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VOLUME 31
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Conflict and Cooperation in a Female-Dominated Society: 
A Reassessment of the “Hyperaggressive” Image of Spotted Hyenas

MARION L. EAST AND HERIBERT HOFER

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CAREL TEN CATE, HANS SLABBEKOORN, 
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Preface

The aim of *Advances* remains as it has been since the series began: to serve the increasing number of scientists who are engaged in the study of animal behavior by presenting their theoretical ideas and research to their colleagues and to those in neighboring fields. We hope that the series will continue its “contribution to the development of cooperation and communication among scientists in our field,” as its intended role was phrased in the preface to the first volume in 1965. Since that time, traditional areas of animal behavior research have achieved new vigor through the links they have formed with related fields and through the closer relationship that now exists between those studying animal subjects and those studying human subjects.

Scientists studying behavior today range more widely than ever before: from ecologists and evolutionary biologists to geneticists, endocrinologists, pharmacologists, neurobiologists, and developmental psychobiologists, not forgetting the ethologists and comparative psychologists, whose prime domain is the study of behavior. It is our intention not to focus narrowly on one or a few of these fields, but to publish articles covering the best behavioral work from a broad spectrum. The skills and concepts of scientists in such diverse fields necessarily differ, making the task of developing cooperation and communication among them a difficult one. However, it is one that is of great importance, and one to which the editors and publisher of *Advances in the Study of Behavior* are committed. We will continue to provide the means to this end by publishing critical reviews, inviting extended presentations of significant research programs, encouraging the writing of theoretical syntheses and reformulations of persistent problems, and highlighting especially penetrating research that introduces important new concepts.

The aspirations of the series are well matched by the current volume. The nature of and evidence for imitation are certainly persistent problems, discussed by Byrne, as is the issue of how animals detect signals in the midst of noise, a remarkable capacity nicely illustrated and illuminated by two chapters (Aubin and Jouventin: Hulse). Behavior borders on ecology in Stoddard’s discussion of the selective forces shaping the signals of electric fish, on neurobiology in Rogers’ review of lateralization, and on physiology in East and Hofer’s discussion of the female-dominated social system of spotted hyenas. Finally, ten Cate, Slabbekoorn, and Ballintijn nicely show how combining field and laboratory studies can shed light on something as apparently simple as the cooing of doves; there is certainly far more to it than meets the uninitiated ear. All of these chapters tackle important topics of wide significance to those interested in the study of behavior.
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Conflict and Cooperation in a Female-Dominated Society: A Reassessment of the “Hyperaggressive” Image of Spotted Hyenas

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I. INTRODUCTION

The spotted hyena (Crocuta crocuta) displays a suite of unusual traits that include female dominance, the masculinization of female genitalia (virilization), and sibling rivalry that can lead to the death of one sibling (siblicide). There has been much speculation about the evolution of these traits, probably because the assumed links between androgens, aggressive behavior, and masculinized traits in spotted hyena females point to fundamental issues concerning the evolution of sex-specific (aggressive) behavior (Gowaty, 1997; Hrdy, 1999). The prevailing assumption has been that elevated levels of androgens in female spotted hyenas produce large, hyperaggressive females that are able to outcompete males in feeding situations and thus acquire absolute dominance over males (Gould, 1981; Glickman et al., 1993; Frank et al., 1995; Frank, 1997; Hrdy, 1999). Some authors have even suggested that the assumed high levels of androgens in adult female spotted hyenas may induce pathological problems during reproduction such as difficulties in completing pregnancies or a delay in the onset of reproduction (Packer et al., 1995). Female spotted hyenas have an enlarged clitoris that is erectile and resembles the penis of the male (Matthews, 1939). The prevailing opinion on the evolution of this “pseudo-penis” has been that it was acquired as a by-product of selection for androgenized, aggressive females (Gould, 1981; Hamilton et al., 1986; Frank et al., 1991; Frank, 1996, 1997). Similarly, a phenomenon described as “habitual neonatal siblicide” in spotted hyenas has also been viewed as a by-product of selection for androgenized, aggressive females (Frank et al., 1991; Frank, 1996, 1997).
<table>
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<td>Behavioral response to territorial intruders</td>
<td>Highly context-specific, ranging from tolerance of intruders in transit to quickly escalated aggressive attacks on intruders at carcasses or kills</td>
<td>One of the few vertebrates where such flexibility has been demonstrated; consistent with game theoretical arguments</td>
<td>Hofer and East, 1993b</td>
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<td>Territorial defense through encounters with neighboring clans</td>
<td>Territorial encounters are won by the side that recruits the largest number of clan members after the encounter begins</td>
<td>Group size, not the physical qualities of the participants, decides the outcome of the encounter</td>
<td>Hofer and East, 1993b</td>
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<td>Acquisition of social status (females)</td>
<td>Linear dominance hierarchy based on aggressive and submissive interactions in female dyads</td>
<td>Independent of body mass, muscular measures, or skeletal body size, but dependent on coalition quality (i.e., the social status of the mother)</td>
<td>Frank, 1986b; Hofer and East, 1995a; Holekamp et al., 1996</td>
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<tr>
<td>Acquisition of social status (immigrant males)</td>
<td>Immigrant males queue for social status: social status is based on tenure, agonistic encounters usually consist of submissive avoidance responses rather than aggressive dominance actions, and social status is independent of body size</td>
<td>Queues contain a much higher number of members and last for a substantially longer period of time than other mating queues in vertebrates, yet queuing discipline is strict in comparison to queues described for other species</td>
<td>East and Hofer, 2001</td>
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<td>Acquisition of social status (nondispersing natal males)</td>
<td>Natal males acquire top rank in the immigrant male social hierarchy when they start competing with immigrant males for access to females</td>
<td>“Nondispersal” natal males do not queue for high social status probably due to the status they acquired from their mothers when cubs. All nondispersal natal males submit to all females, irrespective of their mother’s rank</td>
<td>East and Hofer, 2001</td>
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<td>Category</td>
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<td>Maintenance of social status</td>
<td>Position in queue mostly maintained by coalitions among males and between high ranking males and females. Independent of measures of body size.</td>
<td>East and Hofer, 2001</td>
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<td>Rate of aggression between siblings</td>
<td>Most intense sibling rivalry occurs during suckling bouts; depends on food availability and maternal social status, which determines access to food resources in the territory. Consistent with avian models of facultative sibling rivalry</td>
<td>Golla et al., 1999</td>
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<td>Age at first reproduction</td>
<td>Increases as social status declines. Dependent on coalition quality (maternal social status) when daughters acquired their rank.</td>
<td>Hofer and East, 1996; Holekamp et al., 1996</td>
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<td>Reconciliation</td>
<td>Affiliative behavior after an agonistic encounter is more likely after escalated conflicts; winners of conflicts regularly initiate affiliative behavior with losers of conflicts. One of the few nonprimate species where reconciliation has been documented after conflicts</td>
<td>Hofer and East, 2000</td>
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<td>Commuting system</td>
<td>Clan members regularly forage outside the territory in areas containing large concentrations of migratory herds when such herds are absent from the clan territory. Avoidance of conflict with high-ranking clan members inside the territory</td>
<td>Hofer and East, 1993a,b,c</td>
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<td>Acoustic defense of resources</td>
<td>Rate of loud calling (whoops) by females is related to social status, prey abundance, level of intrusion and food competition, and expected benefits in terms of increased food intake and improved cub survival. The rate of acoustic defense of the territory and the resources it contains vary with both intrusion pressure and expected fitness benefits through the resources that are being defended</td>
<td>East and Hofer, 1991a,b</td>
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<td>Greeting ceremonies</td>
<td>Ritualized greeting in which the erect “penis” is used as a signal of submission and clan members compete for “valuable” greeting partners. Individuals value these affiliative interactions and chose greeting partners likely to provide maximum social benefits in accordance with primate models of optimal partner choice</td>
<td>East et al., 1993</td>
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Given the volume of literature that has promoted the idea that female dominance in spotted hyenas evolved due to selection favoring androg-nized, large, hyperaggressive females, it is perhaps surprising that this idea has received little critical assessment. In this review we will use data from our long-term research on a population of several hundred individually known spotted hyenas in several social groups in the Serengeti National Park, Tanzania to examine this prevailing view. Using current knowledge of the behavior, ecology, and endocrinology of free-ranging spotted hyenas, we will present an alternative evolutionary scenario for the occurrence of habitual male submission resulting in female dominance in this species. We will outline a scenario that links elevated levels of androgens in neonates of both sexes with selection for early sibling rivalry leading to resource-dependent, facultative siblicide (East et al., 1993; Hofer and East, 1995a, 1997; Golla et al., 1999) and producing as a side effect virilized genitalia in female offspring (East et al., 1993; Hofer and East, 1995a).

During our discussion of these scenarios we will consider some of the conflicts that exist within spotted hyena society and the mechanisms used to resolve them. Throughout our review we aim to highlight how both conflict and cooperation shape hyena society and to emphasize that spotted hyenas most likely use social relationships with other group members as an important resource (Table I). This view of social relationships coincides with a major paradigm shift among many animal behavior researchers (Aureli and de Waal, 2000) who view aggression not as the driving force that determines the fabric of social life, but rather as one of several forms of conflict resolution that are in an evolutionary balance with mechanisms of conflict avoidance and with affiliative behaviors that encourage the maintenance of social relationships. This argument is particularly pertinent for long-lived, slowly reproducing, and highly social mammals, such as spotted hyenas, where the social environment may exert as strong a selective force as the natural environment. We thus hope that our review of the evidence relating to the assumed links between aggressive behavior, androgens, and masculinization in spotted hyenas leads to a more balanced appraisal of this topic.

II. SERENGETI HYENA SOCIAL ORGANIZATION

Similar to spotted hyenas elsewhere (Kruuk, 1972; Frank, 1986a; Henschel and Skinner, 1987; Mills, 1990; Hofer, 1998), Serengeti hyenas live in stable social groups called clans that defend territories against neighboring clans (East and Hofer, 1991a,b; Hofer and East, 1993a). Females remain in their natal clan throughout their life. As in other spotted hyena populations (Hofer, 1998), there is a strong social hierarchy among female Serengeti
CONFLICT AND COOPERATION IN A FEMALE-DOMINATED SOCIETY

clan members (East and Hofer, 1991b; East et al., 1993), with high-ranking females maintaining priority of access to food resources (Hofer and East, 1996). Coalitions among Serengeti females are important for the acquisition and maintenance of social status (Table I). As a consequence of such coalitions, the social status of adult females is highly positively correlated with that of their mother (most daughters acquire a social status just below that of their mother). Also, adult females may dramatically decline in social status after the death of a strong coalition partner, such as a mother or adult daughter (Hofer and East, 1996; Hofer and East, unpubl. data). All adult females breed and their cubs are typically reared in a communal den inside the clan territory (Hofer and East, 1995b). Serengeti males normally disperse from their natal clan after reaching sexual maturity at about 2 years of age (Hofer and East, 1995b). When males disperse into a new clan, they join the immigrant male dominance hierarchy at the bottom. Immigrant males do not fight for social status, but instead low-ranking males with short tenure increase in rank as higher ranking, longer tenured males die or leave the clan (Table I). Thus, immigrant males can be considered to queue for social status (East and Hofer, 1991b; East et al., 1993; East and Hofer, 2001). All immigrant males are subordinate to all female clan members; males do not participate in parental care.

III. CONFLICT OVER ACCESS TO FOOD

A. THE COMMUTING SYSTEM

In the Serengeti National Park, the herbivore biomass is dominated by migratory species, chiefly wildebeest (*Connochaetes taurinus*), Thomson’s gazelles (*Gazella thomsoni*), and zebras (*Equus burchelli*), and these species are the primary prey of Serengeti spotted hyenas (Hofer and East, 1993a). Due to the movements of these migratory herbivores, the abundance of prey within clan territories fluctuates markedly. Large numbers of herbivores are present within any given territory for only 22–30% of any year and, during such periods, the abundance of herbivores is high (mean of 238 animals/km$^2$). Irrespective of social status, all clan members forage within the clan territory when large migratory herds are present (Hofer and East, 1993b). When such herds are absent from a territory, the abundance of prey is dramatically reduced to a mean of 31 animals/km$^2$ during periods of medium prey abundance (small herds of migratory and resident herbivores are present) and to a mean of 3.3 animals/km$^2$ during periods of low prey abundance when only resident herbivores are present (Hofer and East, 1993a,b).
Conflict between clan members over access to food resources in the clan territory increases as the abundance of herbivores declines. One method of decreasing conflict over access to declining food resources is to leave the clan territory on short-term (6–8 days for nonlactating animals), long-distance (40–80 km) foraging trips to the nearest concentration of migratory herbivores (Table I). The proportion of clan members regularly commuting to forage outside the territory increases as the abundance of herbivores declines (Hofer and East, 1995b). Individuals of low social status regularly commute when there are moderate densities of herbivores in the group territory. In contrast, females of high social status only commute when conditions of low prey abundance prevail. Although commuting decreases conflict with socially dominant group members, commuting dramatically increases foraging effort. For example, nonlactating, low-ranking females undertake approximately 15–18 commuting trips annually, and such trips entail traveling a minimum average distance of 1000–1300 km per year (Hofer and East, 1993c).

B. TERRITORIAL DEFENSE AND INTRUSION PRESSURE

The evolution of the commuting system in Serengeti spotted hyenas does not indicate near-pathological hyperaggression among females. Rather, it demonstrates considerable behavioral flexibility that allows the year-round exploitation of abundant migratory prey, copes with high levels of intrusion by commuters, and permits a larger group size than would be feasible given the low abundance of resident prey in group territories (Hofer and East, 1993a,b). Clan territory owners have a highly context-specific response to intruding hyenas. Intruders in transit, moving swiftly along recognized thoroughfares through a clan territory, are tolerated or ignored by residents, whereas foraging intruders are usually subjected to low-level aggressive challenges by residents when the latter encounter the former. Territory owners escalate aggressive attacks at food resources if intruders do not immediately relinquish the prey they have killed or carcass they have scavenged (Hofer and East, 1993b). Such flexible, context-specific adjustment of the territorial response to intruders is expected from game-theoretical arguments (Hofer and East 1993b) but, to our knowledge, our study of Serengeti hyena territoriality is the only example where such a flexible territorial response has been demonstrated in a carnivore society (Table I).

Territory owners rarely need to resort to physical contests as they invest in olfactory (Mills and Gorman, 1987; Hofer et al., 2001) and acoustic signals to advertise ownership of resources in their territory (East and Hofer, 1991a,b). Clan females “loud call” or whoop most often when their territory contains a high abundance of herbivores. Thus females adjust their vocal defense of resources in their territory in relation to (1) levels of competition from
intruding commuters and other clan members and (2) the expected benefit that an increased abundance of carcasses provides in terms of food and high cub growth rates (Hofer and East, 1993b,c). High-ranking resident females who stand to benefit the most from ensuring that they have priority of access to carcasses also whoop at the highest rates (East and Hofer, 1991b).

C. Maternal Care

Parental effort (the effort required to obtain resources) and parental input (the quality and quantity of resources delivered to offspring that are converted into growth; Evans, 1990) comprise parental care. Benefits of parental care are usually measured in terms of the survival and reproductive success of the offspring. Although the cost of parental care is the reduced fitness obtained from future offspring caused by the level of care invested in current offspring (Trivers, 1972), parental energy expenditure has often been considered an appropriate approximation of parental costs (Clutton-Brock, 1991). Due to fluctuating levels of conflict over access to food resources in Serengeti clan territories, the options available to females with respect to parental effort and parental care differ according to social status.

During periods of high prey abundance, maternal effort is low, maternal input is high as offspring are nursed each day, and thus, cub growth rate is high irrespective of the social status of mothers (Hofer and East, 1993c, 1996; Golla et al., 1999). In contrast, all Serengeti females, irrespective of social status, regularly leave the clan territory to forage on distant migratory prey during periods of low prey abundance. Maternal effort is high because mothers have to travel long distances to foraging areas and return to the clan territory to nurse their offspring at the communal den. Maternal input is low because commuting mothers are absent from their offspring for several (2–9) days. Mothers do not compensate for infrequent nursing of their young by increasing milk quality or volume delivered during nursing (Hofer and East, 1993c, 1996). Consequently, the comparatively low maternal input during commuting periods results in minimum or even negative growth rates of offspring over periods of several weeks (Hofer and East, 1993c, 1996; Golla et al., 1999).

During periods of medium prey abundance, females of high social status monopolize low-cost foraging opportunities inside the clan territory, whereas females of medium and low status continue to exercise the high-cost foraging option of traveling long distances to feed on migratory prey. By remaining “at home,” females of high status ensure that their parental effort is kept as low as possible, and they continue to nurse their offspring frequently. By comparison, commuting medium- and low-ranking females have a substantially higher maternal effort and lower maternal input. Medium- and low-ranking lactating females undertake between 42–51 commuting trips
annually, traveling a minimum average distance of 2900–3700 km, whereas high-ranking mothers may travel only half this distance (Hofer and East, 1993c, and unpubl. data). These commuting distances exceed the total distance covered by the migratory herds throughout their annual migratory cycle by a factor of 3 or more (Hofer and East, 1995b).

The two foraging options available to Serengeti mothers substantially differ in their consequences for maternal effort (costs to the mother) and maternal input (benefits to the cubs). For instance, the average one-way distance of a commuting trip of 40 km exceeds by an order of magnitude the distance of 4 km that is equivalent to the approximate radius of territories defended by clans in our study (Hofer and East 1993b, 1995b). Similarly, commuting mothers nurse their cubs on average at intervals of 3.4 days, which is substantially less often than mothers feeding inside the clan territory who nurse their cubs typically twice a day (Hofer and East, 1993c). Thus, commuting is clearly the worse option, yet low- and mid-ranking females spend most of the year commuting to avoid conflict over food with high-ranking clan members.

Offspring of high-ranking females generally grow faster and survive better than those of low- and mid-ranking mothers because their mothers only commute during periods of low prey abundance (Hofer and East, 1996; Golla et al., 1999). These effects have far-reaching consequences for the reproductive careers of daughters. Parental input by Serengeti mothers, measured in terms of cub growth rate to independence, is a significant predictor of adult mass, adult skeletal size, and age at first parturition of daughters (Hofer and East, 1996). Age at first parturition is considered a key life history trait (Roff, 1992; Stearns, 1992) because it determines, among other things, the expected duration of the lifetime reproductive period. In species such as spotted hyenas, with small litter size and long interbirth intervals due to their long period of offspring dependence, total duration of the reproductive period is a significant predictor of lifetime reproductive success (Clutton-Brock, 1988). Since daughters of high-ranking Serengeti mothers grow faster, obtain a higher social status, and reproduce earlier than daughters of low-ranking mothers, offspring quality in Serengeti hyenas is strongly and positively correlated between generations (Hofer and East, 1996).

IV. SIBLING RIVALRY: A BY-PRODUCT OF ANDROGENIZATION OR AN ADAPTATION TO FLUCTUATING LEVELS OF PREY?

Intense sibling rivalry, leading to the death of a sibling, has been observed in numerous avian species (Mock and Parker, 1997). Such siblicide has been described as obligate if rivalry invariably results in the death of a sib and
facultative if brood reduction only occurs when parental food provisioning falls below that required to sustain the entire brood (Mock and Parker, 1997). Spotted hyenas are one of the few mammalian species that exhibit sibling rivalry leading to siblicide. Frank et al. (1991) and Frank (1996, 1997) considered siblicide in spotted hyenas to be independent of resources, “habitual” (i.e., presumably obligate) in twin litters composed of cubs of the same sex, and a by-product of selection for large, aggressive, androgenized females that could dominate males.

In contrast, we have described in detail cases of resource-dependent, facultative siblicide in Serengeti spotted hyenas (Hofer and East, 1997). Variation in the intensity of sibling rivalry within Serengeti litters conforms to predictions derived from avian models of facultative siblicide (Golla et al., 1999), and facultative siblicide in Serengeti litters normally occurs within the first 2 months of life (Hofer and East, 1997; Golla et al., 1999). “Habitual” siblicide in same-sex twin litters has not been observed during our long-term study (East and Hofer, 1997; Hofer and East, 1997). Smale et al. (1999) also argued that siblicide in spotted hyenas was unlikely to be “habitual,” and more likely to be facultative, due to the low incidence of siblicide in their study clan in the Masai Mara of Kenya.

In the Serengeti, litter size is one or two, rarely three (Hofer and East, 1997), and cubs are born throughout the year (Hofer and East, 1995b). Mothers normally nurse only their own offspring, and cubs are stationed at the communal den for approximately 12 months (Hofer and East, 1993c). Due to a long period of lactation (12–18 months), Serengeti mothers experience large fluctuations in prey abundance in their territory irrespective of the timing of parturition (Hofer and East, 1995b). The milk of spotted hyenas is highly nutritious (protein content 14.9%, fat content 14.1%, gross energy density 9.70 kJ/g), with a protein content higher than that recorded for any other land carnivore, a fat content only exceeded by Palearctic bears and sea otters (Enhydra lutris), and a gross energy density higher than that of most other land carnivores (Hofer and East, 1995b). Given the considerable maternal investment of spotted hyenas in terms of high-quality milk and long lactation period, the existence of siblicide in this species might be expected, as a siblicidal survivor would gain exclusive access to highly nutritious maternal milk during the prolonged period of lactation.

Although a siblicidal cub might gain an additional share of the maternal milk supply, a cub should only sacrifice a littermate when the increase in fitness acquired by such an act is greater than the fitness cost incurred (Parker et al., 1989; McNamara et al., 1994). Such a situation will occur when maternal food supply is insufficient to sustain the entire litter (Table I), and under such circumstances, the dominant offspring should seek to improve its chance of survival by monopolizing maternal resources (Mock et al., 1990).
Severe sibling rivalry between spotted hyena siblings results in the exclusion by the dominant cub of the subordinate cub from access to maternal teats. This results in large asymmetries in body mass between littermates and the eventual death due to starvation of the subordinate offspring (Hofer and East, 1997). If, as theory predicts, insufficient parental provisioning causes despotic behavior by the dominant offspring (Mock et al., 1990; McNamara et al., 1994; Mock and Parker, 1997), then escalated sibling rivalry within spotted hyena twin litters should be expected when mothers fail to provide sufficient milk to sustain a litter. Consistent with this prediction, rates of aggression among Serengeti littermates increased as levels of maternal input, measured in terms of cub growth, decreased (Golla et al., 1999). Rates of aggression were calculated as the frequency of aggressive behaviors per minute during suckling bouts derived by a bout criterion analysis (Sibly et al., 1990). Also in accordance with this prediction, littermates belonging to high-ranking mothers and receiving high levels of maternal input (see earlier) had lower rates of aggression than those belonging to lower ranking mothers that provided less adequate levels of input (Golla et al., 1999).

Thus all the evidence currently available suggests that siblicide in spotted hyenas is facultative and resource-driven, just as in any other species with facultative siblicide, and not a pathological by-product of selection for another trait.

V. SIBLICIDE AND BIASES IN THE SEX COMPOSITION OF TWIN LITTERS

Facultative siblicide in spotted hyenas is an interesting phenomenon, as enforced starvation does not appear to occur randomly with respect to the sex composition of twin litters. Twin litters may be composed of cubs of the same sex (i.e., both male or both female) or of mixed sex (male and female cubs). Considering the sex composition of 114 twin Serengeti litters at the age of 3 months, when cubs can first be sexed in the field by the shape of their phallic glans (Frank et al., 1990), mixed-sex litters occurred significantly more often than expected, whereas there were too few all-female litters (Hofer and East, 1997). This suggests that facultative siblicide is more likely to occur in all-female than all-male or mixed-sex twin litters. If facultative siblicide most often occurs in all-female twin litters, then many all-female twin litters will be represented by a singleton female after siblicide has occurred (Hofer and East, 1997). The overall sex ratio expressed as the proportion of males in singleton Serengeti litters was 0.429 (N = 91 cubs), a significant female bias consistent with the idea that females are more likely to commit siblicide (Hofer and East, 1997).
If females are more likely to commit siblicide, then the twin litters that survive intact to the age of 3 months should show a male bias. In the Serengeti, the proportion of males in twin litters at this age was 0.557, a bias toward male cubs. James and Hofer (1999) showed that siblicide could only account for the subbinomial variance of the sex composition of Serengeti twin litters at the age of 3 months if the probability of siblicide depended on the sex of the victim, or if it was caused by preparturition processes, as suggested by Smale et al. (1999).

East and Hofer (1997) suggested that if facultative siblicide is most common in all-female litters, then the sex composition of twin litters in spotted hyena populations should alter with the amount of food available to lactating mothers. If so, the low incidence (8%) of all-female litters in a Masai Mara clan, when group size was considered at carrying capacity, and the higher incidence of such litters (41%) after fission reduced group size to below carrying capacity (Holekamp and Smale, 1995), may have been caused by a decline in facultative siblicide after fission (East and Hofer, 1997). A comparison of the sex composition of twin litters in ecosystems with large differences in prey abundance shows that the proportion of all-female twin litters increased as the availability of resident prey increased (Table II, Spearman’s $\rho = 0.886, N = 6, P < 0.05$). The highest incidence of all-female (twin/triplet) litters was observed, as predicted, in a well-fed captive colony of spotted hyenas.

Sex-specific biases in sibling competition may result from unequal investment in offspring of different sex (Clutton-Brock, 1991), causing more extreme competition for parental resources by the sex that receives more parental investment (Mock and Parker, 1997). In Serengeti spotted hyenas, singleton female cubs grow at a higher rate than singleton males, suggesting that investment in females is higher than in males (H. Hofer and M. L. East, unpubl. data). Also, as previously mentioned, females remain in their natal groups and normally acquire a social rank immediately below that of their mother, with social status directly influencing access to food resources. Thus, due to philopatry among females, higher levels of competition may be expected within all-female litters than within all-male litters (Holekamp and Smale, 1995; Golla et al., 1999). Aggression rates among Serengeti cubs within all-male and all-female litters were higher than in mixed-sex litters, but did not differ between all-male and all-female litters (Golla et al., 1999). These results may be due to escalated contests between competitors with identical interests (Maynard Smith, 1982). More likely, they reflect the combined aggressive behavior of both siblings and not the tactics used by dominant and subordinate contestants during competition for access to maternal milk supplies (Golla et al., 1999).
<table>
<thead>
<tr>
<th>Ecosystem</th>
<th>Prey density</th>
<th>Aggression rate</th>
<th>Facultative siblicide</th>
<th>% Mixed-sex</th>
<th>% All-male</th>
<th>% All-female</th>
<th>N</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kalahari</td>
<td>2.6</td>
<td>?</td>
<td>?</td>
<td>89**</td>
<td>11</td>
<td>0$^g$</td>
<td>9</td>
<td>Mills, 1990; Hofer and East, 1993a</td>
</tr>
<tr>
<td>Serengeti</td>
<td>3.3</td>
<td>0.49 ± 0.31</td>
<td>Yes</td>
<td>61**</td>
<td>25</td>
<td>14**</td>
<td>114</td>
<td>Hofer and East, 1993a, 1997; Golla et al., 1999</td>
</tr>
<tr>
<td>Masai Mara$^c$</td>
<td>?</td>
<td>?</td>
<td>Yes</td>
<td>85***</td>
<td>12$^§§§$</td>
<td>2***</td>
<td>33</td>
<td>Frank et al., 1991</td>
</tr>
<tr>
<td>Masai Mara$^d$</td>
<td>153$^e$</td>
<td>0.035$^e,f$</td>
<td>Possible</td>
<td>81**</td>
<td>13</td>
<td>6$^§§$</td>
<td>16</td>
<td>Holekamp et al., 1993; Holekamp and Smale, 1995; Smale et al., 1995, 1999</td>
</tr>
<tr>
<td>Masai Mara$^b$</td>
<td>163$^e$</td>
<td>0.035$^e,f$</td>
<td>No$^g$</td>
<td>48</td>
<td>27</td>
<td>25</td>
<td>48</td>
<td>Holekamp et al., 1997; Smale et al., 1995, 1999</td>
</tr>
<tr>
<td>Ngorongoro</td>
<td>184.2</td>
<td>0.023 ± 0.06</td>
<td>No</td>
<td>49</td>
<td>31</td>
<td>20</td>
<td>35</td>
<td>B. Wachter and O. P. Höner, unpubl. data</td>
</tr>
<tr>
<td>Captivity</td>
<td>Ad libitum</td>
<td>0.05$^e$</td>
<td>Possible$^h$</td>
<td>56</td>
<td>17</td>
<td>28</td>
<td>18</td>
<td>Drea et al., 1996; Frank, 1996</td>
</tr>
</tbody>
</table>

Note: $^g p = 0.075$; $^§§ p = 0.063$; $^§§§ p = 0.058$; $^{**} p < 0.005$; $^{***} p < 0.001$.

$^a$ Sex composition of twin litters from binomial expectations is 50% mixed-sex, 25% all-male, and 25% all-female litters.

$^b$ Minimum estimate.


$^d$ Study period 1988–1990 before clan fission, high competition between females.

$^e$ Derived from graphs or data published in the original citations.

$^f$ Study period 1990–1998 after clan fission, low competition between females.

$^g$ No evidence for siblicide in twin litters but one case in a triplet litter.

$^h$ The subordinate in a twin litter and the runts in all four triplet litters sustained serious injuries and observers intervened.

$^i$ Aggression rates may have been recorded before and after clan fission.
The female genitalia of spotted hyenas are virilized and resemble the genitals of the males. The clitoris is enlarged and forms an erectile pseudo-penis, the labia are fused to form a pseudo-scrotum, and the urogenital tract passes through the pseudo-penis (Matthews, 1939; Neaves et al., 1980; Frank et al., 1990). Female spotted hyenas thus urinate, copulate, and give birth through their clitoris. Several hypotheses have been advanced to explain the virilization of female genitalia in spotted hyenas. The nonadaptive theories view female virilization as an incidental by-product of selection for elevated prenatal androgen levels. Such elevation occurred because (1) it lead to large size, increased aggression, and social dominance of adult females over males (Gould, 1981; Frank et al., 1991; Frank, 1997); it was (2) a consequence of a punctuated genetic translocation (van Jaarsveld and Skinner, 1987); it was (3) favored in the evolution of sibling rivalry (East et al., 1993, Hofer and East, 1995a). Adaptive theories considered the enlarged clitoris to have the direct selective advantage of a conspicuous structure used to facilitate the reestablishment of social bonds (Wickler, 1965; Kruuk, 1972). Another theory, which is an adaptive extension of the nonadaptive theory of Gould (1981), suggests that the virilization of female genitalia evolved as a by-product of selection for androgen-facilitated dominance and that the virilized clitoris was incorporated into greetings, favoring selection for its enlargement and erectile nature (Hamilton et al., 1986).

What evidence is there to support the idea that virilization of the female external genitalia was driven by selection for androgen-facilitated dominance? We will look at the evidence on androgen concentrations in the next section and concentrate here on the behavior. Adult female spotted hyenas are commonly assumed to be highly aggressive (Hamilton et al., 1986; Frank et al., 1991, 1995; Glickman et al., 1993; Monaghan and Glickman, 1992; Packer et al., 1995), even though levels of aggression among female spotted hyenas have not been compared with those of females in other mammalian species living in a similar social context of multimatriarchal groups that live in a fission–fusion society (Goymann, 1999). Rates of aggression among competing immigrant males are low, and males are rarely aggressive to females (East and Hofer, 2001). Thus, females may appear to be aggressive because the aggressiveness of immigrant males is so low (East et al., 1993). In mammalian species other than the spotted hyena (e.g., European mole _Talpa europaea_: Matthews, 1935; platyrrhine monkeys: Ploog and MacLean, 1963) virilization of female external genitalia is rare but where it occurs it is not associated with female dominance (East et al., 1993; Hofer and East, 1996; Teltscher, 1996). In mammalian species, female dominance is uncommon, but does occur in a variety of taxa (Ralls, 1976; Hrdy, 1981) and is typical for
Lemuriformes (Jolly, 1984; Kappeler, 1990; Young et al., 1990). However, extreme masculinization of female external genitalia has not been recorded in any female-dominated species except for the spotted hyena (Teltscher, 1996). Female dominance in other mammals is not dependent on females being larger than males, and dominance is not a function of aggressiveness (Rowell, 1974). Even in spotted hyenas, females are not necessarily larger than males (Hamilton et al., 1986; East and Hofer, 1997, unpubl. data), and body size in males and females is not related to social status in our Serengeti population (East and Hofer 1997, 2001), nor in a clan in the Masai Mara of Kenya (Holekamp et al., 1996). In several primate species (Saimiri, Cebus, Cercopithecus talapoin, Macaca mulatta, Erythrocebus patas), coalitions of females can successfully challenge larger males (Harvey et al., 1987; Smuts, 1987), and in spotted hyenas coalitions are important in the maintenance of female rank (East et al., 1993; Hofer and East, 1996).

VII. VIRILIZATION AND ANDROGENS

It has been argued that spotted hyena females have androgen profiles that are unusual for female mammals. On an interspecific level, they are thought to have higher androgen levels than other female mammals (e.g., Glickman et al., 1993; Packer et al., 1995; Frank, 1996). On an intraspecific level, the quoted “aggressiveness” of females is assumed to be caused by elevated levels of androgens. What is the evidence?

Comparative data demonstrate that testosterone and androstenedione levels in nonpregnant free-ranging spotted hyena females are below or similar to those in a variety of other nonpregnant female mammals, including those in female brown and striped hyenas (Tables III and IV).

In intraspecific comparisons, some studies reported similar testosterone levels in male and female spotted hyenas, whereas others reported significantly higher testosterone levels in males than in females (Table V). Androstenedione levels were similar in females and males in some studies and significantly higher in females than in males in other studies (Table VI). Confusion about androgen levels in spotted hyenas probably stems from three sources (Goymann et al., 2001). First, some studies have not considered the impact of reproductive status on androgen levels in males. This is a problem because androgen levels in young, nonbreeding natal males (“predispersal” males) are significantly lower (Holekamp and Smale, 1998) than levels in older, mostly immigrant, reproductively active males (“post-dispersal” males) (Table V and VI). Second, since the challenge hypothesis (Wingfield et al., 1990) predicts that androgen levels should increase when individuals experience elevated levels of social challenge, androgen levels in
TABLE III
EXAMPLES OF PUBLISHED DATA ON PLASMA TESTOSTERONE (ng/ml) IN NONPREGNANT FEMALE CARNIVORES AND OTHER MAMMALS

<table>
<thead>
<tr>
<th>Species</th>
<th>Plasma concentration (ng/ml)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spotted hyena (Crocuta crocuta)</td>
<td>0.32</td>
<td>Goymann et al., 2001</td>
</tr>
<tr>
<td>Brown hyena (Hyaena brunnea)</td>
<td>0.52</td>
<td>Racey and Skinner, 1979</td>
</tr>
<tr>
<td>Striped hyena (Hyaena hyaena)</td>
<td>0.64</td>
<td>Racey and Skinner, 1979</td>
</tr>
<tr>
<td>Domestic dog (Canis familiaris)</td>
<td>0.05–0.29</td>
<td>Concannon and Castracane, 1985</td>
</tr>
<tr>
<td>Human (Homo sapiens)</td>
<td>0.30–0.60</td>
<td>Feder, 1985</td>
</tr>
<tr>
<td>Chimpanzee (Pan troglodytes)</td>
<td>0.35–0.73</td>
<td>Nadler et al., 1985</td>
</tr>
<tr>
<td>Baboon (Papio hamadryas)</td>
<td>0.15–0.23</td>
<td>Feder, 1985</td>
</tr>
<tr>
<td>Talapoin monkey (Miopithecus talapoin)</td>
<td>2.2–4.0</td>
<td>Batty et al., 1986</td>
</tr>
<tr>
<td>Syrian hamster (Mesocricetus auratus)</td>
<td>0.06–0.09</td>
<td>Feder, 1985</td>
</tr>
<tr>
<td>Musk shrew (Suncus murinus)</td>
<td>0.20</td>
<td>Rissman et al., 1990</td>
</tr>
<tr>
<td>European mole (Talpa europaea)</td>
<td>0.79–1.44</td>
<td>Whitworth et al., 1999</td>
</tr>
</tbody>
</table>

captive (e.g., Glickman et al., 1987, 1992) and free-ranging spotted hyenas may not be comparable. Unlike free-ranging spotted hyenas that live in fission–fusion societies, captive individuals are housed together, have constant social contact, and have limited opportunities to avoid interactions. These socially challenging conditions are likely to result in elevated levels of androgens. Following the same line of argument, Serengeti spotted hyenas that are caught in wire snares set by game meat hunters, but escape by biting through the tethering wire (Hofer et al., 1993), experience an elevated level of social challenge. This is because the snare is often embedded in the

TABLE IV
EXAMPLES OF PUBLISHED DATA ON PLASMA ANDROSTENEDIONE (ng/ml) IN NONPREGNANT FEMALE CARNIVORES AND OTHER MAMMALS

<table>
<thead>
<tr>
<th>Species</th>
<th>Plasma concentration (ng/ml)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spotted hyena (Crocuta crocuta)</td>
<td>2.44</td>
<td>Goymann et al., 2001</td>
</tr>
<tr>
<td>Brown hyena (Hyaena brunnea)</td>
<td>4.70</td>
<td>Racey and Skinner, 1979</td>
</tr>
<tr>
<td>Domestic dog (Canis familiaris)</td>
<td>0.41–0.79</td>
<td>Concannon and Castracane, 1985</td>
</tr>
<tr>
<td>Human (Homo sapiens)</td>
<td>2.25</td>
<td>Cashdan, 1995</td>
</tr>
<tr>
<td>Baboon (Papio hamadryas)</td>
<td>1.2–2.0</td>
<td>Feder, 1985</td>
</tr>
<tr>
<td>Talapoin monkey (Miopithecus talapoin)</td>
<td>3.6–6.0</td>
<td>Batty et al., 1986</td>
</tr>
<tr>
<td>Syrian hamster (Mesocricetus auratus)</td>
<td>1.0–1.9</td>
<td>Feder, 1985</td>
</tr>
<tr>
<td>European mole (Talpa europaea)</td>
<td>1.22</td>
<td>Whitworth et al., 1999</td>
</tr>
</tbody>
</table>
**TABLE V**

**Mean Testosterone Concentrations (ng/ml Plasma) in Male and Female Spotted Hyenas of Different Reproductive State**

<table>
<thead>
<tr>
<th>Female, neither pregnant nor lactating</th>
<th>Pregnant female</th>
<th>Lactating female</th>
<th>Young, natal male before dispersal</th>
<th>Sexually mature, reproductively active male (usually immigrants)</th>
<th>Male of unknown reproductive state</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.76 (5)</td>
<td>1.20 (10)</td>
<td>1.06 (5)</td>
<td>—</td>
<td>—</td>
<td>1.48 (18)</td>
<td>Racey and Skinner, 1979</td>
</tr>
<tr>
<td>—</td>
<td>1.33 (4)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>Lindeque and Skinner, 1982</td>
</tr>
<tr>
<td>0.5(^a) (1)</td>
<td>0.5(^a) (1)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>Gombe, 1985</td>
</tr>
<tr>
<td>0.35 (12)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>3.15 (9)</td>
<td>Frank <em>et al.</em>, 1985</td>
</tr>
<tr>
<td>0.46 (16)</td>
<td>1.24 (8)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.84 (4)</td>
<td>Lindeque <em>et al.</em>, 1986</td>
</tr>
<tr>
<td>0.3(^a,b) (11)</td>
<td>—</td>
<td>—</td>
<td>1.5(^a,b) (16)</td>
<td>—</td>
<td>4.52 (6)</td>
<td>van Jaarsveld and Skinner, 1991a</td>
</tr>
<tr>
<td>0.75 (12)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>4.52 (6)</td>
<td>—</td>
<td>van Jaarsveld and Skinner, 1991b</td>
</tr>
<tr>
<td>1.2(^a) (5)</td>
<td>—</td>
<td>0.6(^a) (6)</td>
<td>1.5(^a,c) (6)</td>
<td>10.5(^a) (3)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>0.4(^a,b) (8)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>3.6(^a,b) (6)</td>
<td>—</td>
<td>Glickman <em>et al.</em>, 1992</td>
</tr>
<tr>
<td>0.3(^a,b) (5)</td>
<td>0.3–7.0(^a,b) (5)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>Licht <em>et al.</em>, 1992</td>
</tr>
<tr>
<td></td>
<td>—</td>
<td>1.7(^a,b) (3)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>Drea <em>et al.</em>, 1998</td>
</tr>
<tr>
<td>0.32 ± 0.12 (7)</td>
<td>0.29 ± 0.02 (3)</td>
<td>0.16 ± 0.02 (24)</td>
<td>0.51 ± 0.20 (4)</td>
<td>4.26 ± 0.77 (19)</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

*Note:* Numbers in parentheses refer to “sample sizes” (i.e., some references may contain repeat samples from the same individual, thus, sample sizes are not necessarily identical with the number of individuals sampled).

\(^a\) The original paper did not supply numeric means; thus, mean values have been approximated from published graphs.

\(^b\) Data from captive individuals.

\(^c\) Described as “resident natal males,” included subadults older than one year.

\(^d\) Labeled as “natal males.”
### TABLE VI
**Mean Androstenedione Concentrations (ng/ml Plasma) in Male and Female Spotted Hyenas of Different Reproductive State**

<table>
<thead>
<tr>
<th>Female, neither pregnant nor lactating</th>
<th>Pregnant female</th>
<th>Lactating female</th>
<th>Young, natal male before dispersal</th>
<th>Sexually mature, reproductively active male (usually immigrants)</th>
<th>Male of unknown reproductive state</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>—</td>
<td>1.18 (10)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>—</td>
<td>11.1 (3)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1.92 (16)</td>
<td>6.79 (8)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>Lindeque and Skinner, 1982</td>
</tr>
<tr>
<td>2.7&lt;sup&gt;a&lt;/sup&gt;&lt;sup,b&lt;/sup&gt; (11)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1.5&lt;sup&gt;a&lt;/sup&gt;&lt;sup,b&lt;/sup&gt; (16)</td>
<td>—</td>
<td>Glickman <em>et al.</em>, 1987</td>
</tr>
<tr>
<td>1.67 (12)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1.14 (6)</td>
<td>van Jaarsveld and Skinner, 1991a</td>
</tr>
<tr>
<td>2.1&lt;sup&gt;a&lt;/sup&gt; (5)</td>
<td>—</td>
<td>1.6&lt;sup&gt;a&lt;/sup&gt; (6)</td>
<td>1.0&lt;sup&gt;a&lt;/sup&gt;&lt;sup,c&lt;/sup&gt; (6)</td>
<td>3.4&lt;sup&gt;a&lt;/sup&gt; (3)</td>
<td>—</td>
<td>van Jaarsveld and Skinner, 1991b</td>
</tr>
<tr>
<td>4.5&lt;sup&gt;a&lt;/sup&gt;&lt;sup,b&lt;/sup&gt; (8)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>2.5&lt;sup&gt;a&lt;/sup&gt;&lt;sup,b&lt;/sup&gt; (6)</td>
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<td>Glickman <em>et al.</em>, 1992</td>
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<td>3.42&lt;sup&gt;b&lt;/sup&gt; (5)</td>
<td>6.06&lt;sup&gt;b&lt;/sup&gt; (5)</td>
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<td>Licht <em>et al.</em>, 1992</td>
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<td>2.44 ± 1.02 (7)</td>
<td>2.32 ± 1.03 (3)</td>
<td>1.14 ± 0.21 (24)</td>
<td>0.18 ± 0.06 (4)</td>
<td>1.57 ± 0.28 (19)</td>
<td>—</td>
<td>Goymann <em>et al.</em>, 2001</td>
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**Note:** Numbers in parentheses refer to “sample sizes” (i.e., some references may contain repeat samples from the same individual, thus, sample sizes are not necessarily identical with the number of individuals sampled).

<sup>a</sup>The original paper did not supply numeric means, thus, mean values have been approximated from published graphs.

<sup>b</sup>Data from captive individuals.

<sup>c</sup>Described as “resident natal males,” included subadults older than one year.
flesh and the wound created by the snare, and the wire protruding from the flesh draw the attention of other clan members, including individuals with higher social status than the snared animal, and contact with the wound probably causes pain. Elevated levels of social challenge may explain why nonpregnant females with snares have elevated levels of androgens in comparison to nonpregnant females without snares (Goymann, 1999). Third, studies have applied different analytical techniques for the measurement of androgen levels (Goymann et al., 2001). Often studies purporting to measure testosterone do not distinguish between testosterone and 5-α-dihydrotestosterone, as common antisera against testosterone cross-react highly with 5-α-dihydrotestosterone, and vice versa, and it requires special techniques to prevent these kinds of cross-reactions from biasing the results. For the first time in hyena studies, Goymann et al. (2001) measured testosterone, 5-α-dihydrotestosterone, and androstenedione concentrations in plasma samples from Serengeti spotted hyenas after partial purification through chromatography by using a modification (Fusani et al., 2000) of the method described by Wingfield and Farner (1975) and thus eliminating the usual cross-reactions. Thus Goymann et al. (2001) provide a highly specific measure of these three androgens. The results show that free-ranging spotted hyena females follow the standard mammalian pattern, with testosterone concentrations in reproductively active males being an order of magnitude higher than in females (Table V), and androstenedione levels being similar in both sexes (Table VI). In summary, there is little evidence to support the idea that androgen levels in adult female spotted hyenas are abnormally high, or likely to cause hyperaggression or pathological problems during reproduction.

We have proposed an alternative idea that links prenatal androgen levels to facultative siblicide in spotted hyenas (East et al., 1993; Hofer and East, 1995a; East and Hofer, 1997). We consider it probable that the elevated levels of androgens (androstenedione in females, testosterone in males) recorded during fetal development, at birth, and during the initial months of life (Glickman et al., 1987; Frank et al., 1991; Licht et al., 1992) have been selected to produce neonates primed for high levels of sibling rivalry (East et al., 1993). High concentrations of circulating androgens (especially testosterone and 5-α-dihydrotestosterone) in adult females during the final period of pregnancy are thought to be one source of testosterone circulating in the fetus (Matthews, 1939; Licht et al., 1992). If this is the case, then we suggest that the elevation of androgens during the final period of pregnancy may have been selected to contribute to the production of neonates primed for sibling rivalry (East et al., 1993).

It has been thought that high androgen levels in female fetuses and neonates were involved in the formation of the hypertrophied clitoris (Frank
et al., 1991). However, as antiandrogen treatment during fetal development has not produced females without a pseudo-penis, it is unlikely that androgen-dependent mechanisms are solely responsible, and androgen-independent mechanisms are likely to play an important role in the development of the enlarged clitoris (Drea et al., 1998).

VIII. The Fitness Consequences of Virilization

When female spotted hyenas give birth, the hypertrophied clitoris ruptures on the caudal side, causing a large, bleeding wound that may be a source of infection. Many primiparous captive females produce stillbirths, whereas subsequent deliveries are easier (Glickman et al., 1992; Frank et al., 1995). In the Serengeti, the loss of a first litter at parturition implies a reduction in terms of lifetime reproductive success of at least 5% (East et al., 1993). Thus, the maintenance of the hypertrophied clitoris entails a fitness cost for females. If so, direct selection pressure must have operated to maintain this large (1% of body weight, Matthews, 1939) erectile organ (East et al., 1993).

A possible selective advantage for females that have the opening to their reproductive tract (urogenital meatus) displaced to a position forward of their hind legs at the tip of their hypertrophied clitoris is that males have considerable difficulty locating and penetrating the clitoris opening (Kruuk, 1972). Although the hypertrophied clitoris is not erect during mating, its presence and position prevent males from achieving intromission without the complete cooperation of the female (East et al., 1993). We have proposed that this provides females with control over the mechanics of copulation and that male mating success might depend on close male–female relationships (East et al., 1993). With strong female control over copulation, the importance of sexual selection for male fighting prowess is likely to be reduced. If males stand to gain little by fighting with each other, because females do not select mating partners on the basis of their fighting ability, then game theory predicts that fights between males should be rare and/or fighting intensity low (Maynard Smith, 1982). This idea is consistent with the observed low levels of aggression among competing males (Frank, 1986b; East and Hofer, 1991b, 2001).

The challenge hypothesis (Wingfield et al., 1990) has successfully explained how different mating strategies may affect patterns of androgen secretion in several avian species, but the hypothesis has rarely been tested in mammalian species. The hypothesis predicts that if direct competition for females is low, as is the case among male spotted hyenas, then there should be no association between male social status and plasma androgen concentrations. Goymann (1999) found no association between plasma androgen levels and male social
status among Serengeti postdispersal males. Similarly, in some stable primate
groups, where challenges are rare among group males, a lack of correlation
between androgens and male social status has also been reported (Sapolsky,
1993).

The challenge hypothesis (Wingfield et al., 1990) predicts a rise in male
androgen levels during periods of mate guarding and courtship, and consis-
tent with this prediction Goymann (1999) found that Serengeti males that
excluded other males from approaching females had significantly higher an-
drogen levels than males that were not defending females.

If a male spotted hyena is more likely to be selected as a mating partner if
he has developed a relationship with a female, then males should actively fos-
ter relationships with females. The high investment by males in the courtship
of specific females and the submission of males to females at food resources
are consistent with the idea that males invest in fostering relationships with
females (East and Hofer, 2001; see later). Thus, in contrast to the prevail-
ing idea that females had to be virilized, large, and aggressive to dominate
males, we suggest that the maintenance of the pseudo-penis imposed on
males a need to cultivate relationships with females, and an important factor
in this process was male submission (East and Hofer, 2001). The activation
of these sex-reversed traits (decreased male aggression, female dominance)
in adult spotted hyenas may be mediated by mechanisms other than elevated
or decreased levels of peripheral androgens (Goymann, 1999).

IX. THE MALE-DOMINANCE HIERARCHY: QUEUING FOR SOCIAL STATUS

We propose that the female pseudo-penis has not only decreased selection
for male aggression, but has also influenced the manner in which immigrant
males acquire social status (Table I). Social status among immigrant male
hyenas is not linked to physical characteristics such as measures of skeletal
size or body mass, and males do not fight to acquire status (East and Hofer,
2001). Instead, the social status of immigrant males is correlated with dur-
ation of tenure, and thus males acquire social status by queuing (East and
Hofer, 1991b, 2001). The queuing convention observed by immigrant males
is relatively strict (cf. Kokko et al., 1998) as successively arriving males wait
their turn to rise in social status and rarely use aggressive contests to increase
in status (East and Hofer, 2001).

Why do immigrant males observe queuing conventions and why do new-
comers not attempt to jump the queue? We have shown that several factors
are likely to contribute to the stability of the male social hierarchy (Table I).
When males reach high social status they form coalitions with other queu-
ing males more often than when they are mid- or low-ranking. High-ranking
males also form coalitions with females against lower ranking males, whereas mid- and low-ranking males do not form coalitions with females. Coalitions among high-ranking males and between high ranking males and the socially dominant females may contribute to the stability of the hierarchy among the males and deter queue jumping (East and Hofer, 2001). Furthermore, greeting ceremonies (see later) among immigrant males chiefly involve individuals of similar social status and may help confirm their relative status to both participants (East et al., 1993).

X. Male–Female Behavior

Immigrant males of high social status invest considerable time in following (shadowing) particular females irrespective of whether or not the females are in estrus (East and Hofer, 2001). Shadowing behavior appears to be a tactic employed by immigrant males to foster relationships with particular clan females. Immigrant males also attempt to exclude possible competitors from the vicinity of females.

High-ranking males shadow and defend females more often than mid- and low-ranking males. High-ranking males also shadow a larger number of clan females and concentrate their shadowing effort mostly on high-ranking females (East and Hofer, 2001). High-ranking males probably prefer to associate with high-ranking females because they are more valuable mating partners, since cub growth rate, cub survival, and reproductive success of Serengeti females increase with social status (Hofer and East, 1993c, 1996; Golla et al., 1999).

Relationships between immigrant males and clan females vary with male social status and tenure. Females are generally more tolerant of males with high social status and long tenure than males with shorter tenure and low social status (East and Hofer, 2001). Males with high social status and longer tenure display higher levels of friendly behavior toward females. Such females in turn are more tolerant of long-tenured males than more recent immigrant males (Table I). Thus there are status-related differences in the quality of relationships between males and females (East and Hofer, 2001). These findings are consistent with our idea that relationships between immigrant males and females are strengthened with increased male tenure (East and Hofer, 1991b; East et al., 1993).

The reproductive success of a spotted hyena male may not be directly linked to his investment in building relationships with and defending females, but rather depend on female mate choice. The strength of male–female bonds may influence female mate choice, but other factors such as genetic quality may also be involved. In the Serengeti, where females commute and breed
throughout the year, female mate choice is likely to be restricted to those males that are present in the clan territory during her period of estrus (East and Hofer, 2001).

XI. **Natal Postdispersal Males**

It was thought that male spotted hyenas always disperse from their natal groups (Kruuk, 1972; Frank, 1986a,b; Mills, 1990). However, in the Serengeti sexually mature males do not always disperse. In contrast to immigrant males, natal males that do not disperse acquire top rank in the male social hierarchy soon after they begin to compete with immigrant males for access to females. Genetic analysis of paternity has demonstrated that these natal postdispersal males father cubs (M. L. East, H. Hofer, T. Burke, and K. Wilhelm, unpubl. data), so a lack of dispersal does not prevent successful reproduction. Holekamp and Smale (1998) have suggested that low levels of testosterone in natal males before they disperse may be due to persistent exposure to female kin, and that following dispersal and exposure to novel sexually receptive females in a new clan, male testosterone levels increase. However, the existence of reproductively active, postdispersal natal males in Serengeti clans suggests that testosterone levels in males may be more closely linked to male–male conflict over access to mates (Goymann, 1999). It is probable that natal postdispersal males gain immediate high rank in the immigrant male hierarchy due to the social dominance they acquired from their mother over all immigrant males during their development. Natal males are dominant to female clan members ranked below their mother, but when natal males start to compete with immigrant males for access to females they habitually submit to and are socially subordinate to the females they previously dominated (East and Hofer, 2001). This reversal of behavior is not due to increased aggressiveness from adult females, but rather because postdispersal males habitually submit when they begin to approach clan females as potential mates.

XII. **Conflict Resolution**

Much has been written about conflict and aggression in hyena society but affiliative behavior, cooperation, and conflict resolution among clan members has received much less attention. There is certainly conflict among members of spotted hyena clans over access to resources, but there is also much cooperation. Coalitions are important for the maintenance of social status in both male and female dominance hierarchies (East et al., 1993; Hofer
and East, 1996; East and Hofer, 2001). Clan members also cooperate in the acquisition and defense of carcasses against intra- and interspecific competition, defense of territory boundaries against neighboring groups, defense of young at the communal den against predators, group hunting and allo-suckling (Kruuk, 1972; Mills, 1985; East and Hofer, 1991b; Knight et al., 1992; East et al., 1993; Hofer and East, 1993c). Thus clan members need to strike a balance between conflicts that arise in competitive situations and the cooperative pursuit of shared interests against clan members, competitors from other clans, and interspecific predators and competitors (Hofer and East, 2000).

When members of a hyena clan meet, they often participate in a greeting ceremony in which two animals stand side by side, head to tail, with their hind legs lifted while they investigate each other’s anal-genital area (Wickler, 1965). We have shown that greetings are ritualized ceremonies in which socially subordinate animals actively signal submission to more dominant group members (East et al., 1993). The distribution of chosen greeting partners is consistent with the distribution predicted by optimality models of primate affiliative behavior that assume that individuals value social relationships as a resource (Table I, Seyfarth, 1977). Thus, hyena greeting ceremonies help to build relationships in a manner reminiscent of grooming in primates, and thus contribute to the stability of the social hierarchy (East et al., 1993).

If female spotted hyenas value relationships with other females in their clan, in a similar manner to that seen in primates (Seyfarth, 1977), then a conflict that is behaviorally expressed as an aggressive encounter might damage that relationship (de Waal and van Roosmalen, 1979). If so, both opponents might be expected to actively repair the damage to the relationship by initiating neutral or friendly reunions after an aggressive encounter. We have shown that the behavior of females after an aggressive encounter differs from that before the encounter. Losers are more likely to initiate a friendly reunion than winners, and the probability of losers initiating a friendly reunion increases if after the initial conflict there is an escalated conflict with further aggression between opponents (Hofer and East, 2000).

In a fission–fusion society, individuals have the option to reduce conflict by simply avoiding possible sources of conflict. For example, in the Serengeti, subordinate females undertake long-distance foraging trips more often than dominants (see earlier) and by doing so reduce possible conflict with dominant females over food resources within the territory. We predict that simple avoidance of conflict may be a more common tactic in fission–fusion societies than in more close-knit societies and that active reconciliation may be a more prominent aspect of close-knit societies (Hofer and East, 2000).
XIII. Conclusion

Previously it has been assumed that the evolution of female dominance, the masculinization of female genitalia, and siblicide in spotted hyenas was driven by selection for elevated levels of androgens that increased female aggressiveness and body size. We argue that current knowledge of the ecology, behavior, and endocrinology of spotted hyenas does not support this view. Adult female spotted hyenas do not have abnormally elevated levels of androgens, and female aggression should not be seen as the only force that shapes hyena social life. Cooperative and affiliative behaviors that foster the maintenance of relationships are equally important in the functioning of hyena society.

To explain habitual submission by males to females we link female control over copulation with their enlarged clitoris or pseudo-penis. As males are unable to mate with uncooperative females they need to cultivate relationships with females. We suggest that habitual submission is an important part of this process. We propose that female control over mating has also reduced selection for male fighting prowess, as relationships with females are a non-transferable resource. This, we suggest, has led to the observed low levels of physical male–male conflict, to a lack of a correlation between social status and plasma androgen levels in immigrant males, and to the evolution of a male social queue.

There is little evidence to support the notion that elevated levels of androgens in both male and female neonates is a by-product of selection for androgenized, large, aggressive adult females. Data from free-ranging hyena populations also cast doubt on the idea that androgenized neonates commit “habitual” (obligate) siblicide in same-sexed twin litters. Sibling rivalry in spotted hyenas is linked to levels of maternal provisioning of milk, and facultative siblicide occurs when the milk supplied by mothers is insufficient to support twin litters.

XIV. Summary

It has been proposed that the evolution of female dominance in spotted hyenas (*Crocuta crocuta*) was due to selection for increased levels of androgens leading to increased aggressiveness and body size as well as to the development of an enlarged penile clitoris. Siblicide in spotted hyena twin litters has also been viewed as a by-product of selection for androgenized, aggressive adult females. These ideas, however, do not fit current knowledge of the behavior, ecology, and endocrinology of this species. We outline an alternative route to female dominance that links female control
over mating (due to their enlarged clitoris) to the need for males to establish relationships with females before successful copulation is possible. This idea provides a likely explanation for habitual male submission to females, for low levels of aggression among competing males, for a lack of association between male social status and plasma androgen concentration, and for the investment by males in establishing relationships with females. Relationships with females improve with male tenure and are a nontransferable resource, and these are factors that are likely to have contributed to the evolution of a queue for social status among immigrant males. Free-ranging adult female spotted hyenas have perfectly ordinary, and thus not abnormally elevated, levels of androgens, and dominance in spotted hyena society is not related to body size. Hence, the assumed link between androgens, aggression, and body size does not exist. Aggression is not the only means of resolving conflicts among females, and there is substantial evidence that social relationships are a resource valued by females. As females that receive antiandrogen treatment during fetal development still develop an enlarged clitoris, androgen-dependent mechanisms are unlikely to be solely responsible for the development of this structure. Elevated levels of androgens in neonates of both sexes do not result in the “habitual” (obligate) death of a cub in same-sexed twin litters, and they are unlikely to result in contrasting behavior in adults (increased aggression in females, decreased aggression in males). Elevated levels of androgens in neonates are more likely linked to sibling rivalry and facultative siblicide when the milk provided by mothers falls below the level required to rear two cubs.

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References


CONFLICT AND COOPERATION IN A FEMALE-DOMINATED SOCIETY


Birdsong and Male–Male Competition: Causes and Consequences of Vocal Variability in the Collared Dove (Streptopelia decaocto)

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I. INTRODUCTION

During the breeding season, many birds produce species-specific, relatively complex and loud vocalizations, usually referred to as “songs.” These vocalizations are predominantly produced by males and serve to attract mates, to compete with conspecifics, and to defend territories by deterring rivals. The structure of these songs may vary widely among species, ranging from the “hoots” of owls and the “coos” of doves and pigeons to the elaborate songs of many songbirds. Signals produced in these contexts are subject to sexual selection and birdsong is no exception. In fact, many aspects of sexual selection have been tested using birdsong. The relative ease with which sound recordings can be analyzed allows for a detailed quantitative description of signal structure and its variation. Recordings can be edited and played back to both males and females to examine their responses. In our studies we also exploit the possibilities that the birdsong model system provides to examine aspects of sexual selection and, in particular, intrasexual selection.

In this chapter we concentrate on the role of birdsong in one aspect of male–male competition: territorial defense. We will first briefly review this subject, arriving at the conclusion that the role of variation in vocal signals in territorial defense and male contest has received limited attention. We outline the questions to be addressed and next introduce our model species, the collared dove (Streptopelia decaocto) and its vocalizations. We describe
the vocal variation in the perch-coo, the prime signal in the territorial behavior of this species. Current knowledge about causes and consequences of perch-coo variation is presented. We end with a discussion of the importance of a better understanding of the linkage between vocal variability and sender quality.

II. SONG: MATE ATTRACTION AND MALE CONTEST

A. MATE ATTRACTION

As a conspicuous secondary sex trait, song is assumed to have evolved because it serves a role in competition over mates (Kroodsma and Byers, 1991; Andersson, 1994; Catchpole and Slater, 1995). This competition for mates occurs if females choose mates on the basis of their songs or if songs are involved in male–male interactions, giving some males a reproductive advantage over others. Song characteristics may thus evolve through both inter- and intrasexual selection, that is, song can be a trait of dual utility (Berglund et al., 1996).

With respect to mate attraction, playback experiments have shown that song attracts females and that some songs or singing styles are more attractive than others (Catchpole, 1980; Catchpole et al., 1984; Eriksson and Wallin, 1986; Eens et al., 1991; Mountjoy and Lemon, 1991; Vallet and Kreutzer, 1995; for a review, see Searcy and Yasukawa, 1996). It is still a matter of debate what benefits females may gain from making such choices and how female choice evolved. Several, not mutually exclusive, hypotheses have been put forward to explain the evolution of elaborate mate attraction signals in general (for reviews see Cronin, 1991; Andersson, 1994; Bradbury and Vehrencamp, 1998; Stearns and Hoekstra, 2000). In the “Fisherian” or “runaway” model (Fisher, 1930; Lande, 1981; Kirkpatrick, 1982) and in the “sensory exploitation” model (Ryan et al., 1990) the signal may, in theory, be arbitrary in the sense that it need not be related to specific qualities of the male. In contrast, some alternative theories hypothesize that signals bear a close relation to male quality. One such hypothesis is the “genetic indicator” hypothesis (Andersson, 1994). This states that conspicuous traits like bright colors or elaborate songs evolve because they reflect heritable viability differences, such as resistance against parasites (Hamilton and Zuk, 1982; cf. Read and Weary, 1990, 1992). Another hypothesis is that elaborate traits may reflect a male’s current phenotypic condition or other qualities (e.g., the willingness to invest in parental care that might be directly beneficial to a female; Grafen, 1990a,b). Both the genetic indicator model and the current quality model are also known as “handicap” models (after Zahavi,
1975, 1977; Zahavi and Zahavi, 1997) because various theoretical studies have shown that such signals only evolve if production of the signal is costly (Grafen, 1990a,b).

Birdsong has been used to examine and test the various previously mentioned hypotheses (for a review: see Searcy and Yasukawa, 1996). So far there is not much evidence that runaway selection has played a role in the evolution of varied songs or elaborate repertoires (Catchpole and Slater, 1995; Searcy and Yasukawa, 1996). Also the role of sensory exploitation in song evolution awaits further study (Searcy, 1992; Gray and Hagelin, 1996; Collins, 1999; Neubauer, 1999). Most studies on the function of song concentrate on the possibility that females may get direct or indirect (genetic) benefits from mating with males with certain types of song or singing styles. In several species, for instance, song repertoires increase with age (e.g., Nottebohm and Nottebohm, 1978; Cosens and Sealy, 1986; Derrickson, 1987; Lampe and Espmark, 1994; Hasselquist et al., 1996; Mountjoy and Lemon, 1996; Eens, 1997). Therefore a female preference for larger repertoires may lead to getting more experienced, or perhaps healthier, mates. Females may also prefer vocal characteristics that might be more demanding to produce, indicating a male of good physical quality (e.g., Gibson and Bradbury, 1985; Vehrencamp et al., 1989; Vallet and Kreutzer, 1995; Vallet et al., 1998).

Several studies have obtained correlational evidence for a relationship between male song features and reproductive success (Horn et al., 1993; Kempenaers et al., 1997; Galeotti, 1998; Hasselquist, 1998; Martin-Vivaldi et al., 1999; Gil and Slater, 2000), but in many of these cases it has not been possible to disentangle the contribution of direct and indirect effects. However, the evidence keeps accumulating that selection through female preferences plays a role in the evolution of birdsong (Searcy and Yasukawa, 1996).

B. Male Contest

In the context of male contest, some processes through which female choice may drive signal evolution, such as selection for “good genes,” are not relevant, or less so. However, the handicap theory in particular provides a good framework to explain signal evolution in the context of male contest.

Birdsong may be used in territorial defense (reviews by Kroodsma and Byers, 1991; Catchpole and Slater, 1995; Searcy and Nowicki, 2000). The first experimental evidence showing this was provided by Peek (1972) who showed that muted red-winged blackbirds (Agelaius phoeniceus) suffered from more territorial intrusions than nonmuted controls. Later studies in this and other species confirmed this finding (Smith, 1979; McDonald, 1989). Krebs (1977) took a different experimental approach. He captured all
territorial great tits (Parus major) from a woodland area and replaced them by speakers playing either song, noise (a whistle), or no sound. The area from which no song or noise was played was the first one to be occupied by new great tits. These experiments and similar ones on other species (Falls, 1988; Nowicki et al., 1998b) indicate that song can have a role in territorial defense, and therefore, that it may be subject to intrasexual selection. They do, however, not show whether some song variants are more effective than others. But, rather than testing whether interindividual variation in song features correlated with aspects of male–male competition, many subsequent studies have focused on interspecific song variation and the function of song in species isolation (e.g., Nuechterlein, 1981; Becker, 1982; Martens, 1996; Miller, 1996; de Kort and ten Cate, 2001). Playback experiments tested whether altering species-specific features, such as temporal structure, frequency range, and syntax, affected the responses of territorial birds (e.g., Becker, 1982; Dabelsteen and Pedersen, 1985; Nelson, 1988). Weaker responses to a modified song were interpreted as being due to a loss of species specificity and the results were interpreted within a theoretical framework of species recognition, testing theories such as the “invariant features” (Nelson, 1989) or the “room for variation” (e.g., Dabelsteen and Pedersen, 1992) hypotheses.

Responding to a species-specific territorial song and not to the songs of other species will usually be of advantage to males. Hence, it is likely that selection will favor the evolution of species specificity in songs, as it prevents the waste of time and energy or the risk of injuries involved in aggressive interactions with birds that are not competitors. However, it is realized more and more that the border between signal evolution under the influence of species recognition and through inter- and intrasexual selection is a gradual one. Various authors state that species isolation has been overemphasized as an explanation for the evolution of secondary sex traits (Ryan and Rand, 1993a; Andersson, 1994, p. 207). Rather, sexual selection may lead to rapid evolution in secondary sex signals in isolated populations, which next may result in speciation (West-Eberhard, 1983; Andersson, 1994; Pfennig, 1998). Hence, we are back to the question of the extent to which the evolution of male territorial signals can be driven by male contest. For a long time, this possibility received noticeably less attention than selection by female choice. Andersson (1994), for instance, in his review of empirical studies of sexually selected traits lists 65 putative cases of sexual selection in birds, of which 55 concern selection through female choice and only 10 through male contest. When limiting the overview to male song, there remain 31 cases, involving only 5 instances where a trait may have been selected through male competition. Berglund et al. (1996) reviewed the studies in which the function of signals for both intra- and intersexual communication has been
examined. They also state that studies on sexual selection are heavily biased to intersexual selection. However, they suggest that many of the signals that serve a dual function first evolved in the context of male–male competition as an indicator of male competitive ability and only later became subject to female choice for high-quality males (see also Borgia and Coleman, 2000). Whether this suggestion is correct or not, it underscores the importance of studying the role of male–male competition on signal evolution. The survey of Berglund et al. (1996) involves, among others, studies of the vocal signals of six bird species. These six cases, and also the five mentioned by Andersson (1994), include the studies by Peek (1972) and Krebs (1977) on the effects of song absence on territorial defense. However, these shed little light on the question of whether the characteristics of vocal signals once they are there have been or still are molded by intrasexual selection. Bradbury and Vehrencamp (1998) also discuss territorial signaling among males. They also emphasize the role of these signals in informing other individuals about the sender’s species, individual identity, motivation, location, or distance; that is, on messages that are predominantly about species recognition and identifying territory owners. Such messages are important in territorial signaling. But does this imply there is no scope for communication about competitive abilities through territorial signals?

Various factors may affect the outcome of a conflict or fight between two opponents. One of them is motivation. In a fight between a territory owner and an intruder of similar strength, the owner will usually win (Krebs, 1982; Enquist and Leimar, 1987; Englund and Otto, 1991). Ownership seems to increase the animal’s willingness to escalate a fight, in line with game-theoretical predictions (Bradbury and Vehrencamp, 1998). However, strongly motivated intruders are also predicted to escalate (Grafen, 1987), and this may lead to long fights. The outcome of such fights will depend on physical strength, and superior intruders may beat owners (Smith and Arcese, 1989; Rosenberg and Enquist, 1991; Olsson, 1992). The factors that determine physical strength thus become important. Such factors are body size or weight, condition, or energy reserves (Austad, 1983; Englund and Olsson, 1990; Haley, 1994). Therefore, if a territory owner can produce a signal that reflects any of these qualities, and that is recognized as such by receivers, then he may suffer less from intrusions, and conflicts can be settled without the need to fight. Apart from reducing the chance of injuries, this also means that more time and energy can be used for activities with a direct impact on reproduction. Just as in the context of female choice, such a signal is only likely to evolve if it cannot be cheated; that is, if the production of songs, certain types of vocal characteristics, or singing styles involves size- or energy-related constraints and have higher costs for low-quality males than for better quality ones. If this is the case, then such features may
evolve through male–male competition. The handicap model thus also applies to male–male contest.

C. Male Song Variation and Male Competitive Ability: A Brief Review

As shown earlier, there are theoretical considerations making it likely that variation in territorial signals reflects competitive ability. But what is known about the relation between male competitive ability and the characteristics of vocalizations used as territorial signals? In addressing this question, we focus on the vocalizations themselves, and their variability, rather than on how they are used during vocal interactions. Todt and Naguib (2000) have reviewed this latter issue. They demonstrate that the relative timing of vocal signals given by two participants in a vocal exchange and the use of specific song patterns in reply to the opponent may have important communicative significance. However, the relation between the use of various singing styles or types of vocal interactions and either male quality or male fitness consequences is still largely unclear and remains to be explored (Todt and Naguib, 2000). For this reason we leave this issue aside and concentrate on the structure of the signals used in such interactions and on whether and how their acoustic features may be shaped by selection through male–male competition.

To assess the hypothesis that selection through male competitive ability may shape the evolution of song features that are related to quality, the following conditions have to be met: (1) males should show interindividual variation in song features; (2) this variation has to correlate with some aspect of competitive ability (e.g., strength); (3) the signal has to be one for which some variants can only be produced by males with the highest competitive ability; and, finally, (4) receivers of the signal, in this case other males, should note the signal variation and differentiate their responses according to the perceived quality of the sender. So, what evidence is available that birdsong meets these requirements and which song features may contain meaningful variation?

1. Repertoires and Male Quality

One song variable examined in the context of male–male interaction is song- and syllable-repertoire size. In both great tits (Krebs et al., 1978) and red-winged blackbirds (Yasukawa, 1981) playbacks of large repertoires were more effective in preventing intrusions into territories than those of small repertoires. Krebs (1977) suggested that the effect was due to the sender creating the impression of being several birds, rather than one. Whether this is really the cause of the observed effect is still unclear (Catchpole
and Slater, 1995), and later observations on red-winged blackbirds are not unequivocally consistent with the hypothesis (Yasukawa and Searcy, 1985). However, other studies have also indicated that larger repertoires may deter rival males. In starlings (*Sturnus vulgaris*), for instance, Mountjoy and Lemon (1991) showed that playback of “complex song” was more effective in preventing males from entering a nestbox than playback of “simple song,” whereas Eens (1997) obtained a positive correlation between repertoire size and proportion of encounters won in a group of captive starlings. So, as with mate attraction, larger repertoires may be more effective in male–male competition. However, whereas females may use a large repertoire to get an older male, with a better territory or of a higher genetic quality, it is not immediately clear whether such characteristics make these males better competitors in a male conflict. Between species, larger repertoire size correlates with size of the HVC (Higher Vocal Center—DeVoogd et al., 1993). There is also some evidence for a correlation between repertoire size and HVC within a species (e.g., Airey et al., 2000), and it has been suggested that only fitter males can afford the costs associated with the increase in brain size (Catchpole, 1996). Such males may be generally stronger as well. But, although repertoire may thus reflect some aspect of quality (e.g., Brenowitz et al., 1995), this parameter need not necessarily bear a relation to the current competitiveness or fighting ability of the singer. A more direct relationship with fighting ability would be expected in vocal parameters that are constrained by body size, energy supplies, and physiological or respiratory limitations.

2. **Song Frequency and Body Size**

Body size may act as a constraint on the production of low-frequency vocalizations. A larger body size will generally be correlated with a larger sound-producing organ and this will allow the production of lower frequency sounds in the same way that larger musical instruments produce lower frequency sounds than smaller versions of the same kind. As body size can be an important component in the outcome of fights, selection may have favored the evolution of low-frequency sounds, indicative of a larger body size, in male contest signals (Morton, 1977). In several groups of animals as diverse as insects, fish, anurans, and mammals, larger species or individuals do indeed produce lower frequency sounds (Davies and Halliday, 1978; Clutton-Brock and Albon, 1979; Arak, 1983; Ryan, 1985, 1988; Robertson, 1986a,b; Wagner, 1989; Hauser, 1993; Myrberg et al., 1993; Simmons, 1995; Brown et al., 1996). In line with this, it has been found that larger bird (sub)species generally produce lower pitched vocalizations and that within a species the larger sex is usually the one that produces lower frequencies (e.g., Ryan and Brenowitz, 1985; James and Robertson, 1989; Rosenfield and Bielefeldt, 1991; Farquhar,
1993; Bretagnolle, 1996; Ballintijn and ten Cate, 1997a; Bried and Jouventin, 1997; Tubaro and Mahler, 1998; Whitehead, 1999). Also, it has been suggested that the tracheal elongation shown by several groups of birds has evolved because sexual selection for large body size gave an advantage to those birds that, by enlarging their vocal apparatus, could fake a larger body size than they actually possess (Fitch, 1999). This phenomenon is very interesting as it suggests that birds may break through the constraints of body size on the production of low-frequency vocalizations. As a consequence, the reliability of low-frequency vocalizations as a predictor of size and competitive abilities is weakened. Thus, most critical to our discussion, is whether within a species larger or heavier individuals really produce lower frequency vocalizations than smaller or lighter same-sexed individuals. This has been found in some studies (Würdinger, 1970; Handford and Lougheed, 1991; Beani and Dessi-Fulgheri, 1995; Appleby and Redpath, 1997; Galeotti et al., 1997). However, others have not found such a correlation (e.g., Bowman, 1979; Shy, 1983; Genevois and Bretagnolle, 1994). In roosters (Gallus gallus domesticus) the relation between competitive abilities and frequency even seems reversed as the most dominant males produce crows with higher frequencies (Leonard and Horn, 1995). Hence, although the expected positive correlation between frequency use and body size has been found in some species, it is not a universal and reliable correlation. This demonstrates that this correlation is not caused by simple allometry. The reason for this may be that birds generate their sounds in more complex ways than insects or anurans. A consequence of these findings is that even if a negative correlation between body size and vocal frequency is obtained it becomes necessary to assess how the relationship is brought about before it can be assessed whether frequency acts as an honest signal of body size. In addition, controlled experiments comparing the effects on other males of playbacks of high- and low-frequency vocalizations that are identical in other parameters are necessary to establish whether the frequency difference has a role in communication. Such experiments are still few and far between.

3. **Condition and Song Rate**

It has been suggested that energetic or physiological constraints are reflected in parameters such as total song output and loudness, repetition rate, and duration of vocalizations (Bradbury and Vehrencamp, 1998). Song rate is a parameter that may be affected by condition or energetic constraints. In line with this, it has been found that condition (weight) correlates with vocalization rate in some species (Galeotti, 1998; Butchart et al., 1999). Correlations have also been obtained between measures of condition and other vocal parameters. Male blue petrels (Halobaena caerulea), for instance, show a positive correlation between body weight and how fast the call is delivered.
(Genevois and Bretagnolle, 1994), whereas in hoopoes \((Upupa epops)\) body condition shows a positive correlation with number of elements in their song (Martin-Vivaldi \textit{et al.}, 1998). However, in these examples the call variation has been examined in relation to female mate choice rather than to male–male competition.

Several studies have reported that food supplementation may increase song output (Reid, 1987; Alatalo \textit{et al.}, 1990; Cuthill and Macdonald, 1990), demonstrating that body condition may affect this parameter. However, it is still not quite clear how expensive vocal production is in birds (Eberhardt, 1994; Chappell \textit{et al.}, 1995; Horn \textit{et al.}, 1995; Eberhardt, 1996; Gaunt \textit{et al.}, 1996). Also, song output may be affected by aspects of condition other than energy, such as parasite load (Møller, 1991). Hence, it is not clear how direct the linkage is between fighting ability, energy, and song rate or other song characteristics. The correlation between weight and song features, as mentioned earlier, may, for instance, not be a consequence of an energetic constraint, but be due to greater strength of heavier individuals. In addition, song rate requires a receiver to invest time to sample this parameter. Therefore, although condition and energy reserves may be a factor affecting fighting potential, their role in the evolution of assessment signals for competitive ability remains to be tested.

4. \textit{Neuromotor Mechanisms and Vocal Characteristics}

Fighting, like vocalizing, requires muscular and respiratory activity. Therefore, vocal parameters that reflect superior muscular or respiratory qualities provide good candidates to serve in assessment.

Studies on the mechanisms underlying vocal production have identified potential constraints in neuromotor mechanisms, such as the coordination between the left and right sides of the syrinx or between respiratory and syringeal muscles, and constraints on vocal tract movements and neuromotor coordination (Allan and Suthers, 1994; Suthers \textit{et al.}, 1994; Podos, 1996, 1997; Suthers, 1997; Suthers and Goller, 1997). However, we still lack experimental evidence (e.g., from playbacks) that these constraints affect meaningful parameters of male territorial signals. Also, for some cases in which particular vocal features correlate with male quality (Appleby and Redpath, 1997; Galeotti \textit{et al.}, 1997; Rehsteiner \textit{et al.}, 1998), the mechanism of vocal production involved is not clear, making it difficult to assess their link to some neuromotor constraint. Nevertheless, studies on vocal production suggest that quality might potentially reflect itself in parameters such as high repetition or trill rates, the occurrence of a large proportion of sound within a duty cycle, long-lasting sounds, and rapid vocal delivery. For instance, Lambrechts and Dhondt (1986) showed that winter dominance in great tits was correlated with a higher number of phrases per song.
Lambrechts has suggested that high repetition rate might lead to muscular exhaustion and hence may reflect superior quality of a sender (Lambrechts and Dhondt, 1987, 1988; Lambrechts, 1996, 1997; see also Hailman et al., 1987). There is some evidence of this phenomenon in frogs (Wells and Taigen, 1986). Lambrechts suggested that muscular exhaustion is also reflected in certain features of great tit song, such as an increase in intersong interval during the course of a bout or a decrease in time spent singing a song with increasing bout length (Lambrechts and Dhondt, 1988; Weary et al., 1991). This phenomenon of “drift” in prolonged singing is also known from other species (McGregor, 1991). However, it is controversial whether the phenomenon really reflects exhaustion (Weary et al., 1988; 1991). Furthermore, it has not been tested whether variation in drift affects receiver responses.

5. Conclusion

To summarize, studies from various perspectives have provided plausible arguments and some correlational support for a linkage between competitive ability and specific vocal characteristics. Nevertheless, the direct evidence for this is very limited, as are experiments demonstrating that the identified vocal characteristics affect the responses of other males. The aim of our studies on coo-vocalizations of the collared dove is to examine the link between interindividual vocal variability, variability in sender quality, and receiver responses in a case study on one specific model species.

III. The Collared Dove as a Model System

We specifically chose a nonsongbird to avoid the complications arising from the sometimes extensive intraspecific song variability in songbirds and from the learning processes underlying their song structure. The vocalizations of Streptopelia doves (turtledoves) provide an excellent model system to examine the relationship between vocal variation and sexual selection. Studying these vocalizations has a long history. Darwin (1871, p. 60) suggested that the vocalizations of the European turtledove (S. turtur) had a role in mate attraction. Craig (1908) identified various functions of cooing, in particular for the ringdove (S. risoria), and also noticed the existence of individual differences in vocalizations. Lehrman (e.g., 1965) and others (e.g., Cheng, 1979; 1986; ten Cate and Hilbers, 1991; ten Cate et al., 1993; Cheng et al., 1998) examined in detail the role of cooing in the reproductive behavior of the ringdove. Other studies showed that the species-specific coo-pattern of ringdoves emerged in deafened birds (Nottebohm and Nottebohm, 1971) and that cross-fostering doves of various Streptopelia species to related
species did not affect their conspecific coo-patterns whereas hybridization did (Lade and Thorpe, 1964; Davies, 1970; Baptista, 1996). These latter findings suggest that genetic differences underly the vocal differences between, and maybe also within, various species. It is this background of knowledge that made us select a *Streptopelia* species that we could study in the laboratory and in the field: the collared dove (*Streptopelia decaocto*).

### A. The Collared Dove and Its Territorial Behavior

The collared dove (*Streptopelia decaocto*) is one of the 17 species in the genus (Johnson *et al.* 2001). It is a sister species to the African collared dove (*S. roseogrisea*), the ancestor of the domesticated ringdove (*S. risoria*). The species originates from the Indian subcontinent. In historical times, however, it had invaded large parts of Asia and Europe (Nowak, 1965), and currently it is rapidly expanding in the United States (Romagosa and McEneaney, 1999). In the Netherlands it was first observed in 1947 and it now is a very common inhabitant of suburban areas (SOVON, 1987). Our study population is located in the village of Oegstgeest (52°11 N, 4°28 E). Blocks of terrace houses with moderately sized front and back gardens characterize the habitat. These gardens, with their mixture of deciduous and coniferous trees, provide shelter, nesting sites, and food. In our study area breeding may start as early as February and continue until October (Slabbekoorn, 1998). During this period, a pair can raise several broods successively.

Male collared doves defend a territory for most of the year, and the same territory may be occupied for several years (own observations). In winter, when attendance at the territory may be absent or very limited, most birds stay in the area, gathering at communal feeding sites and roosts. These feeding sites, often locations where humans provide food, and roosts are used all year round by nonbreeding birds. Even territorial males may regularly leave their territories to visit these sites during the breeding season. Some observations suggest that pair formation may occur at these locations (Hofstetter, 1954), although males may also attract females at their territories. Pair-bonds may last for several years (Hofstetter, 1954), but males and females do not stay in close vicinity to each other all the time. Even during the breeding season females may temporarily leave the territory. The territory is predominantly a breeding territory. As part of the feeding and roosting may occur elsewhere, territory size can be limited. In our study area the number of territories is about 100 per 30 ha, ranging in size from 100–3000 m² (Slabbekoorn, 1998).

Especially when densities are high, territorial conflicts can be observed regularly. If other birds fly over or approach the territory, display flights are given. These are upward flights, accompanied with wing beats, followed by a
downward glide with wings and tail fully spread. These glides may be circular or may lead to escorting an intruder off the territory. Display flights are usually accompanied by calls (see later). Intruders may also be approached directly, usually resulting in a chase. If intruders do not fly off, this may lead to a fight. Obviously, territorial birds may benefit from preventing fights and using displays to advertise territoriality and fighting ability. Display flights fall in this category, but the most prominent role is played by coo-vocalizations.

B. Vocalizations

Four types of vocalizations are linked to territorial behavior and/or mate attraction in the collared dove: three coo-types and one call. The call is mainly produced in flight. It is frequently given during display flights, but also during chases and other flights inside the territory. It has been mentioned as the “excitement call” in the literature (Goodwin, 1970; Cramp, 1985), but we prefer the more neutral term “flight call” (other calls are produced in different contexts, but when we use the term “call” in this chapter, we refer to this call). It sounds like a nasal “weh” and may be given in short series of up to about five calls. Although some authors have described different variants of this call for different contexts (Bodenstein, 1949; Hofstetter, 1954; Nowak, 1965), we have not been able to detect clear context-specific variation in it (C. ten Cate and S. Rantala, unpublished data).

As with many other doves and pigeons (Goodwin, 1970), the collared dove has three coo-types: the perch-coo, the bow-coo, and the nest-coo. These coo-types can be distinguished on the basis of accompanying behavior, by the contexts in which they are shown, and also on acoustic parameters. In some species of the genus *Streptopelia* the three coo-types differ in number of elements and in acoustic structure (e.g., tonal vs trill sound), in others, such as the collared dove, they share the same overall structure, differing in a quantitative way only. In the collared dove, all three coo-types have a three-syllabic, more or less tonal structure with a similar temporal pattern [Fig. 1 provides two examples of perch-coos; see ten Cate (1992) and Ballintijn and ten Cate (1999a) for additional sonograms and sonagrams of bow- and nest-coo].

The perch-coo is by far the most common vocalization (Fig. 1). It is a typical, long-distance advertising display that is predominantly shown by males. They show it from singing posts at conspicuous positions inside the territory, such as trees, chimneys, rooftops, and streetlights. During perch-cooing, the head is kept in front of the body, with the throat inflated and the bill pointing downward. Perch-coos are usually produced in series (bouts) of repeated coos (Fig. 1). Although perch-coo activity may fluctuate during the breeding cycle, it can be heard every day for most of the year. Cooing usually peaks in the morning, and there may be an additional smaller peak in the afternoon (Slabbekoorn, 1998).
The bow-coo is almost exclusively shown by males. It is directed toward another individual at close quarters and accompanied by bowing movements of the head and hopping and trampling movements of the feet. The behavior may be directed at the partner or at an intruder that has landed in the territory. Studies on the ring dove have shown that it is an aggressively motivated behavior, although it plays a role in the initial phase of pair formation (Davies, 1974; Lovari and Hutchison, 1975). Bow-coos are also given in bouts of repeated coos, similar to perch-coos.

The nest-coo of the collared dove is linked to activities and locations related to nesting, such as inspecting potential nest sites, nest building, and nest relief during the breeding phase. It is shown by both members of a pair, but predominantly by males. During nest-cooing the body is tilted forward and the wings may perform a scissoring movement. In the ring dove (S. risoria), male nest-cooing stimulates female nest-cooing (Cheng, 1979), and the latter has a self-stimulating effect on ovulation (Cheng, 1986; Cheng et al., 1998). It thus peaks just before egg laying (ten Cate and Hilbers, 1991), and field observations indicate a similar pattern in the collared dove. Nest-coos are given in bouts that may last for over 50 coos (Ballintijn and ten Cate, 1999a). Within such a bout the interval between coos is variable but almost always longer than the duration of the coos themselves.

Apart from the way a bout is structured, a detailed analysis of the three coo-types of wild caught and first generation offspring of collared doves kept in our laboratory revealed several other acoustic differences between them. These were in the duration and amplitude of the first element (shortest and softest in the nest-coo, longest in the bow-coo, and loudest in the perch-coo) and in the duration of the second element (longest in the nest-coo, shortest...
in the perch-coo) (Ballintijn and ten Cate, 1999a). A first study indicated differences in frequency between the coo-types (ten Cate, 1992), but this could not be confirmed in a later study (Ballintijn and ten Cate, 1999a). Another difference is that elements of the bow- and perch-coo may show so-called “modulations” (Fig. 1); sudden upward shifts in frequency at the start of elements, followed by a decrease toward the end. The proportion of such modulated elements is very small in the nest-coo and significantly larger in bow- and perch-coos (ten Cate, 1992; Ballintijn and ten Cate, 1999a). Also, this proportion decreases significantly from the first to the third element in the bow-coo, but not in the perch-coo (ten Cate, 1992). Finally, perch- and bow-coo series may contain coos lacking the third element (Ballintijn and ten Cate, 1999b) (see also the top sonagram of Fig. 1). This has not been observed for nest-coos (Ballintijn and ten Cate, 1999a).

C. The Perch-Coo and Sexual Selection

The perch-coo has all the characteristics of a long-distance territorial signal. Although pair formation may have occurred outside the territory (Hofstetter, 1954), one function of the perch-coo may be mate attraction, for instance to get extrapair copulations, a phenomenon that has been observed in collared doves (Hofstetter, 1954; H. Slabbekoorn and C. ten Cate, personal observations). A role for intersexual selection on the evolution of this signal thus cannot be excluded. However, an important, if not the main, function of perch-coos is communication between males. For instance, perch-cooing continues after mating, whereas vocalizations serving primarily for mate attraction usually decrease substantially during this period (e.g. Catchpole, 1973; Möller, 1991). Males also respond to each others cooing by cooing themselves, and playback of coos significantly reduces the interval between successive bouts and increases the amount of perch-cooing of territorial males (Gürtler, 1977; Slabbekoorn and ten Cate, 1996). Cooing also occurs in association with agonistic interactions or in response to such interactions in neighboring territories (authors’ personal observations). This signal is thus a very suitable one with which to investigate interindvidual variation and its meaning in the context of male–male competition.

IV. Perch-Coo Variability among Individuals

The starting point of our research was the search for interindivudual acoustic variation that might indicate some aspect of male quality and hence serve as an assessment signal. One parameter that differs between individuals is bout length. A bout is defined as a series of coos in which the pause between
coos is shorter than the duration of the coo. In our study population, the average bout length per individual varied from 4 to 11 coos, with a population mean of 7 coos \((N = 36, \text{ H. Slabbekoorn and C. Goed, unpublished data})\). Similar values were obtained in the laboratory (ten Cate, 1992; Ballintijn and ten Cate, 1999a; ten Cate and Ballintijn, 1996), where we obtained a mean of 8 coos per bout, with significantly different bout lengths between individuals (ten Cate, 1992; Ballintijn and ten Cate, 1999a). Another difference between males is the fundamental frequency of both nonmodulated and modulated elements; this also differs significantly between individuals (ten Cate, 1992). However, although these differences may be meaningful, our attention was drawn to two other conspicuous parameters for which the coos of individuals can differ. Both are related to the structure of the coo: the proportion of modulated elements and the proportion of coos lacking the third element.

A. **Frequency Modulations**

The first researcher who described the two types of elements in the perch-coos of the collared dove was Gürtler (1973, 1977). However, he did not examine inter- and intraindividual variation in any detail. In our study population, the proportion of all elements that were modulated varied between 0 and 100% per individual \((N = 36, \text{ H. Slabbekoorn and C. Goed, unpublished data})\). Wild-caught males kept in the laboratory differed significantly in the proportion of modulated elements (ten Cate, 1992) and the same is true for laboratory-raised males (Ballintijn and ten Cate, 1997b). Again the number of modulated elements varied between 0 and 100% per individual. Although the proportion of modulated elements produced by a male in the middle of this distribution range may fluctuate somewhat between different bouts (possibly depending on the context), the average intraindividual variation is usually smaller than the interindividual variation, even when intraindividual variation between successive years is considered (ten Cate, 1992).

B. **Number of Elements**

Various authors have described from field observations the variation in the number of elements, ranging from 2–4, in perch-coos (Bodenstein, 1949; Dyrcz, 1956; Bettman, 1959; Frieling, 1960; Nowak, 1965). In our study population we also observed such variation. Coos with four elements were rare. A study of one bird showing this variant in our laboratory suggests that in this case three-element coos had an additional first element (Ballintijn and ten Cate, 1999b). A possible interpretation of this variant is that it is some
sort of “stutter” in the motor program underlying the coo, a phenomenon also observed when a cooing dove is interrupted by a distracting light flash (ten Cate and Ballintijn, 1996). In our study population most birds showed two-element coos on an occasional or regular basis. However, there was a clear and consistent interindividual variation in the proportion of coos consisting of two elements only. Of 26 birds recorded in our laboratory, only 4 birds never showed two-element coos, whereas in other birds the proportion reached 50% (Ballintijn and ten Cate, 1999b—see also Figs. 1 and 7).

For both the proportion of modulated elements and the proportion of two-element coos, the variation is noticeable to the human ear. Although this may not mean that it is also noticeable to the doves, it suggests that it is. In our studies we addressed the causes and consequences of this variation in the structure of the vocalizations. We will first address the variation in the proportion of modulated elements (Section V) and then the variation in the number of elements (Section VI).

V. MODULATED ELEMENTS

A. SENDER CHARACTERISTICS

The interindividual variation in the proportion of modulated elements raises the question of their message: does this variation relate to any particular feature of the sender? A first indication of this was obtained when we examined the development of perch-cooing and sex differences in perch-coo parameters in laboratory-reared, individually housed collared doves (Ballintijn and ten Cate, 1997a,b). Young males and females start to coo at around the age of 12–16 weeks. At that time coo-bouts were still short, and coo structure was variable and showed several harmonics. Apart from the frequency level, which was higher in females, there was no clear sex difference in vocal characteristics. Neither males nor females produced any modulated elements at this stage. For females vocal structure changed only slightly when they became sexually mature. Males, on the other hand, changed in vocal structure at around 44 weeks of age. At that point several changes occurred more or less simultaneously, leading to significant differences between male and female coo characteristics. Vocal activity, bout length, stereotypy, and proportion of sound per coo all increased, whereas the number of harmonics decreased (Ballintijn and ten Cate, 1997b). These changes occurred to a greater or lesser degree in all males. At the same time some males started to produce modulated elements. However, other males continued to produce no modulations at all, and this difference remained present when adult
At the same age at which the sexual differentiation in vocal structure became apparent, the first instances of nest- and bow-cooing in males started to occur. The time of occurrence of the first bow-coos correlated strongly with the time of occurrence of the first modulated elements in perch-coos \((r = 0.96, N = 8, p = .001; \text{Ballintijn and ten Cate, 1997b})\). The absence of modulated elements in young doves and in adult females, and their emergence at the same time as other sexually differentiated acoustic traits means that modulated elements can be considered a signal of sexual maturity in males. But not all males showed modulations, even if all other vocal changes suggested that they had reached sexual maturity. So, do modulations carry another, more subtle message, for instance, one about male quality?

Weight in birds can be an indicator of male quality, with heavier males generally being bigger and stronger. For this reason we next examined whether weight (of both males and females) correlated with any of the vocal parameters measured. We obtained a significant positive correlation between male weight and the frequency (pitch) of unmodulated elements \((r = 0.679, N = 9, p = 0.025)\) and a near significant one \((r = 0.563, N = 9, p = 0.067)\) between male weight and the proportion of modulated elements (Ballintijn and ten Cate, 1997b). Both this study and an earlier one (ten Cate, 1992) also showed a positive correlation between these two acoustic parameters. When we extended our sample size, the correlation between modulated elements
and weight became significant (Fig. 3). So, the proportion of modulated elements is an indicator of body weight in males. As weight of animals in general correlates with strength or fighting ability (see Section II.B), these data suggest a link between the presence of modulations and fighting abilities. As we demonstrate later, circumstantial evidence makes this a strong working hypothesis.

The observed relation between weight and the proportion of modulated elements raises two questions: (1) How come heavier males produce more modulations? (2) Is the variation in the proportion of modulated elements detected and responded to by receivers? The first question is important as it may provide insight into whether modulations can only be produced by certain physically superior individuals (i.e., they are handicaps) or whether all males might produce them but some do not for strategic reasons. Such a further examination may also reveal more about which precise qualities are reflected in this vocal parameter. We shall return to this issue in Section V.D, but will first address the receiver side.

B. RECEIVER RESPONSES TO MODULATED ELEMENTS

Various techniques have been used to assess whether a vocal signal functions in territorial competition. A frequently used paradigm is to play back
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The assumption is that owners will show stronger responses (closer approach, more aggressive behavior, more vocal display) to more threatening signals. Gürtler (1973) used this method to examine the responses of territorial collared doves to various coos and artificial coo-variants. Although his pioneering experiments suggest differential responses to different sounds, his data allowed no clear conclusions about the meaning of modulations. Hence, we decided to do an extensive series of more-controlled playbacks. We used a standardized design in which we examined the responses of territorial birds to various sets of two stimuli that differed in a systematic way. The two stimuli were played 2 min after each other, thus creating a paired design. Each stimulus usually consisted of a series of four bouts made up of eight identical coos. A loudspeaker was placed in the territory and the behavior of the owner was recorded from 1 min before the first playback to 2 min after the second playback. Playback sets were controlled for sequence effects and avoided pseudo-replication (see Slabbekoorn and ten Cate, 1996, 1997, for details). As response measures we used the time in flight, the number of calls, and the number of perch-coos.

In our first experiment (Slabbekoorn and ten Cate, 1996), we examined whether and how doves responded to nonmanipulated coos and coo-variants. When the response to dove coos was compared with that to playback of songs of the winter wren (*Trogodytes troglodytes*—a common bird in our study area), the dove sound led to more time in flight and a higher number of calls during playback and to more coos after playback. These results validated our method. We subsequently used this design to test the responses to modulated elements.

If modulations reflect the competitive abilities of senders we would expect territorial males to respond more strongly to modulated coos than to nonmodulated ones. This was indeed the outcome when the responses to playback of modulated coos were compared with those to nonmodulated coos of the same individuals (Slabbekoorn and ten Cate, 1996). However, modulated coos may not only differ from nonmodulated ones by the presence of the modulation, but also in temporal parameters or in amplitude. So, further experiments were needed to control for such factors. To this end, we compared the responses to coos without modulation with responses to the same coos in which an artificial modulation was made in either the first or in all three elements of the coo (Slabbekoorn and ten Cate, 1997). All other parameters of the nonmodulated coo (temporal structure, amplitude) remained intact in the modulated version. Playback of both manipulated coo-variants (i.e., those with one and those with three modulated elements per coo) led to stronger responses than the nonmodulated coos.
Playback of nonmodulated coos, however, led to a significantly increased response compared to the behavior before playback; that is, nonmodulated coos are also a meaningful signal. Whether all three elements or only the first one showed modulations did not matter in terms of response strength (Fig. 4).

In later experiments (Slabbekoorn and ten Cate, 1998b) we showed that coos with modulations in the second element, or with one modulation per coo in an arbitrarily chosen element differing for each subsequent coo, also gave rise to stronger responses than did coos with nonmodulated elements. Although this suggests that the presence of modulations induced the increased responses, there is a caveat. Presence of a modulation also increases the average frequency level of that element. As mentioned in the previous section, heavier birds use higher frequencies in their (nonmodulated) coos. So, was it the higher frequency that produced the stronger response, or was it the modulation as such? This was tested by comparing the response to nonmodulated coos raised in frequency to match that of modulated coos (Slabbekoorn and ten Cate, 1997). An increase in frequency did not lead to a significantly stronger response compared to nonmodulated coos, whereas they induced a significantly lower response than modulated coos did (Fig. 4). Thus, it is the presence of modulations as such and not the use of a high frequency that induced stronger responses to coos with modulated elements. So, this set of experiments showed that presence of modulated elements has a clear and positive effect on the response strength of territorial collared
doves. The effect is in line with the hypothesis that modulations may signal some aspect of better quality or fighting ability.

C. SUPERMODULATIONS?

Some experiments on intersexual selection have shown that signal versions beyond, or at the extreme of, the natural signal range are more effective than the natural signal in attracting mates (e.g., the tail of widowbirds, *Euplectes jacksoni*, Andersson, 1982; the calls of *Physalaemus* frogs, Ryan and Rand, 1993a,b). This phenomenon may drive signal evolution to more extreme versions. Although an established phenomenon in the context of intersexual selection (Andersson, 1994), it is not clear whether the same may occur in the competitive context. Therefore we did some experiments to examine whether it was possible to create modulated elements that lead to a stronger response than naturally occurring modulated elements.

To create “supermodulated” coos, we cannot increase the number of modulated elements beyond three without altering coo structure itself. However, what can be examined is whether the magnitude or frequency level of the modulations affects the response strength. In the experiments described earlier, an artificial modulation was made by a 3% decrease in frequency of the first part of a nonmodulated element (the so-called “base frequency”) followed by an 11% increase in frequency for the remainder of the element (the “modulated frequency”). This leads to a modulation with a magnitude of 14%; that is, the rise in frequency at the start of the modulation is 14% of the frequency of the nonmodulated element. So, when the nonmodulated element had a frequency level of 550 Hz, the magnitude of the modulation was $0.14 \times 550 = 77$ Hz. The 14% was used because it was well within the natural range of modulation magnitudes. For our experiments (Slabbekoorn and ten Cate, 1998a), we varied two parameters of the modulations independently of each other. The first parameter was the magnitude of the modulation, the second was the frequency level of the base frequency. In a first series of experiments, we examined the responses to coos with modulations of 3, 28, and 42% by testing each against nonmodulated coos. Of these values, 3 and 42% are outside the natural range, for which the average is around 20% (Slabbekoorn and ten Cate, 1998a). In a second series, modulations of 3, 21, 28, and 42% were tested against the previously used modulation of 14%. Finally, we tested whether it mattered if the base frequency was within or outside a range of 3 SD (standard deviation) around the population average.

It turned out (Slabbekoorn and ten Cate, 1998a) that receivers were most responsive to modulated coos with a modulation of 14 or 21% (i.e.,
similar to that of the average in the population) and a base frequency within 2 SD of the population average. Responses to other variants were generally weaker, although still of the same magnitude as responses to nonmodulated elements. Only the variants with a base frequency of more than 3 SD above the population average (>650 Hz) produced no meaningful responses. So, altering the magnitude or the base of modulated elements does not create a supernormal signal. This means that intrasexual selection, as mediated by receiver responses, will have a stabilizing effect on modulation characteristics. This raises a new question about the sender, which is whether birds showing modulations within the average species range are the strongest competitors, and consequently, whether those below or above this average are the weaker ones. At this moment we cannot answer this question. However, given the persistently stronger responses to coos with modulated elements and the finding that the proportion of modulations is correlated with weight, we return to the question of why all males do not produce coos with modulated elements.

D. THE SENDER REVISITED: PRODUCTION OF MODULATED ELEMENTS

Modulated elements seem to carry a message about the sender. However, what precisely is this message? Why is weight reflected in the proportion of modulated elements? Does their production require more effort than the production of nonmodulated elements? To address these questions we turned to the mechanisms of vocal production. Here, however, we face the problem that, in spite of all the research into birdsong, there still is no complete understanding about how birds sing and how different sound characteristics are produced (for reviews, see Gaunt and Nowicki, 1998; Suthers, 1999). The reason for this lack of understanding is the difficulty of measuring the processes occurring within the syrinx (the sound production organ) in an actively singing bird. Thus, most of the traditional hypotheses concerning sound production are based on indirect measurements, analyses of acoustic structure and syrinx morphology, and biophysical modeling (Greenewalt, 1968; Stein, 1968; Gaunt et al., 1982; Fletcher, 1988; Brackenbury, 1989). It is only recently that new technologies and methods have become available to measure several features of sound production more directly (Goller and Larsen, 1997; Suthers, 1997). Although this is rapidly changing the existing views on vocal production in birds (Gaunt and Nowicki, 1998; Suthers, 1999), inferences on how vocal variation is linked to sender characteristics are still limited for any bird species.

The starting point for our investigation of the production of modulated elements was that circumstantial evidence suggests that modulated elements
are more difficult to produce than nonmodulated ones. For instance, those birds that produce modulations only in part of their coos have fewer modulations in the very first and last coos of a bout (ten Cate, 1992). During these phases, the birds do not seem to use their full capacity to vocalize. Furthermore, if a cooing bird is interrupted by a light flash, this may cause a modulated element to change into a nonmodulated one, but never the other way around (ten Cate and Ballintijn, 1996). We also noticed that some birds that are transferred to a new cage may temporarily produce fewer modulated elements. So, what can be said about the way modulated elements are produced, and is it really likely that their production requires more effort than the production of nonmodulated elements? To address this question we turn to the dove syrinx and various models that have been proposed for vocal production in birds.

E. Sound Production in Doves

The syrinx of the collared dove, as with that of other Columbideae (Warner, 1972; King, 1989), consists of a number of membranes between several modified rings of the trachea and the primary bronchi (Fig. 5, Ballintijn et al., 1995; Ballintijn and ten Cate, 1997a). Several authors have suggested different prime sources for the sound. Abs (1980), studying domestic pigeons (*Columba livia*), suggested that vibration of the median tympaniformic membranes, caused by airflow along them, was the prime source of sound production. To test this, he constructed an artificial syrinx and showed that a membrane did indeed vibrate and produce sound when air was blown along it. This model also showed another feature. A gradual rise in airflow led to an increase in frequency of the sound that was to some extent proportional to the increase in flow. However, at a certain level of flow, the frequency level abruptly changed to higher frequencies, a phenomenon also known from various types of whistles (Gaunt and Gaunt, 1985). Using the syrinx of a dead pigeon, Abs (1980) demonstrated that here too a gradual rise in air speed led to an increase in frequency of the sound produced, although the sudden change to a higher frequency was lacking. Nevertheless, the finding of higher airflow resulting in higher frequencies being produced, combined with the occurrence of sudden frequency increases, is reminiscent of the findings in the collared dove, where a higher frequency of nonmodulated elements is linked to a higher proportion of modulations (ten Cate, 1992). Fee et al. (1998) showed that nonlinear dynamics may underlie sudden changes from one stable state of the sound production mechanisms to another, a phenomenon also present in the vocalizations of mammals (Wilden et al., 1998). A gradual rise in airflow through an *in vitro* preparation of a zebra finch syrinx led to sudden changes in the acoustic structure of elements at
certain critical flow levels. These observations suggest that a possible hypothesis for the occurrence of modulations may be that the flow through the syrinx reaches a critical level, at which a nonlinear transition in the sound pattern occurs.

This proposed hypothesis is based on the assumption that vibrating membranes are the prime source of sound production in doves. However, this mode of sound production has been seriously questioned for doves. Gaunt et al. (1982) and Gaunt and Gaunt (1985) suggested dove coos to be whistles, with the medial tympaniformic membranes (Fig. 5) acting as a static slot through which air is blown, leading to sound production through formation of stable vortices. They arrived at their conclusion after measuring EMGs of syringeal and abdominal muscles and air sac pressure patterns in

![Diagram of syrinx](image)

**Fig. 5.** Slightly schematic ventral view (left) and horizontal section (right) of the syrinx of an adult male collared dove. In the ventral view the dark structures are ossified tissue, the lighter gray ones are muscles and the light parts of the tracheal and bronchial rings are cartilaginous. Not shown is the dorsal (tracheosyringeal) membrane. See Ballintijn et al. (1995) and Ballintijn and ten Cate (1997a) for more details.
the abdominal air sac of the ringdove (*S. risoria*). As the ringdove is the closest living relative of the collared dove (Johnson *et al.*, 2001), the latter model of sound production may also be applicable to the collared dove. However, our detailed study of the syrinx morphology of the collared dove (Ballintijn *et al.*, 1995), indicated that the system probably cannot function in the way suggested by Gaunt *et al.* (1982). For instance, the structure of the medial tympaniformic membranes is highly elastic, ideal for vibrating rather than for staying in a stationary position to create a slot. For this reason, we decided to put the whistle model to a test in the collared dove. If sound is produced in a whistle-like manner, the fundamental frequency is dependent on resonances which stabilize the acoustic disturbance in the airflow (Chanaud, 1970). Consequently, altering the resonance frequency of the whistle will result in a correlated shift in its fundamental frequency. Such a shift is not expected if vibrating membranes are the prime source for the sound. A way to alter the resonance properties of the vocal tract is to alter the medium from normal air to a gas with a different density, altering sound velocity.

In our experiment (Ballintijn and ten Cate, 1998) we used a closed cage in which we gradually replaced air by heliox (a mixture of helium and oxygen). This mixture allows the birds to breathe normally while increasing sound velocity. The prediction is that if coos are whistled sounds, the frequency should increase in proportion to the heliox concentration. If, on the other hand, a vibrating membrane produces sounds, the frequency should not be affected, or only marginally so. A toy flute could be operated from outside the cage and was used to assess the increase in frequency that a coo would show if it was a whistled sound. We recorded six male collared doves in heliox as well as in normal air. As expected, the frequency for the flute increased in heliox, on average 46%. Nonmodulated coos also showed a significant increase in frequency, but with just 3.6% it was marginal compared to the flute rise in heliox. This demonstrated that, like the pure tonal sounds in several songbirds and the calls of budgerigars (Nowicki, 1987; Nowicki and Marler, 1988; Brittan-Powell *et al.*, 1997), the nonmodulated elements of dove coos are not produced by a whistle-type mechanism. However, we did obtain a substantial and significant decrease in amplitude of the fundamental frequency of the nonmodulated elements (Fig. 6). This finding suggests that, although there was no direct coupling between acoustic resonance and the frequency at the sound source, resonances of some sort may be involved in its amplification (cf. Hoese *et al.*, 2000). The result of the heliox experiment was noticeably different for modulated elements (Ballintijn and ten Cate, 1998). The first phenomenon we observed was a significant reduction in the number of modulated elements. However, the most remarkable effect was a systematic change in the frequency profile of the modulated elements...
Fig. 6. Comparison of sonagrams and amplitude envelopes of coos in normal air (left) and in heliox (right) of two collared doves. Dove 111 produced nonmodulated elements only. The heliox atmosphere did not affect frequency, but the amplitude was strongly reduced. Dove 015 produced coos with a modulation in the first element in normal air. In heliox, the modulated first elements (arrow), but not the nonmodulated ones, show a higher frequency level than in normal air. Again, the amplitude is strongly reduced in heliox (note the different amplitude scales in normal air and heliox for this bird). From Ballintijn and ten Cate (1998).

(Fig. 6). With increasing heliox concentration, the frequency of the modulated part of the elements increased to about 1.5 times the frequency of the base of the elements, after which the increase stopped (Ballintijn and ten Cate, 1998). This change occurred in each of the four birds that showed modulated elements. Although the results show details that raise questions about what precisely is going on, the observed changes are different from the predictions of the whistle model.

So, the whistle model of sound production, suggested by studies of the ringdove, can be discarded for the production of modulated as well as nonmodulated elements. This is also suggested by experiments on feral pigeons, Columba livia, using endoscopic techniques (Goller and Larsen, 1997; Larsen and Goller, 1999). Direct observations of vocalizing in anesthetized pigeons, induced by brain stimulation, showed that opening and closing of the lateral tympaniformic membranes (Fig. 5) was correlated with sound production (Larsen and Goller, 1999). This suggests the vibrating movement of these membranes produces the sound, possibly in a way similar to the vocal folds in mammals.
So, to summarize, the coos in doves are not produced by a whistle-type mechanism. At the same time, the different response to heliox by modulated and nonmodulated elements suggests that different, albeit it as yet unspecified, modes of production of resonance may underlie their production. It confirms that the complexity of the processes underlying vocal production is greater than earlier models suggested (Gaunt and Nowicki, 1998). To return to the hypothesis that an increased flow of air through the syrinx may induce the occurrence of modulations, this is still a feasible one, with nonlinear processes being a candidate principle for their origin.

Assuming for the moment that the hypothesis is correct, is the production of modulations so demanding that some males are unable to produce them, that is, are they true handicaps? One constraint on signal production may be the energetic costs (see Section II.C.3). But one may wonder whether energetic costs make much of a difference between the production of modulated and nonmodulated elements and also whether such a difference is really worth broadcasting. If a signal is needed to broadcast superior energetic reserves, then a high output rate (i.e., a high amount of singing) may be a much better signal than a specific sound variant. However, if a high airflow is required to produce modulations, then the prime message conveyed by modulations might be about respiratory muscle strength: a bird able to produce a higher driving force may also be a stronger fighter in case of a conflict.

It will be obvious that the mechanism of sound production has to be understood before the cause of individual differences in vocal structure can be fully assessed. Nevertheless, we tentatively conclude that modulations may act as an honest signal of fighting ability.

VI. VARIATION IN ELEMENT NUMBER

A. RELATIONSHIP TO SENDER CHARACTERISTICS

We now turn to the second parameter for which noticeable individual variation is present: the number of elements within a coo. In our laboratory colony, coos consisting of two elements are quite common. Out of 26 individuals, only 4 never produced a two-element coo. In 15 individuals, two-element coos, if produced, were always the last ones of a bout (Fig. 1). Finally, seven individuals showed two-element coos in other positions during a bout, usually toward the end (Ballintijn and ten Cate 1999b—Fig. 7). Two-element coos not only occurred more toward or at the end of coo-bouts, but the chances of having a bout ending with one or more two-element coos increased with increasing bout length (Ballintijn and ten Cate, 1999b). Over
all birds there was a significant negative correlation between body weight and proportion of two-element coos per bout (Fig. 8).

A detailed comparison of the temporal structure of coos and coo bouts with and without missing third elements revealed that the duration from the beginning of one coo to the beginning of the next one did not differ between the two (Ballintijn and ten Cate, 1999b; see also Fig. 7). This suggests that while no third element is heard, the underlying rhythm of coo production is maintained. For one bird we measured the pattern of tracheal airflow and pressure in the abdominal air sacs simultaneously with sound production. This showed that the pressure pattern, but not the flow pattern, of coos with two and three elements had the same duration (G. Beckers, R. Suthers, and C. ten Cate, unpublished). This supports the idea of constancy in the underlying rhythm, at least partly. But why is no sound produced if at least some aspects of the underlying pattern of neuromuscular actions seem maintained?

Three, not necessarily mutually exclusive, mechanisms may account for this phenomenon. The first one may be declining motivation, resulting in a reduced intensity of the signal during prolonged reiteration of the coo. Although this hypothesis cannot be excluded it does not readily explain why decreasing motivation results in incomplete coos rather than in short bouts. Nor does it explain why elements disappear only toward the end of long bouts, and not short ones. Finally, the observed correlation between body weight and the occurrence of two-element coos does not fit a motivational explanation.

A second hypothesis to account for the findings is the “neuromuscular exhaustion” hypothesis proposed by Lambrechts (Lambrechts and Dhondt,
FIG. 8. Male body weight correlates negatively with the proportion of coos lacking the third element. Stars: individuals that never produced two-element coos; open circles: individuals that produced two-element coos only at the end of bouts; closed circles: individuals that produced two-element coos at various positions during bouts ($r = -0.41, p = 0.036, N = 26$). From Ballintijn and ten Cate (1999b).

1988; Lambrechts, 1996). As discussed in Section II.C.4, this hypothesis postulates that high repetition rates of vocal elements may lead to exhaustion in some of the muscles involved in their production. The repetitive coo pattern might be a candidate to suffer from this phenomenon. This hypothesis would explain the pattern of more missing elements toward the end of long bouts. Also, heavier or stronger males might suffer less from exhaustion than lighter ones. The exhaustion hypothesis thus provides a potential explanation for the findings. However, direct measurements of muscle activity and metabolism are necessary to confirm it. Such measurements are also required to test a third and related hypothesis. This hypothesis is that with increasing bout length the bird may run into problems with keeping up the respiratory activity required to vocalize. Sound production is strongly coupled with respiration (e.g., Brackenbury, 1989; Wild et al., 1998). Rather than a constraint at the level of syringeal muscle activity, as postulated by Lambrechts’ hypothesis, the constraint may be an inability of the respiratory system, causing the bird to run out of breath (Ballintijn and ten Cate, 1999b).

In summary, although not conclusive yet, the data suggest that differences in the number of elements may reflect honest differences in sender quality.
B. Receiver Responses

To test whether coos lacking elements were perceived as less threatening by receivers, we used the same methodology as we did to examine the effect of modulated elements. Playbacks were done, comparing the effect of two coo-variants, differing in one parameter (Slabbekoorn and ten Cate, 1999). In this case the manipulated parameter was presence or absence of a particular element. A total of five different tests were done each against a matched control series of nonmanipulated coos. The experimental manipulations involved three series, which were: (1) the first, second, or third elements of coos were removed and replaced by a silent interval, (2) removal of the third element led to a corresponding shortening of the interval between coos, and (3) the pause between elements one and two was exchanged with the pause between elements two and three (Fig. 9).

In contrast to our expectations, replacing the third element by silence did not affect receiver responses. Territorial males responded equally strongly to coos with and without the third element. When the second element was replaced by silence we obtained the same response. It was only when the first element was replaced by silence that territorial males showed significantly weaker responses. Weaker responses were also obtained in response to shortened coos and to coos in which the pauses between the elements were exchanged (Slabbekoorn and ten Cate, 1999—Fig. 9).

The finding that replacing the first element by silence has a stronger effect is in line with results obtained in other species. Several studies, both

![Fig. 9. Responses to playbacks of stimuli with manipulated temporal structure against a nonmanipulated control. (Left) Schematic representation of the various stimuli. NM = nonmodulated coos with normal temporal structure (control); NM-3, NM-2, NM-1 are nonmodulated coos for which, respectively, the third, second, and first element are replaced by silence. In NM-3* the third element is also removed, but not replaced by silence. NM* is a nonmodulated coo in which the pause between elements one and two is exchanged with that between two and three. (Right) Percentage of time spent in flight during playback of the stimuli [see Slabbekoorn and ten Cate (1999) for details]. * Indicates significant differences at \( p < 0.05 \).]
in the field and in the laboratory, have shown that modifications in the first part of songs lead to a stronger decline in response than modifications to later parts (Schubert, 1971; Brémond, 1972; Helb, 1973; Wolffgramm and Todt, 1982; Johnsrude et al., 1994). Also, laboratory studies of zebra finches (*Taeniopygia guttata*) have shown that replacing part of a song by silence may go seemingly unnoticed (Cynx, 1993). This latter phenomenon is reminiscent to findings in humans. Obliteration of words in a sentence, replacing them by noise or silence may go unnoticed by listeners (Warren et al., 1972; Bashford et al., 1988). Finally, studies on other species also indicate that affecting element or interval duration of songs, or the rhythm of sounds, may reduce responsiveness (Falls, 1963; Reinert, 1965; Emlen, 1972; Heidemann and Oring, 1976; Romanowski, 1979; Brenowitz, 1983; Hulse et al., 1984). So, in several respects the results of our experiments on the collared dove are comparable to those obtained in other species. At the same time, however, the outcome raises questions when the communicative context is taken into account.

From a functional perspective it makes sense for males to respond only marginally to shortened coos or altered pause durations. These coo variants are outside the species typical range as we observed it in the field and the laboratory. At the same time, differences in temporal parameters are the most distinguishing features among the perch-coos of the various species of the genus *Streptopelia* (Slabbekoorn et al., 1999). So, unless there are instances of interspecific competition with related species, there is no benefit and there may even be a disadvantage in responding to coos with considerably modified temporal characteristics. Various *Streptopelia* species do indeed show reduced responding to the perch-coos of other members of the genus (de Kort and ten Cate, 2001). Also, laboratory studies indicate that temporal features are one parameter that *Streptopelia* species use to distinguish coo-like sounds (Beckers and ten Cate, 2001). However, as outlined in the previous section, it may benefit a receiver to differentiate between coos with a third element and coos without a third element, but with the same overall duration. Intruders that produce three-element coos only, should be more of a threat than intruders producing two-element coos. Why this is not reflected in the responses to playbacks is not clear. The findings of other species might be taken to suggest that replacing an element by silence goes perceptually unnoticed. If so, lack of a difference in response to stimuli carrying different messages is due to a perceptual constraint. An alternate, and to us more plausible, explanation is that the difference may be noticed by the birds, but is not reflected in their response or in our measurements. In our experiments we used nonmodulated coos. As shown in Section V, such coos give rise to weaker responses than modulated coos. Maybe the response to nonmodulated coos with a third element represents the weakest
response given to any vocalizing intruder. Weaker responses were only obtained in experiments with stimuli outside the species range and indicate the virtual absence of any reactions. If a “floor effect” is the reason for finding no difference in response, then we predict that replacing the third element by silence in a modulated coo will reduce the response to playbacks. So, whether the lack of differentiation between two- and three-element coos is a general phenomenon remains an open question.

VII. Vocal Variability and Male Contest: Conclusions

The aim of our study was to examine whether variability in territorial signals provides information about sender quality and whether receivers take this information into account.

We have shown that two features of the perch-coo of the collared dove—the occurrence of modulations and the number of elements—are related to weight of the sender. Weight is a potential indicator of competitive strength. As either more muscle strength or a higher respiratory capacity may be needed to produce modulated elements and coos with three elements, the interindividual vocal variation may be an honest reflection of sender quality. Although the currently available evidence thus fits the hypothesis that vocal signals used to deter rivals carry information about competitive ability, several aspects of the system await further investigation. For instance, our playback experiments show that receiving males are not only very sensitive to the presence of modulations, but also that male responses to modulated elements are tuned to modulations with a magnitude similar to the population average. We do not know whether the magnitude of modulations is in any way related to other features of males. Further study is also required to analyze whether modulations and element number really affect the success of intruders or defenders in acquiring or defending a territory. Nevertheless, our study shows, at least, the potential for intrasexual selection in shaping territorial signals. It indicates that, in general, more attention should be given to the possibility that the structure of such signals is not arbitrary (cf. Bradbury and Vehrencamp, 1998), but shows linkage to their content, and that interindividual variation is related to differences in quality.

Another issue requiring further study concerns the precise linkage between vocal variation, physiology, and strength or competitive abilities of the sender, not just in the context of male–male contest, but also in that of mate choice. The production of vocalizations requires an appropriate morphology of the vocal tract, precise neural coordination, and extensive muscular activity. Vocal variation may thus potentially reveal individual differences in a whole range of morphological, neural, and physiological parameters that
are also relevant for the fitness of the sender. Just as some aspects of within-individual motivational variation may give rise to a physiological state that is inextricably linked to the ability to produce certain types of vocalizations (Morton, 1982), physiological and morphological differences between individuals may have the same effect. Examining such relationships provides a challenge for future research, as our current understanding of such links is still limited (see also our review in Section II.C). It will help to understand whether partially correlated variation in separate sound parameters reflects different underlying mechanisms or whether these are a consequence of a common causal factor. It will also help to get a better understanding of the precise messages in interindividual vocal variation. Such variation may originate from very different sources. For instance, certain aspects of a vocalization may depend on the morphology of the sound-producing system (e.g., its size or its membrane structure), whereas others depend on the way the system is operated. While the first may reflect something about the conditions of the birds during rearing (Nowicki et al., 1998a), the latter may reflect current condition. Knowing the relationship between vocal parameters and their main determinant may thus allow a much more detailed interpretation of the information present in the signal. This will improve an assessment of their potential or actual relevance in various contexts. It will also reveal whether birds that learn their vocalizations, such as songbirds, differ in this respect from birds that do not, such as doves. This may shed more light on the advantages or disadvantages of song learning.

Further studies on the relationship between vocal parameters, vocal production, physiology, and morphology are also relevant to assess whether vocal signals contain redundant information. Redundancy occurs when several parameters of a signal carry the same type of information (Bradbury and Vehrencamp, 1998). Redundancy can be seen as an adaptive trait, evolved to guarantee that receivers detect a message. It is undoubtedly true that signal efficacy might be improved by adding features that exploit “receiver psychology” (Guilford and Dawkins, 1991). In examining potential cases of such redundancy, vocal signals have, for instance, been considered as one component and movement or morphology as another (e.g., Fusani et al., 1997; Møller et al., 1998). One general problem with assessing redundancy is that its assessment is based upon disproving the alternative that the separate components carry different messages (Møller and Pomiankowski, 1993; Johnstone, 1997). One can imagine that the more detailed the level of analysis of the message of a signal, the less likely one is to find redundancy. Another issue with particular relevance to vocal signals is whether they are single signals. We suggest that vocalizations, through their complexity and, hence, multitude of sound parameters, might better be viewed as multicomponent signals, potentially carrying multiple messages. When examined in
some detail, certain vocal parameters may turn out to provide one particular message, others another. In such a case, these different messages may be addressing different audiences, for example, potential competitors and potential mates. So, although at one level “song” can perhaps be seen as one signal with “dual utility” (Berglund et al., 1996), at a different level it can serve as carrier for multiple messages for different audiences. When such messages may give rise to conflicting selection pressures, the result may be the evolution of different singing styles or songs for different contexts—a phenomenon present in several bird species (e.g., Morse, 1970; Catchpole, 1983; Groschupf, 1985; Kroodsma et al., 1989). There are certain systematic differences between songs serving for mate attraction and songs involved in territorial behavior (Catchpole and Slater, 1995). It is, however, still hardly explored whether these differences also reflect different qualities of the senders.

More generally, the conclusion can be that understanding signal content and whether and how it links to signal design still represents a challenge for future research. In spite of all the progress that has been made with respect to theories about why and how animals communicate, there is still a lot to be discovered when it comes down to explaining why birds sing the way they do.

VIII. Summary

Bird songs are assumed to have a dual function: attracting mates and deterring rivals. Hence, they are likely to be subject to sexual selection. Most studies on signal evolution through sexual selection concentrate on the first function: mate attraction. In this chapter we concentrated on vocal signals involved in male–male competition, and, in particular, territorial defense. Broadcasting species or individual identity and territory ownership are usually considered to be the main functions of territorial signals. Far less is known about whether such signals may also act as assessment signals, providing honest information about the sender’s competitive abilities. On theoretical grounds, such a function is to be expected.

We review the evidence that interindividual variation in vocal characteristics may provide a message about male competitive ability. This evidence is fragmentary. Some vocal parameters may be suitable indicators of differences in such abilities, but few studies demonstrate that they are actually used in this way. As a case study on this issue, we examined the role of vocal variation in the territorial “perch-coo” vocalization of the collared dove (Streptopelia decaocto). The perch-coo consists of three elements that are produced in series. Heavier males show a higher proportion of perch-coo
elements with a “modulation,” a sudden increase in frequency at the start of an element. They also show fewer coos in which the third element is lacking. The available evidence about how doves vocalize suggests that production of both modulated elements and three-element coos require greater strength or respiratory capacity. Playback experiments show that coos with modulated elements give rise to stronger responses from territorial males, that is, they are perceived as originating from a stronger competitor. The strongest responses are given to modulations with a magnitude close to the population average. Presence or absence of the third element only leads to different responses when combined with reduced length of the coo. These results show that at least part of the interindividual variation in acoustic parameters of the perch-coo conveys meaningful information about sender quality to receivers. This demonstrates the potential for intrasexual selection as a factor shaping territorial signals.

The findings highlight the point that the study of signal variation in a competitive context is a neglected but fruitful area for research. The challenge for future studies will be to link vocal variation to specific modes of vocal production and to relate it to more specific aspects of “sender quality.” This will help us to understand the relationship between signal content and signal design and may shed light upon the role of birdsong as a multicomponent signal.

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References


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Imitation of Novel Complex Actions: What Does the Evidence from Animals Mean?

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I. INTRODUCTION

Despite a flurry of interest in imitation of bodily actions by nonhumans, little clear agreement has resulted as to its cognitive mechanism, adaptive function, and species distribution (Galef, 1988; Heyes, 1993; Heyes and Ray, 2000; Meltzoff, 1996; Mitchell, 1987; Tomasello et al., 1993; Whiten and Ham, 1992; Zentall, 2001). These three deficiencies may be interlinked: What is meant by imitation varies significantly in different theoretical formulations, affecting both the possible adaptive value of having the capacity to imitate and the range of mechanisms that are sufficient to account for it. Ambiguities about the species distribution of imitation, in turn, impede understanding of the phylogeny of imitation. In textbook accounts of animal behavior and animal mind, too often the topic of imitation is still consigned to a small and isolated subheading. By contrast, in developmental psychology imitation has long been considered a hallmark of intelligent function in children (Piaget, 1945/1962; Vygotsky, 1962); yet, even there, clear models for its operation are often lacking.

The purpose of this chapter is to put forward a mechanistic theory that can explain the most challenging data on imitation, that is, how novel motor behavior with complex organization may be learned by observation. This is the kind of imitation that enables us to learn by apprenticeship, patiently watching a skilled practitioner. The question of whether, and to what extent, nonhumans share this ability can best be judged when the phenomenon is better understood. A secondary aim, therefore, is to articulate a process model clearly enough to aid proper interpretation of animal behavior, in the hope of avoiding the danger that “imitation” becomes a wastebasket
category of those behaviors that cannot be understood in any other way. It is not intended that imitation of novel, complex motor behavior should be seen as the only kind of imitation, and it will, in fact, be argued that several types of imitation serve different adaptive functions and may have different evolutionary origins. If imitation has evolved in more than one functional context, it is expected that its properties and underlying mechanism will be different in each case, and conflating them in a single category will be unhelpful. (These words are partly offered as an apology for introducing yet more novel terminology.)

It may reasonably be asked why this should be necessary: Why is there not already a range of adequate process models for imitation of novel, complex behavior that require only to be tested against evidence? At least three reasons may be offered. First, much research has been phenomenon-driven, focusing attention on isolated behaviors that are labeled “imitation” and need to be explained (or explained away). This has distracted from the overall context and adaptive functions of social learning in general and has led to reliance on contrived laboratory tasks or unusual natural circumstances as gold-standard indicators of “true imitation.” If these phenomena were indeed pure cases of imitation, this might be a good research strategy, but that is most unlikely. This is the second point: It is unlikely that it will ever prove possible to devise a demonstration of imitation uncontaminated by other social influences and ways of learning. In the untidy world that real animals inhabit, such tidy partitionings are rare: Behavior that is entirely imitated cannot be expected any more than can behavior that results entirely from nature or entirely from nurture. Instead, it is more likely that several different mechanisms contribute to the development of any single behavior. Even if one of these mechanisms is imitation, the acquisition process will also be influenced by genetic predispositions, other learning mechanisms, and other social influences. Third, clarity has not been increased by the ambiguity and vagueness of the terms employed in this arena, in particular, the word imitation itself. Even now, there is no consensus on whether, to count as imitation, behavior needs to be a close physical match to the behavior that was demonstrated, and, if so, how exact this match should be; whether it need involve new learning or merely evocation of already practiced actions; and whether or not imitation implies some form of empathy or identification of mental state with the imitated individual (see peer commentaries to Byrne and Russon, 1998).

The net result is that, although an abundance of different categories of social learning have now been defined, based often on somewhat hairsplitting differences (see Whiten and Ham, 1992, for an attempted taxonomy of this plethora), less progress has been made on how imitation works, mechanistically, and why, functionally, it has evolved in some species. Numerous hypothetical mechanisms have, in fact, been proposed to avoid attributing
imitation to nonhumans and to account, in a simpler way, for animal behavior suggestive of imitation. Often the existence of these mechanisms lacks independent validation, and the precise meaning of “simpler” is not often explored; there is thus heavy reliance on Lloyd Morgan’s canon, rather than on discriminatory data, when deciding between explanations (Roitblat, 1998). Since the everyday meaning of imitation is loose, this is to some extent understandable; but, if making advances in scientific understanding of social learning is regarded as a process rather like peeling off unwanted layers of husk, then the current concern must be whether the kernel will finally be palatable. As Heyes and Ray (2000) have shown, the majority of theoretical models of imitation do not fit long-established data, and many models are not well-enough specified even to qualify as explanations at all.

In this chapter, I first set out what is not in serious contention: the explanation, by means of quite simple and now well-accepted learning mechanisms, of much behavior that is still called imitation in lay circumstances. Then, I use a distinction found useful in the vocal learning literature, contextual versus production learning, to resolve a controversy as to what is or is not good operational evidence of imitation. This will clear the way for a discussion of two forms of imitation, which are apparently widely divergent in adaptive function: social mimicry and method learning. A theoretical treatment is offered of how and why they might differ in mechanism. Finally, narrowing the focus to the production learning of complex, novel behavior, I discuss several different process models, emphasizing their strengths and limitations, with the aim of enabling proper categorization of animal imitation in the future. Throughout, attempts will be made to integrate imitation with wider cognitive domains and wider evolutionary functions: “imitation for action,” not for its own sake.

II. Social Learning without Imitation

Before sharpening the focus toward observations that have been treated as motor imitation in the research literature, I think it is useful to recognize a baseline of agreement on a range of other phenomena to which the term is sometimes applied.

It has long been understood by animal learning theorists that a general tendency to respond more vigorously (stimulus enhancement: Spence, 1937) or attend more closely (local enhancement: Thorpe, 1956, 1963) toward those parts of the environment with which a conspecific is seen to interact will usually have the beneficial consequence of speeding learning in social circumstances. More rapid learning in social species makes it more likely that local traditions of dealing with the environment can develop and persist, giving rise to differences in characteristic behavior patterns between family
lines or populations ("cultures"; see Roper, 1983). Popular accounts of these differences normally refer to imitation (and also teaching), but the mere existence of such differences does not on its own constitute evidence for imitation in any of the senses in which the term is used by ethologists or psychologists.

Similarly, imitation is often popularly attributed when individuals are seen to do the same thing together, a coincidence of action which may be due to many things, including environmental prompting (e.g., when several birds on a bird feeder table all peck at seeds because that is their purpose in flying there, not because they imitate the others). Zajonc (1965) proposed that animals and people were often seen to do things together because of a general tendency for the presence of conspecifics to increase the activity level of all of them, an effect he called social facilitation. The existence of this phenomenon has been doubted (e.g., Byrne, 1994, 1995), but it has been shown under controlled conditions in capuchin monkeys (Visalberghi and Addessi, 2000). The researchers suggest it may play a role in overcoming neophobia. However, neophobia itself presumably evolved as a protection mechanism, so the trade-off may not be simple. In different species, synchrony of behavior might be adaptive for a number of reasons (reduction of predation risk, enhanced prey capture rate, locomotor efficiency, etc.). According to current theoretical treatments, social facilitation, as with stimulus enhancement, may result in behavior that mimics the results of true imitation, but may be explained away by simpler means (Galef, 1988).

Moreover, it is recognized that interactions with humans may influence animals in unintended ways. Where wild or feral populations are provisioned, the distribution of food items by people can potentially condition behavior patterns, giving rise to behavioral traditions that appear to be the product of learning by imitation. This has been advanced as a possible explanation of the dialects found in Japanese macaque monkeys (Green, 1975). Three populations show identical call repertoires except for their food-associated calls, which are quite different in form in each population. The rewarding consequence of food, applied differentially toward the more noisy and conspicuous individuals, may have resulted in a learned association between vocalization and food; coincidental differences in the particular calls that attracted human attention resulted in each population's "food calls" developing from different founding vocalizations (coos in one, screams in another, and so on). Further, as Green noted, this might also apply to the various feeding skills, which are unique to the provisioned monkeys of Koshima Islet and have often been attributed to imitation (but see Huffman, 1984, for a behavioral tradition that appears to have spread without human influence). Further doubt has been cast upon the idea that these traditions resulted from motor imitation, based on the slowness of their original spread (Galef, 1990, 1992).
Rapid social learning, frequently observed co-action, and population-specific traditions of behavior will no doubt continue to be attributed to motor imitation in popular accounts. Although demonstrating the negative is always problematic, researchers in animal behavior now routinely require stronger evidence (Heyes, 1993). In particular, the demand is for control data, to show that the opportunity for observation of a skilled model is essential, and evidence that the effect of having a model to observe is mediated by more than individual learning bolstered by general tendencies such as stimulus enhancement and social facilitation. If genetic differences and other potential confounds can be ruled out, then population-specific traditions provide control for the availability of skilled models, but innovations in artificially provisioned populations must remain suspect. Even under conditions unaffected by human intervention, such as the insect-gathering and nut-cracking traditions of tool use in wild chimpanzees, maintenance by imitation may be disputed, since even long-standing traditions might potentially be maintained by socially enhanced individual learning (Tomasello, 1990). Further, population isolation introduces concern about genetic differences in some cases. For example, all records of nut-cracking in chimpanzees are in the Western subspecies *Pan troglodytes verus*, so it is possible to argue that *P. t. troglodytes* and *P. t. schweinfurthii* lack some innate capacity that makes learning to use hammers peculiarly straightforward for *verus*. In the light of these problems, many researchers have turned to laboratory experimentation for incontrovertible evidence of imitation.

III. LEARNING WHEN AND LEARNING HOW

Use of controlled experiments has shown that, even with these concerns removed, there remains a wide range of circumstances in which an animal, if allowed to see another individual performing a particular motor behavior, is likely itself to show behavior of the same form; whereas if it is denied that sight it does not do so. These cases have typically been hailed as “true imitation” in literature (e.g., Voelkl and Huber, 2000), but rejoicing may be premature. Several different evolved mechanisms may produce behavior that fits the basic pattern of “A does X after seeing B do X, but not otherwise.” Lumping all cases together leads to expectations that a single explanation will serve for all, which may be quite wrong. Moreover, some mechanisms that can explain the experimental results are inadequate to account for everyday imitative learning.

Instead, I propose that drawing two distinctions may aid our understanding of evolutionary function and cognitive mechanism in the different cases. The first of these is a distinction already found useful in the literature on vocal imitation, it is that between contextual and production learning.
(Janik and Slater, 2000). The second distinction, separating production learning into two types according to whether the imitation is action-level or program-level, derives instead from studies of primate skill acquisition (Byrne, 1994, 1999; Byrne and Russon, 1998). Taken together, they create three categories of imitation: contextual imitation, production learning by action-level imitation, and production learning by program-level imitation.

In contextual learning, there is a change in the circumstances in which an action is performed; the action itself is not new but was present in the existing repertoire of the animal. Applying this to imitation, contextual imitation would amount to learning to employ an action already in the repertoire in different circumstances, but not learning its form. Consider the progressive narrowing down during development of the range of referents to which vervet monkeys, Cercopithecus aethiops, give eagle alarm calls (Seyfarth and Cheney, 1986). Young infants give these alarms to any looming airborne object, even a falling leaf; juveniles restrict their use to a range of broad-winged soaring birds; finally, adults reserve them specifically for the martial eagle, Polemaetus bellicosus, the major predator of the monkeys. If this developmental change is to be ascribed to imitation, it is imitation of context not product; the acoustic form of the call appears to be independent of any social learning. Contextual imitation may aid problem solving as well as reliable communication: A behavior in the species-typical repertoire might be applied to a novel problem, or be used in novel circumstances, after observation of a conspecific doing the same. A range of experiments has shown that a bird, seeing a conspecific using one particular action to obtain food from an unfamiliar container, will use the same action when it is given the chance to open a similar container, whereas individuals shown another efficient action acquire that technique instead (Dawson and Foss, 1965; Galef et al., 1986; Lefebvre et al., 1997; Palameta and Lefebvre, 1985; Zentall, 1996). In several species of primate, also, observing a demonstration has been shown to cause individuals to apply a particular technique to an unfamiliar problem; these include chimpanzees (Whiten et al., 1996), capuchin monkeys (Cebus apella; Custance et al., 1999) and marmosets (Callithrix jacchus; Bugnyar and Huber, 1997; Voelkl and Huber, 2000). For instance, seeing a human use a twisting motion, to remove a bolt that locks a box containing food, makes the nonhuman primate observer more likely to twist rather than pull the bolt out, and vice versa. Crucially, for both bird and primate examples, the two methods are equally effective. This two-action methodology (the label is retained even if more than two methods are tested) has become the paradigm case for experimentally demonstrating “true imitation.” Indeed, these data have been described as the best evidence for motor imitation in animals (Heyes, 1993, who explicitly defines imitation as including both this “R–S learning” (response–stimulus) and “learning of novel R”). However, if the differences between experimental groups are to be ascribed to imitation,
it must be to contextual imitation—contextual learning by observation. In none of these cases is there evidence that a new action has been added to the individual’s repertoire; rather, in every case it may simply be that a familiar action is applied to an altered range of environmental stimuli. The result under many circumstances will be improved fitness, since effective actions are prompted into use, but no learning of new actions necessarily occurs; contextual learning is therefore a feasible and arguably simpler explanation.

Moreover, contextual learning of motor behavior can be explained at a cognitive level in a remarkably simple way (Byrne, 1994, 1995, 1998), one closely allied to stimulus enhancement. Stimulus enhancement may be viewed as priming of brain records of environmental stimuli, such that subsequent attention to these stimuli is increased and exploratory behavior is directed more toward them. In the same way, the data of the two-action methodology, described as “true imitation,” may instead be treated as response facilitation. In this case, observation results in the priming of brain records of motor behavior, with the result that these motor actions will more likely be elicited if similar circumstances recur. A proviso is that there must be a straightforward way of recognizing that the action is “the same”: a clear overlap in perceptual features between the act as done by another and by the self, or some other way of making the link. This is not an all-or-nothing distinction. Although one’s own vocalizations, perceived through the skull as well as the air, do not sound the same as those of others, heard through air alone, the two are similar and the differences are highly predictable ones. Correspondingly, hand actions done by a conspecific and by the self do differ in visual perspective, but they retain many invariances. The difference between self- and other-view is greater for movements of the head and beak in birds, although the sounds made by pecking or tearing at environmental objects will be much the same whether self or other performs the action. For the human facial gestures imitated by newborn babies the feature overlap is presumably nil (Meltzoff and Moore, 1977). Heyes and Ray (2000) introduce the useful term perceptual opacity for this dimension of variation. In response facilitation, the correspondence between an act in the observer’s repertoire and one performed by another individual automatically triggers an increase in the likelihood of the observer performing the act (Byrne, 1994). (Thus it is not strictly a learning process at all—although, if the observer thereby gains reward, as with the experimental two-action methodology, then contextual learning would occur.)

This interpretation is consistent with the discovery of mirror neurons in monkey cortex, a population of cells that respond equally to a purposive gesture whether performed by the monkey itself or by another (Gallese et al., 1996; Rizzolatti et al., 1996). These researchers believe that all goal-directed motor actions in a monkey’s current repertoire will be matched by mirror
neurons, so that any action the monkey can perform will trigger an appropriate mirror cell even when it is seen done by another. Given the nontrivial differences in perspective between self and other, it may appear that the existence of mirror neurons simply shows that the matching occurs, not how it is achieved. However, Laland and Bateson (2001) have used a neural net simulation to test the idea that such matching can indeed result from past experiences, in which self and other simultaneously performed the same action, with encouraging results (note that they label the effect “imitation,” rather than response facilitation, as herein): If their conclusions are accepted, the origin of mirror neurons is not problematic. Rizzolatti (2001) suggests that mirror neurons enable a monkey to understand the dispositions of others (intentions in his terms, but there is no implication of mental state attribution) and thus to anticipate their next actions. This provides a very different explanation of the adaptive function for copying familiar acts, shown in experiments designed to reveal “true imitation,” than the usual assumption of instrumental learning. If mirror neurons underlie response facilitation, as argued by both Byrne (2001) and Rizzolatti (2001), then the tendency to copy observed motor acts is a by-product of a mechanism whose primary adaptive function is to reveal behavior’s purpose (in the sense of its immediate consequences). This would account for one apparent paradox. It would seem to be an inevitable prediction, in the case of an individual showing a general tendency to copy the actions of conspecifics, that its trial-and-error exploration should be reduced in social circumstances, thus reducing its chances of discovering novel and effective solutions. No such conservatism has been noted to be a consequence of group living. However, if the effect of observation was to reveal the purpose of an act, in many cases copying would be inappropriate. In the wild, only where the immediate consequence was a previously unattainable reward would copying the actions pay. In most tasks used by psychologists to demonstrate this sort of imitation experimentally, the end result is indeed normally a reward (food), so copying brings rewards and does make sense; thus contextual learning is seen. The limitation on this contextual learning is that the motor act must already exist in the individual’s repertoire, and it must be recognizable as similar when seen performed by another (Byrne, 1994). (In neuronal terms, this means mirror neurons for the particular action do exist which automatically trigger when self, or other, performs an action which largely resembles it.)

In contrast, Heyes and Ray (2000) suggest a model in which pairings between observed and copied actions are arbitrary because they are acquired by association learning. Whereas normally the result is a link between an act as seen and the same act as done, in principle quite different links could be learned. For instance, repeated sight of one’s face with a particular expression, viewed in a mirror, may become linked to the kinesthetic experience of making that facial expression, despite minimal lack of perceptual feature
overlap (see also Mitchell, 1987). Thus, with appropriate experimental manipulation, Heyes and Ray predict that it would be possible to produce an animal whose “imitations” were distinctively unusual: for instance, it might do action X when it sees action Y, and vice versa. This interesting idea has yet to be tested.

Neither response facilitation nor Heyes and Ray’s related theory can account for neonatal imitation, where highly specific facial gestures of an adult are imitated by very young babies, since in this case not only is there minimal perceptual overlap in visual appearance, but the phenomenon is found long before the infant has access to mirrors which could allow the stimulus–response pairing to be learned (Meltzoff and Moore, 1977, 1983). One possibility is that matching behavior is the result of a few innate linkages between trigger-features and fixed action patterns (which happen to look the same to external observers), an account favored by those who dispute the generality of the infants’ copying (Anisfeld, 1991). Alternatively, the child might be equipped at birth with a very general mechanism for making a 1 : 1 correspondence between body movements of others and the muscular contractions needed to match them in the self, an account favored by those who consider that the range of gestures that can be copied is limited only by the restricted motor repertoire of the child (Meltzoff, 1988a). This latter possibility, of course, envisages a sufficiently powerful mechanism to underwrite production learning even of novel actions. (Neonatal imitation is sometimes of “novel” actions, in the trivial sense that the infant has never performed them, but there is no doubt that the facial movements are in the child’s latent repertoire and would be shown at some point without any need to see a demonstration.)

With contextual learning by imitation, no new motor behavior is acquired. By contrast, in production learning, the result of observation is to learn a new action. The evidence for production learning of motor behavior in animals is much sparser and more controversial, but I suggest that one reason for this has been the conflation of several different processes, each underwritten by a different mechanism and each probably evolved in response to different environmental demands. New distinctions need to be introduced to capture these differences. To begin, we consider the function of copying behavior from another.

IV. IMITATION: SOCIAL MIMICRY AND PICKING UP METHODS

As is clear from everyday experience, imitation can serve a social function, by increasing identification between the imitator and the imitated. Signaling may be directed at third parties, where the identification is used to comment upon some aspect of the imitated, for instance, in the theater or in
the use of imitation for playground mockery. A purely dyadic interaction is also possible, and here increasing the meshing of behavior between two individuals may serve to build up or cement their relationship (see papers in Giles, 1984). Such a function has been argued to be central to both the unconscious tendency of adults to match the body posture of their interlocutor (Bull, 1987) and the tendency of neonates to copy facial gestures of adults (Meltzoff, 1990; Meltzoff and Moore, 1994). In this social mimicry, the copying is not a matter of improving individual performance, so acquiring new actions from what is copied is not important. Instead, even if this is not a conscious process, the copy must be seen as a copy and treated as a signal. The fidelity of the match is what is crucial for such an interpretation.

Social mimicry seems peculiarly important to humans, from birth onward (Meltzoff, 1996). Even at birth, human infants copy some of the mother’s expressions and facial movements, and during childhood the prominence of imitation is striking (Meltzoff, 1988b; Meltzoff and Gopnik, 1993) and clearly serves at times to allow experimentation and practice with the social roles and actions of adult life. Copying the actions of other significant individuals, apparently for the pleasure of copying, is almost as prominent in the behavior of human-reared great apes. Neonatal imitation of facial gestures of human caretakers has been carefully documented in infant chimpanzees (Myowa, 1996; Myowa-Yamakoshi and Matsuzawa, 2000). Juvenile and adult gorillas, orangutans, and chimpanzees, after being exposed to everyday human living, copy a bewildering range of human actions, including tying shoelaces, brushing teeth with toothbrush and paste, sawing wood, lighting a fire by fanning embers dipped in kerosene, washing clothes with soap, and many other examples (Hoyt, 1941; Russon, 1996; Russon and Galdikas, 1993; Savage-Rumbaugh, 1986; Savage-Rumbaugh and Lewin, 1994). In some cases, it may be difficult to sharply distinguish copying for its own sake from copying for performance reasons (compare Russon, 1999; Tomasello, 1996), and this is also true of imitation by human children. Indeed, Meltzoff argues that there is a continuum between neonatal imitation of facial gestures and the ability of older children to learn novel manual skills and to copy intended actions rather than performance errors (Meltzoff, 1995; see also Want and Harris, 2001). This interpretation is by no means established: The extent to which children do learn novel skills by imitation, rather than by socially enhanced individual learning, has not been explored in children and is no easier to decide than in the case of animal learning. It is just as plausible that the “adult version” of neonatal imitation is ideomotor behavior (the phenomenon in which, for instance, seeing a car about to crash causes depression of the braking foot in pedestrian observers); the function throughout development may remain a purely social one, increasing identification and empathy, at all stages of development. On such an interpretation, social mimicry has nothing to do
with method learning, in either its ontogeny or its functional origin; imitation of methods is a separate phenomenon.

Certainly, in most cases of social mimicry, skill repertoire is not affected, and the function appears instead to be that of influencing the social relationship or immediate social interaction between mimicker and mimicked. This creates a clear parallel with vocal production learning in birds and mammals. Bottlenose dolphins, *Tursiops truncatus*, imitate the individually distinctive signature whistles of others, apparently as a means of engaging their attention (Janik, 2000). Mated pairs of bou-bou shrikes, *Laniarius*, develop elaborate duets, but the fact that social mimicry is important in this process is evident from the fact that each member of the pair can sing the complete duet when alone (Thorpe, 1967). Indeed, one major function of expert mimicry in birds, for instance parrots and mynah birds, has been suggested to be in developing and retaining a social bond (Bertram, 1970). In both gestural and vocal cases of social mimicry, since matching to the visual or acoustic form of the observed behavior is crucial, copying the surface form rather than the underlying organization is sufficient for adequate function and may be necessary to achieve high fidelity.

Precisely which cognitive models can account for social mimicry depends upon the novelty, perceptual opacity, and complexity of what is copied. If the mimicked action is one already in the individual’s repertoire, and there is a reasonably transparent perceptual relationship between the action as done by model and by mimic, then response facilitation by behavior priming is a sufficient explanation. (As noted earlier, this may apply to most of the experimental demonstrations of “true imitation” of motor actions in primates and birds.) Neonatal imitation of facial gestures is perceptually opaque, and theatrical mimicry of adult humans and vocal imitation by dolphins and many birds are of signals that are highly complex: In these cases, a cognitively more complex process is required, and what this might be is discussed in the next section.

V. PRODUCTION LEARNING BY IMITATION

To researchers in the human sciences, acutely aware of the technological gulf between humans and other animals, the possibility that humans possess an evolved suite of superior learning processes is an attractive one. Along with pedagogical teaching and apprenticeship, imitation has often been invoked as part of this repertoire. In this case, it is specifically *production learning of methods* that is implied: the case where an individual augments its repertoire of useful ways of dealing with the world by observation of a skilled practitioner. Instead of a painstaking, incremental process of building
up a novel skill by individual experimentation, crucial aspects of the skill of another individual can be directly acquired by the imitator plagiarizing the success of another. Of course, most complex activities also require individual practice to perfect the skill, and pedagogical teaching if available may be the most efficient aid; however, imitation may play a significant part. Here, the means to acquire novel behavior is essential, and in most cases the acquired behavior is liable to be complex in organization, since it is in this circumstance that individual learning fails and imitation can give advantage. For behavior that is not complex in organization, but needs to be performed with precise timing and force, optimization by individual practice is likely to be efficient, since the resulting optimum will be adjusted for the precise mechanical capabilities of the learner. (When methods are copied by imitation, especially of an adult by a child, there is always the risk that the actions will be unsuited to the size and power of the learner, raising actual impediments to progress.)

To account adequately for the production learning by observation of novel and complex behavior is a considerable challenge, whether the function of the imitation is to acquire new methods of dealing with the world or for the purpose of social mimicry. Although in principle one powerful mechanism could subserve both functions, the possibility needs to be kept in mind that two or more separate evolutionary trajectories have converged on one final outcome, the ability to copy complex, novel behavior. If so, very different processes may be involved, with contrasting strengths and weaknesses.

A. E M U L A T I O N

Among the ways in which an animal might acquire novel, complex behavior by observational learning, most attention has been devoted to a process that has, in fact, been set up in opposition to imitation; that is, emulation (Tomasello, 1990; Tomasello et al., 1993). Although defined by the Oxford English Dictionary as “to imitate zealously,” emulation in this technical sense means to copy a result, but not necessarily the behavioral method of achieving it.\(^1\) How the result is copied is less clear.

In the simplest sense (called goal emulation by Whiten and Ham, 1992), observation might simply bring a desirable result to the animal’s attention as

\(^1\)Tomasello refers the term emulation to the developmental psychologist Wood (1989) whose meaning was, however, somewhat different. Wood distinguished it as one form of imitation, in which the aim is to achieve similar effects on the world as the model, in contrast to impersonation, in which the aim is to behave “as like someone else as possible” (p. 72), and he notes that some children do this so well that they may one day become professional impersonators. Others have used emulation in yet other ways: Lloyd Morgan describes it as “a desire not only to imitate but to improve upon the copy” (Morgan, 1896, p. 173), which seems to suggest intelligent modification of a copy.
a possible goal, after which the animal would itself work toward this new goal in its own way. This may be modeled as a matter of priming brain records, in much the same way as can stimulus enhancement and response facilitation (Byrne, 1994, 1995). In the example originally used to illustrate the distinction, seeing another individual using a rake to pull in peanuts caused an observer chimpanzee to rake peanuts itself—but not to copy the precise detail of the movements (Tomasello et al., 1987). However, it is unclear in this case whether what was learned was a result, juxtaposition of rake tip and peanut, as argued by Tomasello, or a behavior, the raking action, as suggested by Byrne and Russon (1998; see also Whiten and Custance, 1996).

A better example, showing the utility of the distinction, comes from vocal learning. Mynah birds copy human speech so accurately that the formant transitions of speech (pitch changes in the bands of major energy) are clearly visible on a spectrogram (Bertram, 1970). However, formants in speech are produced by resonance in the different areas of the human supralaryngeal tract which can be independently varied in size and shape, thus filtering the original sound signal (Fry, 1979). Formant transitions correspond to changes in the shape of the supralaryngeal tract. Mynah birds, however, must use the avian syrinx, a very different anatomical structure, to copy the human voice. Nevertheless, they are able to produce the same sound pattern to a high degree of fidelity; a similar case could be made for song thrushes copying the electronic ringing tone of some telephones (Slater, 1986). These remarkable cases suggest that, more generally, imitation in birds may be mediated by copying the final result, not the behavioral means of achieving it. In birds which learn species-typical songs party by imitation, they will of course tend to produce these sounds by using similar muscular movements, but this may be a by-product of attempting to duplicate the end result. Indeed, in some species there is a steady improvement in match to the original model with practice, even without further opportunity to hear the original, and auditory feedback is necessary for full song to develop (Marler, 1976b): both these findings suggest that what the bird does is to modify its output toward ever closer match to a remembered original. This perfectly meets the original definition of emulation and suggests one cognitive mechanism that can generate emulation: trial-and-error modification of behavior until it meets a criterion of match to a remembered template, itself learned from another individual.

However, since the term emulation was first applied to animal learning, its meaning has changed somewhat. In addition to goal-setting, it is now used to include observational learning about the “affordances” of objects (Tomasello, 1998). Affordance, a term borrowed from the perceptual psychology of J. J. Gibson, refers to what can be done with an object. Seeing a chimpanzee smash a nut between two stones, for instance, reveals that some nuts are breakable and that they contain edible kernels. This revelation,
rather than any ability to copy the movement of hammering, may cause the observer to take up nut-cracking, whereas other chimpanzees may never discover the rich food source within hard nuts. What is learned may be cognitively complex, including in this instance the notion of containment and information about the structural form of an unfamiliar object; or, it may be no more than an association between nuts and eating a new and delicious food. In either case, the important distinction from other kinds of imitation is that motor behavior per se is not copied. Thus, in principle, emulation could be as effective if the behavior were not seen—if the nut fell by gravity, for instance, and broke as a result. This points to an obvious experimental control for emulation, but note that the spontaneous movements of objects (especially contrived gadgets in psychologists’ laboratories) may be intrinsically of less interest to animals than the actions of conspecifics, so care is needed in interpretation of negative results. (Moreover, for complex tasks, elaborate videographic editing would be needed to present the unfolding of subtle, sequential transformations of an object with no hand visible.)

B. **Action Level Imitation**

Where it is clear that copying rather than learning about the world has taken place and that novel behavior rather than its physical consequences has been copied a final distinction needs to be introduced. This is the question of whether it is the surface form that is imitated, *action-level imitation*, or the underlying organization of behavior, *program-level imitation* (Byrne and Russon, 1998). In neither case are there many, well-articulated cognitive models as candidates.

A close match to the surface form of observed behavior is crucial to social mimicry, but even for production learning by imitation this may be all that is required for success. How might this action-level imitation be achieved? The following two processes have been suggested, differing in the nature of what is supposed to be copied.

1. **Copying a Fluid Movement**

Complex behavior as performed by a skilled practitioner appears as a fluid whole, and any highly practiced act is literally a single continuous movement in its surface form. It has often been proposed that imitation might be an empathic process, in which the observer can directly “identify” with the movement that is seen and so copy it. The cognitive mechanism would be some form of kinesthetic-motor mapping (Mitchell, 1987). In humans, this elaborate 1:1 visual-kinesthetic mapping of movements has been proposed to be innately prespecified (Meltzoff, 1996), so no further explanation is needed to account for human imitative ability, that is, provided the body of
the observer and model approximately match. Although this may be sufficient to account for social mimicry and some forms of production imitation, such as gaining sporting prowess by bodily imitation, the lack of any analytic power limits the usefulness of such a mechanism for skill learning.

2. Copying a String of Beads

If instead the fluid movement is seen as a series of single, discrete actions, and each one of these actions were something that the observer could already do, then the sequence could be copied—and thus novel behaviors could be imitated. Although the underlying structure would be lost, complex behaviors can nevertheless be imitated in this way, by dissection into a string of component, simpler sequential parts that are already in the observer’s repertoire (Byrne and Russon, 1998). An associative version of this model has been developed by Heyes and Ray (2000), in which the correspondence between the seen-version and the done-version of each action is learned by association. They do not consider how the fluid movement is segmented into the “string of beads,” each action of which can be copied (see Fig. 1a). Response facilitation by mirror neurons provides a straightforward explanation of how, and precisely under what circumstances, this segmentation could take place. Specifically, the segments (“beads”) will be just those sections of the model’s fluid behavior which map onto actions already in the observer’s repertoire, and thus already have corresponding representation.

![Diagram](image_url)

**Fig. 1.** Schematic illustration of indications of underlying planning structure, visible in strings of separately recognized actions. Each action is coded by a letter: A, B, C, . . ., I. (a) “String of beads,” no organization discernible; (b) modular structure can be shown by interruptions; (c) shorter and longer pauses; (d) omissions; and (e) iteration can be signaled by repeated strings.
as mirror neurons. Thus the coarseness or fineness of segmentation will be automatically prescribed by the observer’s existing motor knowledge: experienced observers, whose motor repertoire already includes quite elaborate actions, chunk observed behavior into fewer segments and are confronted with a simpler sequence learning task as a result. The fact that some animals, as well as humans, have a tendency to copy sequences of familiar actions when engaged in trying to solve a novel puzzle was shown by Whiten (1998) for chimpanzees.

It appears difficult to decide between these two theoretical accounts, particularly in cases of social mimicry. However, note that the decision to copy one particular segment of observed behavior presupposes that some sort of segmentation has taken place, before kinesthetic-visual matching could take place. Thus, even where it appears that fluid movements are copied, this may always equate to string-of-beads copying: a large number of very small 1 : 1 correspondences, between observed and performed movements, produces a smooth action in the final output. Kinesthetic-visual matching may never be more than a convenient label for a process of action-level imitation which is essentially a matter of matching segmented units of behavior.

C. Program Level Imitation

For production learning of methods in general, it is ideal to acquire not only the surface form but also the underlying organization appropriate to the task. The hierarchical organization that mountain gorillas show in processing plant foods gives an illustration of this sort of complexity (see Fig. 2, and Byrne and Byrne, 1993). If behavioral organization could be discerned in the actions of a skilled practitioner, then the observer would be able to copy a whole range of alternatives: (1) one particular subprocess, filleted out; or, (2) the whole operation at a broad-brush level of description, with details filled in by individual trial and error; or, (3) the whole operation exactly as seen, including both the underlying organization and the surface form. But is it possible to “see” underlying organization in behavior?

As noted by Heyes and Ray (2000), although a number of models have been put forward to explain such ability, the mental transformations involved have never been clearly specified; indeed, most of these models have a somewhat magical quality, in which the crucial elements are never specified. In contrast, Byrne (1999) proposes an entirely mechanistic model of program-level imitation that is held to be sufficient to account for imitation of the underlying hierarchical structure as well as the surface form of novel, complex behavior. This model is called string parsing.

The model begins from the assumption that behavior observed in another individual can be seen as made up of a sequence of simpler elements. The
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Fig. 2. Mountain gorilla nettle leaf processing. The technique used by gorillas is to rapidly amass a bundle of leaf blades, without the stems of petioles that host the strongest stings, and fold the bundle, so that only a single leaf underside is exposed when the parcel is popped into the mouth (Byrne and Byrne, 1993). This minimizes the number of stings that contact the palm, the fingers, and, especially, the lips. The cognitive organization of the task must include at least the level of organization shown here, on the basis of current observational data. “Get leaf blades” and “fold blades” are both known to be separate modules because they are separated by the optional action, “clean.” In addition, “get leaf blades” may or may not be iterated, again implying that it is a distinct module. “Get leaf blades” itself is a routine composed of at least two modules: we know that “strip stem” and “tear off petioles” are separate modules because “strip stem” may or may not be iterated.

The most straightforward way in which this might be achieved is by means of an array of units, each of which responds to an action that matches the corresponding action in the observer’s own repertoire: response facilitation. As with action-level imitation, the system of mirror neurons in premotor and associated temporal cortex of macaque monkeys (Gallese et al., 1996; Rizzolatti et al., 1996; see also Rizzolatti et al., 2000) provides a feasible neural basis for the process of segmenting fluid action into a string of discrete elements, each one an action in the observer’s repertoire—effectively, “reading the letters” of action by means of response facilitation, action by action. (Alternatively, every possible visible movement in a conspecific’s musculature may be prewired to alert the motor program for a corresponding movement in the observer, as in Meltzoff’s account of neonatal imitation; or arbitrary pairings may be learned, between seen movements and performed actions, which may or may not visibly correspond, as in Heyes and Ray’s account of action-level imitation.) At some level of detail, any action must be composed of units which a conspecific has in its repertoire, so that response facilitation is sufficient to allow segmentation of all actions that might be seen. As noted in the case of action-level imitation, the level of segmentation
would be determined by the observer’s experience, and hence its preexisting repertoire: If existing repertoire units are already large and complex, observed behavior would be segmented into only a few chunks, and vice versa.

String parsing operates on the resulting linear sequences of elements. Sequences are compared in a search for data reduction by the discovery of patterns; thus the model assumes that, in some sense, sequence orders of elements can be retained, but this may not involve explicit remembrance. Although the underlying structure of any one string is entirely ambiguous, as more and more strings are cross-correlated the persisting regularities of pattern can betray the organization. Over time and the observation of a number of these one-dimensional, linear strings of elements, an organized structure is generated, in which the links are correlational—a “statistical sketch” of the action. The regularities exist because the underlying structure, present in the brain of the individual that generated the behavior, imposes a distinctive signature on the linear sequence of elements that serves to show how the fluid stream of action may appropriately be “carved at the joints” (Byrne, 1999; and see Fig. 1).

In a hierarchical organization, modules occur in which the elements seem to be more tightly bound together, whereas at a junction between modules the link is weaker (Dawkins, 1976; Lashley, 1951). Interruptions occurring at these junction points allow smooth resumption once the distraction is past; in contrast, interruptions within a module will force the animal to “begin at the beginning again,” at either the beginning of the module or the entire program. Interruptability is a correlate of structure: Interruptions will thus tend to occur between, not within, modules (Fig. 1b). Even when behavior is not interrupted, relatively tighter or weaker linkage will betray itself in the pause structure of output behavior (Fig. 1c). Moreover, hierarchical organization of behavior may allow flexibility, so that unnecessary stages or modules can be omitted on the basis of local circumstances (Dawkins, 1976). So, in repeated strings that are broadly similar, certain sections will occur in some strings but not in others, and the omissions signal the underlying modular structure (Fig. 1d). If we represent a modular structure as $A = B — C = D — E = F$, where elements joined by “$=$” are more tightly bound together than those joined by “$—$,” then interruptions will tend to occur more at B/C and D/E than at other points, and omissions will tend to give rise to shorter strings such as A,B,E,F as well as the full sequence A,B,C,D,E,F. Thus, analysis of sequence orders and of pause structure, including interruptions, can betray an underlying modularity of organization.

Hierarchical organization allows modules to be used as subroutines in a larger organization. For instance, they may be applied iteratively until some criterion is reached (cf. the test-operate-test-exit unit of Miller et al., 1960). When control “loops” around a subroutine in this way, a distinctive pattern
of sequential elements is generated: a series of repeated sequences, embedded within the main sequence (Fig. 1e). Using the same conventions as before, the sequence A,B,C,B,C,B,C,D,E signals that B = C is an iterated subroutine within the main program. Hierarchical organization allows efficiency, in that modules may be omitted if they are not required, on the basis of local circumstances at execution time; this is reflected in sequential orderings, with omissions signaling underlying structure. Finally, hierarchical organization enables a subroutine to be used in more than one program or one program to be used as a subroutine in another. Again, this can aid detection of structure in observed behavior. Once some strings have been identified as forming discrete modules or more complex structures, these familiar patterns can be picked out in as-yet-unparsed strings of elements and serve to reveal their structure.

It is a truism of motor psychology, that every execution of a behavior is slightly different. The variation is necessarily minor and trivial, or else the behavior would fail in its purpose. This leads to another way of detecting underlying structure from string parsing. Because of this structure, deviations at some points will be far less innocuous than at others, and the range of variation over repeated strings will indicate which points are most constrained. The invariant features, occurring in regular positions in every string of elements leading to the same outcome, can therefore be identified as necessary ones, whereas those that are not are revealed as relatively unimportant ones. This means that, by comparing a series of strings that lead to the same outcome, the ordered sequence of necessary elements that leads to it can be identified. (Where the behavior serves to modify some environmental object, as in food processing, the recurring states will be visible as physical objects as well as behavior actions. It may be easier for observers, both human and nonhuman, to attend to objects than to body movements; see Byrne, 1999.) To an adult human observing the process, these necessary intermediate steps are probably seen as “subgoals,” achieved along the route of a successful completion of the main goal. To an organism that has no conception of goal and intentions, invariant features of sequence can nevertheless reveal their existence and sequential order, mechanistically and automatically.

Thus, without any prior understanding of goals and intentions, an observer with string-parsing capability is able to extract the underlying structure from repeated observations of organized behavior (but from random actions, nothing can be extracted). The process is one of pattern-matching, and any such process is aided by extrinsic information about starts and ends of sequences. Cues to these features are often present in goal-directed behavior. Often, the goal is a consummatory activity of some sort (e.g., eating a food item), coming after a sequence of elements, and so a proper end to that sequence is indicated. In some cases, the proper start to a sequence might also
be visible in behavior, if no other activity occurred immediately beforehand; thus some “complete” strings of elements corresponding to goal-directed behavior can be identified. More generally, in this way indication of the appropriate phase in which sequences need to be compared to detect any recurring patterns can be obtained.

The adequacy of string parsing to detect structure has been partially tested by Furse (2001), who constructed an algorithm which operated according to some of these principles and was effective in simulating some aspects of children’s learning of arithmetical procedures, such as long division, by observation of worked examples. Moreover, Saffran et al. (1996) have shown that 8-month-old human infants are sensitive to recurring patterns in spoken strings of nonsense syllables: they learn repeated patterns quickly, with only 2 min of exposure necessary to pick up the statistical regularities.

In a rather literal way, therefore, the organization of complex behavior can in principle be “perceived.” Such organization includes the starting conditions, the outcome or goal, the modular structure, any use of modules as iterated subroutines, and, in general, the statistical regularities of elements that connect start to goal. In this manner, the behavior may also be copied—at program level (Byrne, 1998). A string-parsing algorithm which is sensitive to these regularities will generate a statistical sketch which tends to mirror the actual organization of any planned, complex behavior. If each element were an action in the observer’s repertoir, as would necessarily be the case if segmentation took place by mirror neurons, the use of the statistical sketch to build a novel behavioral routine is particularly straightforward. If the output of segmentation by mirror neurons were the input to the string-parsing process, then the statistical sketch would mirror behavioral organization directly. The major limitation on string-parsing is that numerous instances are liable to be needed to provide sufficient data to extract all the crucial regularities: “One shot” imitation of complex behavior is not possible, if imitation depends on string parsing.

It has already been noted that there may be circumstances in which it is easier for observers to see changes to objects than the movement of a limb or other effector. String parsing could also operate in this case. If each perceived element were a state of the physical world—for example, how an object looked after some manipulation had been applied to it—then the statistical sketch would specify the organization and sequence of transformations necessary to reach the goal. What actions are needed to make each transformation would then still need to be acquired, based on prior knowledge of how to attain these subgoals, or by a process of trial-and-error learning. It would probably be unhelpful to distinguish this possibility as “program-level emulation,” however, because even in this case the organization, by which the actions are assembled into a behavioral routine, would
be derived by string parsing: that is, repeated observation of a sequence which was itself generated by behavior. With videographic technology, it is possible to produce sequential object transformation in the absence of any view of the transforming bodily agent, and sequential transformation behavior on an invisible object, but the extreme artificiality of these things is some indication of the irrelevance of this distinction in everyday behavior.

VI. WHAT LIMITS PRODUCTION LEARNING BY ImitATION?

The emphasis of this chapter has been on mechanistic devices by which observational learning of complex and novel behavior can be achieved, in a relatively automatic and wholly nonmysterious way—in particular, copying of hierarchical organization by means of string parsing to extract statistical regularities. The associative mechanism underlying classical conditioning has been interpreted as a system evolved for extracting correlational structure from sequences of observed behavior (see Dickinson, 1980). If repeated sequences reveal underlying complex organization, when subject to correlational analysis, does this mean that almost any animal should be capable of program-level imitation? Not necessarily.

It might be that the underlying correlation–extraction mechanisms do overlap considerably between classical conditioning and string parsing in many species which nevertheless differ widely in other capacities, and it is these other capacities that limit the use that they can make of observational learning. Some species, those lacking the flexibility to augment an innately prescribed repertoire of actions, may be capable of contextual learning by observation; their “imitation” being restricted to changes in the circumstances and frequency of deployment of their behavioral repertoire (as indexed by the two-action methodology). Other species may be capable of learning new actions by sequential combination of existing elements in their repertoire, but yet be unable to learn novel hierarchical structure because they cannot mentally manipulate hierarchical structures. Such a limitation would be a matter of working memory capacity and so could be indexed by memory experiments, in addition to direct tests of program-level imitation. These species should show production learning by imitation, but the results would have the “string-of-beads” organization of action-level imitation, without hierarchical structure. This would be entirely adequate for the conformity needed in social mimicry but of more limited use in acquiring novel skills. Only species with the capacity to manipulate subgoals mentally into novel structures—in other words, to plan—would be capable of gaining full benefit from string parsing and thus of production learning of methods by program-level imitation. In many cases, this would be hard to distinguish from the
results of action-level imitation, without careful analysis. Pause structure might betray modularity, but its absence would be inconclusive. Experimentally, interruption could be used to interrogate the underlying organization: If interruption at any point had the same effect, whether this were catastrophic or minimal, then string-of-beads organization would be indicated. Perhaps most tellingly, an individual that can imitate at program level has the facility to copy selectively from a complicated sequence of observed behavior, extracting the module or subroutine that particularly serves its current need, and integrate this into an existing structure of behavior. Thus, when we watch an expert mechanic deal with our blocked carburetor, we do not copy every mannerism of undoing bolts or maneuvering within the engine—only the method of freeing the blockage.

Currently, at a time when many of the distinctions used here are rather new, it is unlikely that evidence exists to state categorically which species have these various capacities; moreover, experimental tests inevitably lag behind observational evidence. From observational data, it has been argued that all great apes, not just humans, show program-level imitation (Byrne and Russon, 1998). No experimental evidence so far supports this, but chimpanzees do apparently have quite humanlike working memory capacity (Kawai and Matsuzawa, 2000). On the hypotheses of this chapter then, they should be able to manipulate mental representations of plans and thus benefit from string-parsing dissections of the structure of behavior of skilled practitioners. Many of the clearest examples of production learning by imitation come from birdsong learning. Evidence from avian imitation of human speech suggests that when birds show very exact imitation of sound strings, their copying should technically be classed as “emulation.” However, many oscine passerines acquire their song patterns by imitation: often, sounds matching a broadly specified innate template are memorized by fledglings and performed and improved with practice in the first breeding season (Marler, 1976a; Slater, 1983). Since new elements can sometimes later be inserted into these early learned structures, some hierarchical organization is implied, and indeed experimental interruption of birdsong suggests this is the case (Cynx, 1990; Riebel and Todt, 1997). Whether this implies that birdsong learning depends sometimes on program-level imitation (as has been argued by Todt, 1998) is not yet clear; if so, their behavior might be expected to show flexibility in other ways, whereas the bird taxa with the greatest known flexibility (parrots and crows) are not those for which evidence of hierarchical song structure is available. Several mammalian species show contextual learning by motor imitation, but so far no sign of production learning by imitation. When it is clear just which species do show program-level imitation, the crucial test of these ideas will be the corresponding measures of working memory capacity.
VII. WIDER IMPLICATIONS

From title onward, I have tried in this chapter to treat the various mechanisms hypothesized to underlie imitation, not as special-purpose explanations of singular phenomena in laboratory experiments or field observations, but as parts of a functional cognitive system in which imitation is only one small part of the repertoire. Imitation is not an isolated and peculiar capacity, but one manifestation of a broader suite of capacities—and not even necessarily the evolutionary driving force that enabled them to evolve. Taking this broader perspective, where does production learning by program-level imitation “fit in”?

Program-level imitation is built upon a more primitive ability to identify discrete units in fluid streams of observed behavior. If this primitive ability is accepted as a matter of response facilitation by mirror neurons, then its evolutionary function must be something within the capacity of rhesus monkeys—which does not on present knowledge include program-level imitation (Visalberghi and Fragaszy, 1990). Rizzolatti (2001) has instead suggested that mirror neurons act to pick out “intentions” in the goal-directed action of conspecifics, by which evidently he means dispositions toward certain future actions rather than the embedded attribution of second-order and higher intentionality (Dennett, 1983). Monkeys show extensive ability to predict and react appropriately to the actions of their social companions (Cheney and Seyfarth, 1990; Dunbar, 1988), so this hypothesis makes good sense. That monkeys and birds are slightly more likely to perform an action which is observed demonstrated several times, as shown in the two-action methodology of testing for imitation (Bugnyar and Huber, 1997; Dawson and Foss, 1965; Whiten et al., 1996; Zentall, 1996), would thus be an epiphenomenon of a mechanism whose primary adaptive function is for social categorization.

String parsing, acting on the products of this evolutionarily more ancient mechanism, enables organizational structure to be detected, and hence copied, by any species with the ability to construct hierarchically embedded programs of motor action (Byrne, 2001). Those abilities are part of a much wider constellation of general planning and problem-solving mechanisms, which have yet to be studied in any detail in animals. (In humans, they have largely been studied in the context of verbal reports or quasi-mathematical tasks: Byrne, 1983; Newell and Simon, 1972.) But string parsing itself may not simply be part of an imitation mechanism, since what it delivers is of far more general utility. Just as mirror neurons enable “perception” of disposition and immediately likely future actions, so string parsing enables perception of hierarchical programs lying behind output behavior. This is a crucial part of discerning the plans of other individuals, if those plans can be imagined.
Discerning the plans of others and copying their skills are both plausible functional origins of string parsing; currently, it would be premature to judge their relative plausibility.

On this interpretation, string parsing paves the way for identification of the intentions of other individuals, including the level of intentionality that is sometimes called “theory of mind.” It may therefore be that all species that show program-level imitation can also represent the intentions of others and thereby compute new actions based on these unobservable constructs; this possibility remains a target for future research.

VIII. SUMMARY

Underlying the various behaviors that are classified as imitation, there may be several distinct mechanisms, differing in adaptive function, cognitive basis, and computational power. Experiments reporting “true motor imitation” in animals do not as yet give evidence of production learning by imitation; instead, contextual imitation can explain their data, and this can be explained by a simple mechanism (response facilitation) which matches known neural findings. When imitation serves a function in social mimicry, which applies to a wide range of phenomena from neonatal imitation in humans and great apes to pair-bonding in some bird species, the fidelity of the behavioral match is crucial. Learning of novel behavior can potentially be achieved by matching the outcome of a model’s action, and it is argued that vocal imitation by birds is a clear example of this method (which is sometimes called emulation). Alternatively, the behavior itself may be perceived in terms of actions that the observer can perform, and thus it may be copied. If the imitation is linear and stringlike (action level), following the surface form rather than the underlying plan, then its utility for learning new instrumental methods is limited. However, the underlying plan of hierarchically organized behavior is visible in output behavior, in subtle but detectable ways, and imitation could instead be based on this organization (program level), extracted automatically by string parsing. Currently, the most likely candidates for such capacities are all great apes. It is argued that this ability to perceive the underlying plan of action, in addition to allowing highly flexible imitation of novel instrumental methods, may have resulted in the competence to understand the intentions (theory of mind) of others.

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References


IMITATION OF NOVEL COMPLEX ACTIONS


Lateralization in Vertebrates: Its Early Evolution, General Pattern, and Development

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I. Introduction

Over the past two or three decades, a large number of examples of left–right differences in brain functioning and responding have been reported for a range of vertebrate species. This has provided convincing evidence against the earlier held notion of lateralization as a unique characteristic of the human species that is associated with tool use, language, and consciousness. It is now possible to see that there is a basic pattern of lateralization common to all vertebrates, including humans.

This chapter is concerned with asymmetry of the behavioral responses, in some cases dependent on structural asymmetry either of the central nervous system or of physical features but, mostly, not associated with any known structural asymmetry. It may be manifested as left- or right-side differences in responding or in differential responsiveness to various forms of sensory stimulation according to whether those stimuli are perceived by receptors on the left or right side of the animal’s midline.

The evidence reported in this chapter shows that there is a common basic pattern of lateralization among vertebrates, indicating that the lateralization of birds and mammals is homologous, that is, it is inherited from their common ancestor. The possible advantages and disadvantages of being lateralized are considered.

A. Individual and Population Lateralization

There are two distinct kinds of lateralization. The first is present in the majority of individuals in a population (or species), but there is no lateral bias
Fig. 1. Frequency plots to show distributions characteristic of individual lateralization, not present at the population level (A and B), and population lateralization in which the majority of individuals are lateralized in the same direction (C and D). The lateralization index is plotted on the x-axis (L – R/L + R).

in the population as a whole. Paw preference in rodents (some strains but not all; Waters and Denenberg, 1994) is the best-known example of this form of lateralization: Half of the individuals prefer to use the left paw to reach into a tube to retrieve food and the other half prefer to use the right paw (Bulman-Flemming et al., 1997; Collins, 1985). Thus, a frequency histogram of right minus left values (or of the laterality index, right minus left divided by right plus left) is bimodal with peaks on either side of the no-bias value (Fig. 1A and 1B). The majority of individuals have a paw preference but the population has no handedness (“pawedness”).

The second kind of lateralization is present in the population (or species) as well as in individuals. The population bias results from the fact that most individuals are lateralized in the same direction, as in the case of right-handedness in humans. A frequency histogram of the lateralization index in this case has an obvious skew to the right side of the no-bias point (Fig. 1C). A similar rightward skewed bias at the population level is seen in the data for
righting responses of the frog *Litoria latopalmata* (discussed later; Fig. 4). Other such examples of population lateralization are skewed leftward of the no-bias point (Fig. 1D), as is known to be the case for foot preference in holding food in several species of parrots (Harris, 1989; Rogers, 1980) and for hand preferences in orangutans (*Pongo pygmaeus*) when they manipulate parts of their face using finger flexion and fine movements of the fingers (Rogers and Kaplan, 1996). Such left-handedness has also been found in prosimians when they reach out to grasp food (Ward *et al.*, 1990).

The first type of lateralization (present in individuals but not in the population) is referred to as “individual lateralization” to distinguish it from “population lateralization.” The term “antisymmetry” is also used to refer to asymmetry at the individual level occurring with no consistent side bias (i.e., with no lateralization at the population level) (Møller and Swaddle, 1997). It should be noted that antisymmetry (Fig. 1B) differs from fluctuating asymmetry, of interest to evolutionary biologists (Swaddle, 1999), in that all or most of the individuals have some degree of asymmetry. Fluctuating asymmetry refers to populations in which lateralization occurs in only a small percentage of the population and with random bias to the left or right side. It is, therefore, characterized by a bell-shaped curve (see Palmer, 1996, for further explanation). In populations with fluctuating asymmetry, symmetry in the population is maintained despite the vicissitudes of development (e.g., of lateralized disturbances caused by chance injury or parasite attack) that lead to some individuals, but not the majority, being lateralized in one direction and others in the other direction. “Individual lateralization” does not refer to this kind of population but instead to antisymmetry (e.g., asymmetry of claw size in fiddler crabs; Neville, 1976). Nevertheless, the bimodal distribution of hand preferences in mice has been considered in terms of chance effects occurring during the course of development, leading to lateralization at the individual but not at the population level (Collins *et al.*, 1993). Provided such influences were common enough to affect the majority of the individuals in the population, this could be a possible explanation for the population distribution of paw preferences, but, usually, the chance effects of lateralized disturbances of development are less severe and affect only a minority of the population. Therefore, although fluctuating asymmetry resulting from chance influences on development may apply to some forms of functional lateralization, it seems rather unlikely to apply to paw preference in mice and rats because one might expect to find many individuals that have escaped the chance effects of lateralized disturbance of development and so show no preference. This is not the case; there are very few rats and mice that are ambipreferent (Fig. 1A). Paw preference in rodents is, therefore, an extreme example of antisymmetry with a substantial number of individuals showing zero bias.
Research conducted over the years has provided us with a large number of examples of behavioral lateralization at the population level (i.e., directional asymmetry; Palmer, 1996). Contrary to the initial impression made, primarily, by earlier work showing bimodal distributions of paw preferences and turning biases in rats, it now seems that directional bias of populations is the more common type of lateralization in brain function and behavior. For example, it had been thought that primates acquired individual hand preferences through practice (Walker, 1980), until closer examination of the evidence for hand preferences in primates revealed that population biases were present in a number of species (McNeilage et al., 1987). It remains possible, of course, that individual preferences could be enhanced by practice effects in the case of some lateralized characteristics, on some tasks and in some species.

Even in species with bimodally distributed motor biases (as for paw preferences in rodents), there may be clear population lateralization for attention, sensory processing, and emotional responses. Rats provide a clear example of this (Bianki, 1988; Denenberg, 1981). Despite the absence of a population bias for paw preference to retrieve food, rats are lateralized at a population level for emotional responding, spatial ability, and a number of other cortical functions (discussed later).

Many of these population biases fit a general model applicable across vertebrate species. Examples of population lateralization in different species will be discussed later, but, before this, it should be helpful to give a general framework into which most, if not all, of the examples may be fitted (also outlined in Andrew and Rogers, 2001).

B. GENERAL MODEL OF HEMISPHERIC SPECIALIZATION

It is hypothesized that the left hemisphere (Lhemi) is preferentially involved in the control of responses that require weighing out alternative options before responding. To do this it must be able to inhibit responding until the appropriate decision has been made. This includes inhibiting responses to inappropriate stimuli (e.g., objects that are inedible) and directing responses to appropriate stimuli (e.g., food objects). The Lhemi appears to achieve this outcome, in part by its ability to inhibit the right hemisphere (Rhemi). Also, as the data discussed later indicate, use of the Lhemi causes the animal to focus its attention on local features of the stimulus and to analyze information sequentially.

The hypothesized general model assigns an entirely different set of functions to the Rhemi. Use of the Rhemi appears to be characterized by diffuse (or global) attention and control of responses that are spontaneous, given without inhibition and without weighing out alternative possibilities.
In other words, the Rhemi controls intense responses to stimuli that release species-typical behavior. Thus, it seems, the Rhemi is used in the expression of intense emotions. It also attends to spatial cues that can be used to construct a topographical map of the animal’s surrounding environment. In fact, the constellation of Rhemi functions is, apparently, designed for escape or attack responses. Intense expression of fear, under control of the Rhemi, would be expected to lead to immediate escape responses, or attack responses if escape is not an alternative, and use of the Rhemi enables processing of topographical information to guide locomotion along known escape routes. This would occur in the absence of inhibition by the Lhemi.

These complementary hemispheric specializations are characteristic of humans (Hellige, 1993) as well as other vertebrates. As the following examples show, the hemispheric specializations are expressed in some animal species as side biases, or as eye and ear preferences. The various ways of revealing lateralization include unilateral insult of the hemispheres, monocular or monaural testing, head turning to achieve optimal sensory inputs for the task at hand, and measurement of motor biases.

The following sections attempt to discuss lateralization from an ecological perspective, first by considering responses essential for survival and, where possible, by considering the evidence for lateralization in species-typical behavior performed in the natural environment. Second, the probable advantages and disadvantages of being lateralized are discussed. As avian species, and especially the domestic chick, have been the most studied in terms of lateralization, birds are considered first under each heading. This approach allows discussion of the detailed pattern of lateralization before extending the discussion to other vertebrate species.

Although, in the following sections, lateralization may often be discussed as if it were an absolute phenomenon, this is merely to facilitate expression, and the reader is reminded that all of the examples are probabilistic and refer to a significant population bias away from symmetry.

II. Feeding and Prey Capture

Feeding requires considered responses to be made after recognition processes have been completed and alternative responses have been assessed; for example, grain has to be discriminated from similar inedible objects and living prey has to be identified and discriminated from toxic species with characteristics similar to the prey. Food items must also be discriminated from background. Several examples show that feeding responses are controlled by the Lhemi, and, in some species and conditions, they are directed preferentially to the animal’s right side.
A. Birds

Specialization of the Lhemi for control of feeding responses was first demonstrated in the young, domestic chick. The original method was to administer cycloheximide to the left or right hemisphere and examine the long-term effect of this treatment on the chick’s ability to peck at grain and avoid pecking at the pebbles forming a background among which the grains had been scattered (Rogers and Anson, 1979). Treatment of the left hemisphere impaired the chick’s ability to perform this task, whereas treatment of the right hemisphere had no effect. The same effect was caused by uni-hemispheric treatment with a low dose of glutamate (Howard et al., 1980), and localized injections of very small volumes and concentrations of glutamate in various regions of the forebrain have revealed that the effect of the treatment is located in the visual Wulst region of the left hemisphere (Deng and Rogers, 1997). This is the region of the brain receiving the thalamofugal visual projections, as opposed to the other visual region, the ectostriatal region of the hemispheres, which receives input from the optic tectum (Fig. 2). Apparently, both cycloheximide and glutamate treatment renders the left Wulst dysfunctional, not merely by lesioning it but by causing proliferation of inappropriate neural connections (for details on the mechanism involved see Khyentse and Rogers, 1997; Rogers, 1993, 1996). It appears that the right Wulst is forced to assume control, and so the chick is unable to inhibit pecking at pebbles.

A large number of such experiments have demonstrated a clear role of the Lhemi in controlling both pecking at grain and avoiding pebbles. To perform the task, the chick has to inhibit any spontaneous pecks that might be directed at pebbles, and so make a considered decision each time before a peck is delivered. The difficulty of the task is important, therefore, because a key feature of the task is that the grains and pebbles are hard to distinguish, differing only in texture and not shape, size, or color. Although a chick pecks rapidly in the task, it would appear that each peck requires decision making. In fact, the chicks are often seen to inhibit a peck directed at a pebble just before their beak hits its target. This type of response control is a feature of the Lhemi and not the Rhemi. Were no such decisions necessary on each peck, the chick might well use its Rhemi (see later).

The same lateralization of feeding responses in the same task has also been revealed by monocular testing, and this is possible because the optic nerve fibers decussate completely in birds and, therefore, input from one eye goes, at first, entirely to the opposite (contralateral) side of the brain (thalamus or optic tectum). Figure 2 summarizes the visual inputs to the chick forebrain hemispheres. In the tectofugal pathway, the rapidly conducting (myelinated) projections send input exclusively to the hemisphere contralateral to the eye.
Fig. 2. The two visual pathways of the chick are presented diagrammatically to give an impression of the projection of information to each hemisphere of the forebrain. The black symbols indicate a strong projection: note that each eye sends this information to its contralateral hemisphere. The gray symbols indicate a lesser projection (less detailed information), going from each eye to its ipsilateral hemisphere. The dotted cross in A (left hemisphere) indicates an even less well-developed projection from the left eye (LE) to its contralateral hemisphere (i.e., showing the asymmetry in the thalamofugal visual projections). LE and RE refer to the left and right eyes. The thickness of the lines with arrows gives some indication of the number of projections.
providing those inputs. Then, after a short delay, inputs from that eye are sent to both hemispheres via slowly conducting (unmyelinated) projections. This secondary bilateral input may be the mechanism allowing the animal to shift its attention (and turn its head) to the other hemisphere should the task demand it (Deng and Rogers, 1998a). As Kinsbourne (1975) hypothesized for humans, the nature of the task may determine which hemisphere processes the information and controls responses.

It is noted from Fig. 2 that, although a “sketchy” visual input is transmitted from each eye to its ipsilateral hemisphere via a lesser number of fibers that recross the midline at thalamic level (in both visual pathways), the main input from each eye goes to its contralateral hemisphere. In addition, the input from each eye to its contralateral hemisphere is conducted rapidly through myelinated fibers, whereas the recrossing fibers, in the tectofugal system at least, are slower conducting, unmyelinated fibers (Deng and Rogers, 1998a,b). This means that the primary visual input from each eye is processed by its contralateral hemisphere, and this is the case for both sets of visual projections to the forebrain.

Note also that, as shown in Fig. 2A, there is a structural asymmetry of the thalamofugal visual projections of the chick. There are more projections from the left side of the thalamus to the right Wulst than from the right side of the thalamus to the left Wulst (Adret and Rogers, 1989; Rogers and Deng, 1999; Rogers and Sink, 1988). This structural asymmetry underlies some of the lateralized functions of the chick (Rogers, 1990). Asymmetry of the organization of the visual projections to the forebrain has also been found in the adult pigeon but the location of the structural asymmetry in adult pigeons differs from that in the chick: It is present in the tectofugal system only, in the projections from the optic tecta to the rotundal nuclei (Skiba et al., 2000).

It is not the focus of this chapter to discuss the neural correlates of visual lateralization in detail, but it is important to mention that, at least to some extent, the structural asymmetries determine lateralizations of visual responses and that they underlie lateralization revealed when birds are tested monocularly.

In line with the results obtained by injecting cycloheximide or glutamate in the hemispheres, monocular testing has demonstrated that chicks can avoid pecking at pebbles, and so peck preferentially at grain, when they use the right eye (RE) but not when they use the left eye (LE) (Mench and Andrew, 1986; Rogers, 1997). Given ethical considerations for research using animals, the technique of monocular testing lends itself to revealing lateralization in other species with similar decussation of the optic nerves. Such species include fish, amphibians, and mammals that have their eyes placed laterally so that they have a small degree of binocular overlap and large lateral monocular fields of vision.
In fact, by careful choice of testing procedures, it is possible to reveal biases in responding by the LE and RE in animals with laterally placed eyes. A study by Andrew et al. (2000) showed that chicks searching binocularly for grains scattered over a floor prefer to peck at grains located by the RE, even when no eye patches are applied and the chicks can use both eyes. Andrew et al. (2000) also showed that, when chicks have to manipulate an object to obtain a food reward, they display a bias in their direction of approach that enables preferential use of the RE. The object that had to be manipulated was a lid on the food dish, and, in a series of tests, it had to be removed in different ways, such as by grasping a corner and displacing it or by lifting it by a short string at the top. The direction of approach to the dish and the eye used for viewing was determined by videotaping the chick from overhead and then using frame-by-frame analysis of the tape. In all cases, the RE (and Lhemi) was used prior to performing the manipulation act. When the food was presented in a dish without a lid, the chicks approached it with the opposite bias, using the LE and Rhemi. The researchers concluded that preferential eye use was determined by the need for visual guidance of the bill to grasp and manipulate an object. This explanation would be consistent with the general model in that use of the Lhemi would allow inhibition of spontaneous, and misdirected, pecks to allow manipulation of the lid. When the food can be seen during approach, there is no need for inhibition of immediate pecking and the Rhemi is used.

Similar specialization of the RE and Lhemi for controlling feeding responses has been shown in the pigeon, *Columba livia* (Güntürkün, 1985), and also in the zebra finch, *Taeniopygia guttata* (Alonso, 1998). Güntürkün and colleagues tested pigeons monocularly on a task used to reveal laterization in chicks (Güntürkün, 1985; Güntürkün and Kesch, 1987). Adult pigeons were trained to discriminate safflower seeds from pebbles. The seeds were mixed in with the pebbles, and so the bird had to inhibit pecks that might have been misdirected toward pebbles. The pigeons were given several trials, and the pecking rate as well as the number of seeds ingested was scored. The pigeons using their RE consumed significantly more seeds and pecked more accurately and faster than pigeons using the LE. Further testing showed that this difference in performance between pigeons using the LE or RE was not due to differences in visual acuity between the eyes. On a visual acuity task using high-contrast, square-wave gratings, no significant difference was found between birds using the LE and those using the RE (Güntürkün and Hahmann, 1994). This lateralization for control by the Lhemi in the seed–pebble test appears to be located at higher levels of neural processing, as shown earlier in the chick by administering cycloheximide or glutamate to the Wulst regions of the forebrain (see earlier discussion). It is also associated with the ability both to make considered decisions and to inhibit responses to the negative stimulus.
Entirely consistent with this interpretation is the finding that pigeons perform better in a reversal learning paradigm when using the RE than when using the LE (Diekamp et al., 1999). The birds were trained on a color discrimination operant task and then reverse tested by rewarding the previously negative key and not rewarding the previously positive key. Another study has shown that such reversal learning is a function of the Wulst region of the forebrain (Shimizu and Hodos, 1989), which is consistent with the role of the Wulst in the Lhemi of the chick in performance of the pebble–grain task (see earlier discussion).

Pigeons also have better recall of a complex visual discrimination task when they use the RE than when they use the LE (Fersen and Güntürkün, 1990), consistent with an earlier finding of the same result in chickens, tested on a much simpler discrimination task (Gaston and Gaston, 1984). It is likely that this particular specialization of the Lhemi for recall reflects its role in controlling feeding responses that involve inhibition (considered decisions) rather than specialized involvement of the Lhemi in memory storage.

Tests on a food storing bird, the marsh tit (Parus palustris), demonstrate a similar RE (Lhemi) superiority in recall some 50 h after the tits have been allowed to cache food when binocular (Clayton, 1993). The marsh tits tested using the LE only might, possibly, have access to memory of the sites in which they had previously cached seeds but be unable to inhibit responding to potential cache sites that they had not used. This interpretation differs from that given by Clayton (1993), who preferred the alternative hypothesis that birds using the RE have no access to long-term memory of the cache sites (i.e., no memory store in the Rhemi). Although there is, so far, no available evidence in support of either one of these alternative explanations, the data for marsh tits would be consistent with that of chicks and pigeons if the first explanation is correct.

In fact, there is an even more striking demonstration of the role of the RE of birds in feeding responses that require discrimination and manipulation. Hunt (1996) discovered that New Caledonian crows (Corvus moneduloides) manufacture and use two different kinds of tools, hooked tools made from twigs and probing tools made from pandanus leaves, and that the RE guides the birds’ responses during tool manufacture. The crows use these tools for probing holes in trees or the debris around trees to find insects to eat. Unfortunately, eye use during probing for food has not been studied but eye use in making the tool from pandanus leaves has been deduced by examining the shape of the cutouts on the leaves. The bird uses its beak to sculpture a piece of pandanus leaf from the right edge of the main leaf. To do this, the bird must angle the beak to cut in a series of different directions. Hunt (2000) has shown that the crows make their tools to a standard shape by following a system of rules and that they have a form of handedness. The
crows cut more tools from the left edges of the pandanus leaves than they do from the right edges (left and right being determined when looking down at the upper surface of the leaf and outward from the trunk). Since more tools are cut from the left edges of the pandanus leaves and the birds start at the narrow end of the tool working away from the trunk, it can be deduced that they use their right eye to guide their tool manufacturing behavior and that they primarily use the right side of their beak for cutting (for details and an illustration see Hunt, 2000). This interesting finding suggests that the Lhemi is used to control the cutting behavior and to ensure that the tool made matches a template. This specialization of the Lhemi may be a more complex evolution of the basic pattern described in chicks by Andrew et al. (2000); viz., use of the Lhemi when manipulation using the beak is required to obtain food from a dish. We also note here Hunt’s conclusion that crows have “handedness” for tool manufacture, as was known previously to be the case only in humans. Andrew and Rogers (2001) extended this view to draw attention to the involvement of the Lhemi in skilled manipulation in birds (right “eyedness”) and humans (right-handedness).

Here it is worth mentioning a preliminary result (A. Hoffman and L. Rogers, unpublished) showing that juvenile Australian magpies (Gymnorhina tibicen) may display a significant preference to approach on the parent bird’s right side when begging for food (out of six birds observed, all were biased to approach on the parent’s right side). Although a larger sample size is required to confirm this observation, it suggests that lateral asymmetries might influence social behavior. In this case, the juvenile might position itself on its parent’s right side to ensure that the parent uses skilled manipulation of its beak when feeding the juvenile.

All of these results, obtained from five different species of bird (and perhaps six, if the magpie is included), fit with the general pattern of Lhemi specialization for control of the beak when manipulation is required or for feeding responses that require selection of food targets and inhibition of pecks at inedible targets. The same seems to apply to other vertebrate species.

B. AMPHIBIANS

Toads (Bufo bufo and Bufo viridus) strike preferentially at prey to their right side, suggesting control by the Lhemi (Vallortigara et al., 1998). Each toad was tested by placing it inside a glass cylinder and moving a live prey around it, outside the cylinder, in either a clockwise or counterclockwise direction. Tongue strikes were aimed at prey within the binocular field. The angle between the toad’s lengthwise axis and the line between the point of contact of the tongue on the glass cylinder and midway between the toad’s eyes was determined (Fig. 3). When the prey was rotated clockwise
Fig. 3. Striking at prey by two species of toads. The position of the strike has been determined by noting the point of contact of the tongue on the glass cylinder, outside which the prey is rotated, and by measuring the angle of this from the toad’s midline. The shaded areas represent the binocular field of vision, and the white areas represent the monocular fields. Note that, when the prey is rotated clockwise (figures on the left side), striking is in the right hemifield region of the binocular field. When the prey is rotated counterclockwise, the strikes are more widely distributed within the binocular field. Modified from Vallortigara et al. (1998).

(as viewed from above the toad), almost all strikes were to the right of the toad’s midline (i.e., in the right visual hemifield). This was true for both species. When the direction was counterclockwise, no obvious side bias was seen, although in *Bufo viridis* there was still a tendency for more strikes to be directed to prey to the right of the midline than to left of the midline (Fig. 3).
Although all strikes are made in the toad’s binocular field, the processes that lead to striking may be initiated when the toad first catches sight of the prey in its extreme lateral, monocular field. We might consider this as initial priming for the response, which is not given until the prey advances into the binocular field. If so, it is interesting to note that priming in the left monocular field (Rhemi) leads to a delayed response, not occurring until the prey passes the toad’s midline and enters the right hemifield (i.e., for clockwise rotation of the prey). Priming in the right monocular field is more likely to trigger a response before the prey passes the midline, particularly in *Bufo viridis*. Considered together, these results suggest that the Lhemi is specialized to control prey catching responses in toads, as it is in birds.

The prey striking responses of *Bufo marinus* have also been tested in the same way with prey rotated around the toad (Robins and Rogers, manuscript in preparation). In this species, clockwise rotation of the prey led to frequent striking at the prey, although not until it had entered the right visual hemifield. This indicates that in *Bufo bufo*, as in the other two species of toads, striking at prey is controlled by the Lhemi. When *Bufo marinus* was tested with the prey rotating counterclockwise, very few strikes were made. In this case, it seems that initial detection of the stimulus in the right, monocular visual field leads to an inhibition of feeding responses. Although this result is consistent with the Lhemi’s ability to inhibit responding, it differs from the results obtained with the other two species, perhaps because the prey used in testing *Bufo marinus* (a cricket tethered to a vertical rod) was less preferred by this species.

This bias of toads to strike at prey rotated clockwise only after it has passed the midline deserves further discussion. Some strikes are on the midline but, for clockwise rotation of the prey, the midline represents a clear dividing point with strikes to the right side and not the left side (Fig. 3). In contrast to the avian species discussed earlier, the toads tested have a large binocular field of vision (approximately 70° in *Bufo viridis*, 90° in *Bufo bufo*, and 110° in *Bufo marinus*) resulting from location of their eyes somewhat frontally and toward the top of the head (Lippolis *et al.*, 2001). Therefore, the side biases in toads make an interesting contrast to those found earlier in birds. In toads, the lateralization is seen clearly in the binocular field (i.e., not in the lateral, monocular fields of vision, as is the case in birds discussed earlier, but in relation to the animal’s midline). It is as if the toad suffers from hemineglect syndrome, described for humans (Myslobodsky, 1983), for prey on its left side. These results suggest that toads may have mechanisms operating with respect to the midline and extracorporeal space, as reported previously only in humans. The midline of extracorporeal space is obvious in humans, despite the wide binocular field and, more importantly, the fact that each eye sends input to both sides of the brain (Heilman *et al.*, 1985; Mesulam, 1985). The midline division of responding may depend on different cognitive processes.
or mechanisms in toads and humans, but, as it is an aspect of lateralization not considered previously in nonhuman species, it deserves further investigation in species with wide binocular fields.

C. Fish

The rightward bias for feeding responses has been traced to an appearance during evolution as early as teleost fish. Fish direct bites at small “prey” objects to their right side. Zebrafish (*Brachydanio rerio*) use the RE to fixate on a target, a small bead, that the fish intends to bite, presumably for feeding (Mikløsi and Andrew, 1999). There is a strong, positive association between biting and RE use. No such eye bias occurs if the fish does not bite at the bead. The researchers found that the RE preference disappeared as the fish habituated to the bead (ceased to bite it) and reappeared when the bead was changed in appearance in a way that elicited biting again. Thus, use of the RE and Lhemi is associated with the decision to bite or not to bite the small bead. These bites were likely to be feeding bites, and not aggressive bites, since the fish had been fed previously at the site where the testing bead was located.

Other experiments have shown that zebrafish use the LE to view scenes and larger objects at a distance when no considered decision about responding has to be made (Mikløsi *et al.*, 1998). By contrast, a novel scene evokes RE viewing when seen for the first time, when the fish has to decide whether or not to respond to it. Presentation of the same scene a second time requires no such decision making and evokes viewing by the LE.

This finding, along with a large number of other discoveries of lateralization in fish of various species (summarized in Bisazza *et al.*, 1998a; also see later), attests to an early evolution of lateralization. In fact, Andrew *et al.* (2000) have hypothesized that lateralization evolved in association with the first visually controlled predation. They have argued that the brain of the earliest chordates may have been as asymmetrical as their viscera. Taking amphioxus as an example, they note that the position of the mouth is on the left side in the larval stages of development and it sends its neural inputs to the Lhemi. The mouth of an amphioxus does not migrate to the midline until the adult stage is reached. Andrew *et al.* (2000) reason that this asymmetry in the larval form put the left side of the brain in control of feeding responses, which are largely tactile in amphioxus, and that this lateralization was retained when visually guided predation evolved. Thus, the earliest visually guided motor responses for feeding were, Andrew and associates suggest, controlled by the RE and its inputs to the left hemisphere.

It is noted that this hypothesis for the evolution of lateralization departs radically from the alternative, and currently accepted hypothesis, that
vertebrates evolved to become increasingly more lateralized (Corballis, 1991). Given the numerous and now well-documented examples of lateralization in lower vertebrates (Vallortigara et al., 1999), including teleost fish, there seems to be no reason to adhere to the notion of increasing lateralization as vertebrates evolved. As Andrew (2001) has pointed out, the nervous systems of the earliest vertebrates may have been strongly lateralized.

D. Nonprimate Mammals

No research has specifically investigated lateralization of feeding responses in nonprimate mammals, although many of the tasks with which Bianki (1988) tested for lateralization in rats relied on conditioning for a food reward. His approach was to cause cortical spreading depression to the left or right hemisphere. The results showed that rats with spreading depression in the Rhemi (and therefore using their Lhemi) were superior in conditioned reflexes and that they adapted to the reward procedure better than those forced to use the Rhemi.

Right-side responding was found to be better in rats trained to intercept a beam of light with their snouts. The rat had to hold its snout in a central hole until a light was illuminated on its left or right side, at which time it had to move its head to the side of the light and this intercepted a photocell beam that delivered a food reward (Mittleman et al., 1988). This result is suggestive of Lhemi specialization for responses akin to manipulation for a food reward, as described for the chick. Certainly, it would be predicted from the general model for lateralization of feeding responses.

Response to sickness induced by injecting lipopolysaccharide is, perhaps, more relevant to discussion of specialization of the Lhemi for feeding responses. Nevue et al. (1998) found that the sickness response, characterized by depressed social behavior, increased immobility, and reduced intake of food for 6 h following the injection, is more pronounced in right-pawed mice than in left-pawed mice. This suggests that it is controlled by the Lhemi. This conclusion is based on the reasoning that preferred use of one paw activates its contralateral hemisphere or that it may reflect a precondition for higher activity in that hemisphere, as suggested for handedness and hemispheric activity in primates (Hellige et al., 1994; King, 1995; Ward et al., 1990; discussed in detail in Section III.E). In fact, research has shown that this is, indeed, the case at least in the motor cortex and during movement of the hand: In humans, movement of the preferred (dominant) hand is associated with a greater volume of activation of the contralateral motor cortex than is movement of the nondominant hand (Dassonville et al., 1997). It is not unreasonable to assume that the activation extends to other regions of the cortex, although further research is required to confirm this assumption.
It is, of course, recognized that all of these examples of lateralization of feeding-related responses in rodents may have other explanations not strongly related to specialization of the Lhemi specifically for feeding responses. Nevertheless, they are not inconsistent with the specialization of the Lhemi for control of responses requiring manipulation of objects and inhibition of responding while the animal decides on the appropriate response.

E. **Primates**

Primates represent a special case because most of their feeding and prey catching responses use the hands, at least in the initial grasping of the prey, whereas all of the examples preceding refer to species in which a single effector is used to obtain food (e.g., the mouth in fish, the beak in birds, and the tongue in toads).

Bias to the right side and control by the left hemisphere might be expected to put the right hand of primates in control for grasping food, but in lower primates, for example, the left hand is used more often than the right. Prosimians seize moving prey with a bias for the left hand, using a ballistic movement of the hand and arm (Ward, 1999). Squirrel monkeys also use the left hand to capture swimming fish (King and Landau, 1993). One can only assume that the ability to use two effectors (hands) severed the link between Lhemi control and right-side bias for control of the effector organ. It would be logical to predict that primates when prey catching would make use of the Rhemi’s advantage in processing topographical cues and so use the left hand (Andrew and Rogers, 2001). In fact, a similar preference to use the left hand for grasping or tracking moving objects has been reported in other species. Cats also show an advantage when using the left paw to reach for a moving target (Lorincz and Fabre-Thorpe, 1996), and humans have superior ability with the left hand for throwing (Watson and Kimura, 1989) and producing ballistic movements (Guiard et al., 1983).

Planned manipulation requiring visual guidance may, by contrast, remain under the control of the Lhemi and so be carried out by the right hand (Andrew and Rogers, 2001). This means that it may reflect the ancient evolutionary pattern of specialization of the Lhemi and not, in essence, be determined by postural demands, as proposed by McNeilage et al. (1987). Lhemi control of visual manipulation may, thus, explain right-handedness in humans for writing and other visuomotor tasks and maybe also right-handedness for fine manipulation in higher primates (Hopkins and Morris, 1993). Captive chimpanzees (*Pan troglodytes*) exhibit a right-hand preference for manipulating a joystick (Morris et al., 1993), but no such handedness has been seen in wild chimpanzees (Marchant and McGrew, 1996).

Hand preferences in the apes remain controversial. The left-handedness of orangutans when manipulating parts of the face (Rogers and Kaplan, 1996)
seems to be opposite to the prediction of Lhemi control of manipulation but this response is not visually guided. Instead it relies on tactile feedback, shown in other primates and contexts to be a function of the left hand and Rhemi (Lacreuse and Fragaszy, 1996, 1999), as mentioned previously.

III. PREDATOR-ESCAPE AND FEAR RESPONSES

As the evidence presented later shows, predator-escape and a broad range of fear responses are primarily controlled by the Rhemi, and, in the case of species with lateral placement of the eyes, they are elicited more rapidly and strongly by stimuli on the animal’s left side.

It is possible that the function of the Rhemi in fear and predator-escape responses is one aspect of this hemisphere’s specialization for expressing intense emotions and is closely linked to more effective control of sympathetic outflow by the Rhemi, compared to control of parasympathetic outflow by the Lhemi (Wittling, 1997). The Rhemi’s control of sympathetic mechanisms of the heart has been shown in humans (Hugdahl, 1995), dogs, and cats (Lane and Jennings, 1995).

A. BIRDS

Phillips and Youngren (1986) investigated fear responses of chicks following placement of a lesion in the left or right archistriatal region of the forebrain. The lesioned chicks were placed in a novel environment and fear-induced peeping (distress calling) was scored. Peeping was reduced to a greater extent by lesions of the archistriatum on the right side than by lesions on the left side. Hence, it would seem that the Rhemi is specialized for the expression of distress and fear responses. Entirely consistent with this result, chicks peep more when they detect a novel stimulus in the left, lateral visual field than when they detect it in the right, lateral visual field (Andrew, 1983), although age is a factor in this response (Andrew and Brennan, 1983).

As there have been no published reports of experiments testing whether predator-escape responses of birds are lateralized, it is appropriate to mention here a study of young domestic chicks completed in my laboratory (Lippolis and Rogers, in preparation). The test involved positioning the chick in the center of a circular arena with its head through a hole in a small piece of card standing vertically. A simulated predator resembling the head of a snake was introduced to the arena at various points from behind a wall constructed of cloth and advanced into the chick’s left or right monocular field. The model was moved mechanically by a motor programmed to advance it a fixed distance at two speeds. The latency from the first appearance of the model in the arena to the time when the chick withdrew its head from the
hole was scored from video recordings and found to be significantly shorter for presentations on the chick’s left side compared to the right side.

This result indicates that the Rhemi is specialized for control of predator-escape responses as well as for expressing fear responses. A similar result was found in another experiment in which a novel stimulus was advanced toward the chick from behind while the bird was feeding (Rogers and Anson, 1979). On each trial the stimulus entered the monocular field of either the LE or the RE. The distance of the stimulus from the chick at the time when the chick stopped feeding and showed the startle response was measured and found to be greater for the LE than for the RE. Thus, the Rhemi is also more responsive to novel stimuli. As it is not possible to separate this specialization from that of the response to a model predator, it might be preferable to see the Rhemi as being specialized to control immediate or spontaneous responses that are elicited by novel, and potentially dangerous, stimuli. These responses do not require any form of manipulation to be carried out by the animal, as discussed previously for feeding, but are rapid responses made without weighing up possible alternative responses. Lateralization is, thus, a matter of the amount, as well as the kind, of attention given to a stimulus on its first detection in the left or right visual fields.

Consistent with these specializations of the Rhemi, adult chickens have been found to scan overhead using the LE when they hear their species-specific alarm call signaling the presence of an aerial predator. Evans et al. (1993) played recorded aerial alarm calls to hens and noted that they responded by tilting their heads to look overhead using the LE. This engages the Rhemi in detection as well as the rapid motor responses that may be required to escape the predator. In other words, the alarm call puts the Rhemi in charge and so makes use of its specialization for a number of linked functions; viz., novelty detection, rapid responding, fear expression, and predator-escape responses.

A recent study (A. Hoffman and L. Rogers, in preparation) has found a similar lateralization in the fear/escape responses of wild Australian magpies. The experimenter walked toward the bird (sample size of 34 birds) from behind when it was feeding. The eye used by the bird to view the experimenter could be determined easily since the bird turns its head and fixates using one or the other monocular visual field. After looking thus, the bird ran away a few paces; the human then approached again allowing a new score of eye use to be obtained. Between 10 and 30 scores were obtained per bird. Although some of the magpies displayed a significant eye preference, there was no bias in the population and many of the birds showed no significant preference. Alarm calling was also recorded. The percent RE preference was determined for each bird and these scores were correlated with alarm calling (scores adjusted for the number of recorded events of eye use).
The percent RE preference correlated negatively with alarm calling \( (r = -0.43, p = 0.01) \), indicating that fear and escape responses are elicited more strongly when the LE (and Rhemi) is used than vice versa. This result forms a basis for testing experimentally the hypothesized role of the Rhemi in control of fear responses in other avian species in their natural environment.

The Rhemi is also more likely to control immediate responses to noxious olfactory stimuli (Rogers et al., 1998). Chicks were presented with a novel blue bead mounted on a hollow rod from which the irritant odor, clove oil, was released and could be detected by the chick as it pecked the bead. The chicks were tested with either the right or the left nostril occluded. Those using the right nostril only reacted to the odor by shaking their head in a characteristic disgust response, whereas this response was rare in those using their left nostril. Since olfactory input from each nostril goes only to the ipsilateral hemisphere, it can be concluded that the innate disgust response is elicited more readily when the Rhemi is processing the information. The Lhemi is able to suppress this response and, presumably, direct the chick’s attention to the colored bead. Although head shaking in response to an odor is not a fear response, it may be associated with the same fundamental specialization of the Rhemi for expression of intense emotions.

B. AMPHIBIANS

Toads also are more reactive to predators advancing from their left side than to those advancing from their right side. This left-side bias may demonstrate that the Rhemi responds sooner to a potential predator and expresses fear more strongly. This result was obtained by testing toads (three species of *Bufo*) in a circular arena by advancing a mechanical model of a snake (the same one used for the chicks) toward the toad in its midline (binocular) or in the left or right lateral monocular fields (Lippolis et al., 2001). The toads were more likely to react, most often by jumping away, when the simulated predator was in their binocular field or left monocular field than when it was in their right monocular field. It can be suggested, therefore, that toads might be somewhat more likely to succumb to predators approaching them from their right side than from their left side. In fact, predators might exploit this side bias, present at a population level, by preferentially approaching their prey on its right side and turning to strike leftward. There has been no research addressing this possibility. Also, it is not yet known whether the lateral bias for reactivity to the simulated predator is present only in the monocular, lateral fields of vision or whether, as for the lateralization of striking at prey, the toad’s midline is the dividing point. Given the large binocular overlap in most species of toads (including the three species tested so far), it would be important to determine whether the lesser reactivity on
the right side is confined to the relatively small monocular field or whether it extends over the entire right hemifield of vision. If it is confined to the monocular field of the right eye, it would be tempting to suggest that toads minimize the side bias in reactivity to a predator by maximizing the size of their binocular field in the horizontal plane.

The preceding discussion has considered lateralization of reactivity (whether or not an escape response occurs) to an advancing predator but not lateralization of the motor response itself. The motor responses elicited by an advancing predator may also be lateralized in some anurans. Dill (1977) scored the direction of jumping in Pacific tree frogs, *Hyla regilla*, evoked by swinging a ball toward the frog along its midline. Leftward jumps were more common, a result that Dill attributed to the frogs having a longer right than left hindlimb, although there was no direct concordance of this character and the lateralized jumping scores within individuals. Later experiments have found no such motor bias for jumping in *Bufo marinus* faced with an advancing model predator in the frontal field (Lippolis et al., 2001) even though *Bufo marinus* does exhibit a right hindlimb preference for initiating a successful righting response from a supine position (Robins et al., 1998).

Motor biases in righting responses seem to be common in anurans, as shown by the limb or side preference in righting in three species of toads (Bisazza et al., 1996, 1997b) and two species of Australian tree frogs (*Litoria caerulea* and *L. latopalmata*). As shown in Fig. 4, *Litoria* sp. show a population bias to rotate their body around its right side when righting on a dry surface. It is relevant to consider that an anuran might be required to right itself from a supine position as part of its repertoire of predator-escape responses. Therefore, it is worth noting that rotation around the right side of the body allows the frog to continue viewing the predator using its LE. This might be coincidental, but it is suggested on the basis of the Rhemi’s specialization for predator monitoring and control of escape responses in other species, especially relevant in the case of the teleost ancestors of anurans (discussed later).

Tadpoles also show lateralized escape responses, after they have surfaced to breathe air. Wassersug et al. (1999) tested two species of frog tadpoles in water with reduced oxygen content, which forces the tadpoles to rise to the surface to gulp air. They found a significant population bias for bullfrog tadpoles (*Rana catesbeiana*) to turn leftward during the C-turn escape response that follows the air-breathing but no such bias in clawed frog tadpoles (*Xenopus laevis*). The difference between the two species could, as the researchers suggested, be attributed to placement of the spiracle through which water that enters the mouth is expelled. Bullfrog tadpoles have a single spiracle on the left side of the body, whereas clawed frog tadpoles have a spiracle
LATERALIZATION IN VERTEBRATES

Fig. 4. Motor lateralizations in toads and tadpoles of the Australian tree frog *Litoria* sp. is presented. The two species *Litoria latopalmata* and *L. lesueurii* were tested. (A) Righting responses in toads from a supine position: the number of turns around the right side of the body out of a total of 10 trials is plotted on the x-axis. Note the population bias for a right-side preference. (B) Direction of turning in tadpoles scored for escape turns given to a visual stimulus and for turns after breathing air at the surface of the water. As individuals could not be identified, the number of tadpoles recorded as turning left or right is plotted. Note the significant rightward turning bias to escape and the significant leftward bias of turns after breathing air. These data were collected from toads in their natural environment, Glenreagh, New South Wales.
on each side of the body. However, this explanation would be unlikely if
the direction of turning in a given species varies with the context in which
it occurs. This is the case in *Litoria* sp.: As in the bullfrog tadpole, *Litoria*
tadpoles have a population bias to turn leftward after breathing air and a
population bias to turn rightward in escape turns elicited by a visual stimulus
(Fig. 4; L. Rogers, in preparation).

A tadpole breathes air by first drifting up to slightly below the surface of
the water and then it swims rapidly to the surface, gulps air, and turns rapidly
in a C-turn, and swims down to deeper levels in the water. It is probable that
the rapid-turning phase is triggered by the activity of the Mauthner cell on
one side of the body. This response may not be driven by visual inputs. A vi-
sually driven escape response was elicited by waving a hat to elicit the escape
response from tadpoles in a pond. *Litoria* tadpoles often remain stationary
at the surface of still water in a pond, possibly because it is warmer, and a
sudden visual stimulus overhead elicits rapid turning followed by swimming
downward or first along but just under the surface of the water away from
the stimulus and then downward. As shown in Fig. 4, more tadpoles turned
right than left, the position of the stimulus being randomized with respect to
the position of the tadpole. This rightward turning, when vision is used, fits
with the toad’s greater reactivity to predators seen in the lateral field of the
LE and with use of the LE during escape turning in the teleost ancestors of
anurans (see later). It suggests the presence of a population bias toward use
of the Rhemi during escape in both tadpoles and toads of various anuran
species.

C. Fish

The turning preferences of poeciliid fish, *Girardinus falcatus*, in escaping
from a model predator have been tested by presenting the model to each fish
from in front as it was swimming toward the stimulus (Cantalupo et al., 1995).
After detecting the simulated predator in the frontal field, the majority of the
fish escaped with a rightward turning bias, significant at the population level.
As Vallortigara and Bisazza (2001) suggest, this bias is likely to be generated
at the level of the optic tectum, where visual information is processed before
being relayed to the Mauthner cell that drives the C-start ballistic escape
turning movement (Zottoli et al., 1987). There is a Mauthner cell on each
side of the brain, and the axon of each one crosses the animal’s midline to
innervate the musculature on the contralateral side of the body (Canfield and
Rose, 1993). This means that rightward turning is caused by greater activity
in the left Mauthner cell compared to the right, and so it may be generated
by excitatory inputs to the left Mauthner cell from the left optic tectum and,
thus, originally from the RE. This implies that the Lhemi is controlling the response, although, once the fish has turned rightward, it would engage the LE and right side of the brain in continued monitoring of the predator.

After repeated presentations of the simulated predator, *Girardinus falcatus* shifted to leftward turning, again with a bias at the population level (Cantalupo et al., 1995). By this stage, it was likely that the fish had habituated to the stimulus and were no longer treating it as a potential predator.

The results obtained with *Girardinus falcatus* are consistent and explicable in terms of the general model for hemispheric lateralization (see earlier discussion) only in so far as during turning the LE and Rhemi are used by the fish. Escape responses in fish might, however, be rather variable from species to species, depending on whether or not the species schools and on the habitat it occupies. The teleost fish, *Jenynsia lineata*, exhibits individual, but not population, lateralization of turning responses when faced with a simulated predator (Bisazza et al., 1997a). Half of the group tested turned leftward, and so continued to fixate on the predator with their right eye, and the other half turned rightward. These preferences were retained when the same fish were tested 1 month later. In fact, Bisazza et al. (2000) have conducted a study of 16 species of fish presented with a predator model behind a barrier with vertical bars. Ten of the species showed a significant population bias for turning but only six of these turned rightward. The eye and the hemisphere driving turning may, of course, depend on whether the model predator was seen as a potential predator or not by each particular species, since habituation to the model leads to a change in the direction of turning (see earlier discussion). The direction of turning to go around the barrier must depend on when the final decision to approach is made. It may be made at the point of turning and, depending on the species, with or without further monitoring as the fish swims around the barrier. The most notable finding of this study by Bisazza et al. (2000) was that a population bias for turning (left or right) was present in all of the species that school but in less than half of the species that do not school (discussed later).

It is interesting to note that more scars have been reported to occur on the left side of the whitefish, *Coregonus nasus* and *C. clupeaformis* (Reist et al., 1987). This asymmetrical distribution presumably indicates unsuccessful attempts at predation by lampreys, birds, or bears, as claimed by the researchers. It is impossible to tell whether the lateralization results from less successful leftward escape responses by the fish (leftward escaping fish might, actually, succumb to the predator), more successful rightward escapes by the fish (if the rightward ones escape unscathed), or rightward prey-catching responses of the predators. However, all of these alternatives assume that there is no population bias for turning. If there is a population
bias to turn rightward, as for *Girardinus falcatus*, whitefish may be more likely to be damaged on their left side since that side would be next to the predator.

In some circumstances approaching a potential predator, instead of escaping, occurs, and here fish show a preference to use the RE to view the predator. Some fish leave their school in twos or threes to approach a predator and examine it more closely. Bisazza *et al.* (1998b) have shown that poeciliid fish turn leftward when they reach a barrier separating them from a simulated model predator. This direction of turning allows the fish to view the predator using the RE (Facchin *et al.*, 1999). As an approach would demand inhibition of the escape response, it is entirely consistent with the general model that the Lhemi is engaged to perform the task. Added to this, a mosquito fish (*Gambusia holbrooki*) will approach the predator more closely when it can see a conspecific with its LE at the same time that it approaches the predator. Bisazza *et al.* (1999) discovered this by placing a mirror on the left or right side of a tank in which a mosquito fish could approach a predator fish in an adjoining tank. The test fish approached the predator more closely when the mirror was on its left side than when the mirror was on its right side. This preference for a fish to position itself so that a conspecific (actually, the fish’s own image in a mirror) is on its left side appears to be a general characteristic of teleosts: It has been found in females of five other species of teleosts in the absence of predator inspection (Sovrano *et al.*, 1999) and confirmed to occur in the mosquito fish in the absence of a predator (De Santi *et al.*, 2001).

The preferred eye for viewing a conspecific during inspection of a predator, however, appears to vary with the fish’s prior experience with the predator. Guppies bred in captivity and given prior experience with a hungry predator in their home tank showed more tendency to approach the predator when the image of a conspecific was on their right side (De Santi *et al.*, 2000). They had a preference to use their LE to view the familiar predator and so could respond to it spontaneously and rapidly. However, this does not explain why the fish should approach the familiar predator unless the escape response had been inhibited by the absence of chemical or other cues of the predator fish because it was in a separate tank. There is clearly a need to investigate the responses of fish to predators in more detail: They are an excellent group for systematic investigations.

**D. Nonprimate Mammals**

There have been no specific tests to see whether nonprimate mammals have lateralized predator-escape responses, but some tests have shown that rats display heightened fear and withdrawal responses after lesioning of the
Lateralization in vertebrates

Lhemi, thus forcing use of the Rhemi only. The first experiment showing this relied on a learned withdrawal response—that of taste aversion to a sweet solution (Denenberg et al., 1980). Lithium chloride treatment was used to induce the taste aversion and the left or right hemisphere of the rat was ablated before retention was tested. Aversion and withdrawal behavior was greater in the rats with an intact Rhemi than in those with an intact Lhemi. Of course, there may be alternative explanations for this result.

The role of the Rhemi in fear responses at a physiological level is shown by that fact that lesions of the Rhemi and not the Lhemi decrease circulating noradrenalin levels (Robinson, 1985). Added to this, it is apparent that the Rhemi has greater control of the hypothalamic-pituitary-adrenal axis than the Lhemi, as shown by the fact that, in response to stress induced by physical restraint, plasma corticosterone increases to a higher level in left-pawed mice compared to ambidextrous and right-pawed mice (Nevue and Moya, 1997).

These data for rats do not provide strong evidence in support of the hypothesized general model associating the Rhemi with control of fear responses, but they do not contradict it.

E. Primates

Primates express fear more strongly on the left side of the face, as found in rhesus monkeys (Macaca mulatta) (Hauser, 1993), common marmosets (Callithrix jacchus) (Hook-Costigan and Rogers, 1998) and also in humans (Sackheim et al., 1978). Also, as shown in rhesus monkeys, the left side of the mouth opens before the right during facial expressions of fear made alone or together with a vocalization (Hauser and Akre, 2001; see also Weiss et al., 2001). Since the musculature of the left side of the face is controlled by the Rhemi, this asymmetry reflects specialization of the Rhemi for the expression of intense emotions. Although the facial expression is one of fear, this cannot be used as direct evidence that the Rhemi controls fear responses in a more general sense, but it does, at least, suggest that this may be so. The validity of this suggestion is, of course, strengthened by the evidence for Rhemi control of fear responses in a range of species. Also, fear responses have been shown to be expressed more strongly in left-handed primates.

Hand preferences in primates are usually measured as the preferential use of one hand over the other for simple tasks, particularly tasks involving picking up and holding food (Ward and Hopkins, 1993). Hand preference is used to indicate dominance of the contralateral hemisphere, on the grounds that consistent use of one hand in a number of tasks either activates the contralateral hemisphere, which controls that hand, or reflects a precondition of higher activity in that hemisphere (Hellige et al., 1994; King, 1995; Ward et al., 1990). To say this in another way, preferential use of a hand...
is associated with an attentional asymmetry that extends to higher cortical levels in the contralateral hemisphere (Peters, 1995). Thus left-handed individuals might show diffuse attention and intense emotional responses, including fear responses and withdrawal, whereas right-handed individuals might be better able than left-handed ones to inhibit fear and withdrawal to allow exploration of novel objects and situations (Davidson, 1992, 1995). Results obtained by testing chimpanzees (Hopkins and Bennett, 1994) and marmosets (Cameron and Rogers, 1999) suggest that this is, indeed, the case.

Hopkins and Bennett (1994) found that the right-handed chimpanzees approached novel toys with a shorter latency than non-right-handed (i.e., left-handed and no preference) chimpanzees. The right-handers also touched more toys than the non-right-handers. Thus, approach behavior and exploration appeared to be associated with greater activation of the left hemisphere, and avoidance behavior appeared to be associated with greater activation of the right hemisphere.

A similar result has been found in common marmosets (*Callithrix jacchus*). Individual marmosets display hand preferences consistent over time and in similar tasks, but there is no population bias in this species. Half of the population is left-hand preferent and half is right-hand preferent (Box, 1977; Hook and Rogers, 2000; Hook-Costigan and Rogers, 1995, 1996; Rothe, 1973). Cameron and Rogers (1999) found that marmosets with a right-hand preference for holding food displayed a shorter latency to enter, on their own, a novel room containing novel structures and objects, touched more objects, and performed more touches and more parallax movements than subjects with a left-hand preference. The same marmosets were tested 2 years later and, again, the left-handed subjects took significantly longer than the right-handed ones to emerge from their nest box into an unfamiliar room (J. Hall and L. Rogers, paper in preparation). In fact, left-handed males had the longest latency to emerge.

The results obtained with chimpanzees and marmosets support the hypothesized specialization of the Rhemi for expressing fear and other intense emotional states and thus its association with withdrawal from novel situations and novel objects. The Lhemi inhibits fear and so its activity permits approach of novel objects and entry into unfamiliar environments.

In humans, Rhemi control has been variously associated with intense emotions or negative emotions and withdrawal (Davidson, 1992, 1995). Dimond *et al.* (1976) have found that the use of the left visual field to view a film resulted in more negative assessment than did use of the right visual field to view the same film. Frontal and anterior regions of the Rhemi are selectively activated during withdrawn emotional states involving fear and disgust and, consistent with this, PET scans have revealed elevated activation of the Rhemi during resting in panic-prone subjects (Davidson, 1995). Also,
schizotypy with social and emotional withdrawal is associated with Rhemi dominance, seen in terms of scoring better memory of faces than words and poverty of speech (Gruzelier and Doig, 1996). Damage to the frontal region of the Lhemi, presumably forcing the equivalent region of the Rhemi to take control, leads to decreased interaction with other people and difficulty in initiating voluntary actions (Davidson, 1995). Moreover, patients with injury to the left hemisphere resulting from stroke are significantly more depressed than those with equivalent injury to the right hemisphere (Robinson and Price, 1982; Robinson et al., 1984). Rhemi involvement in human emotion, therefore, seems to be associated with negative and intense states and with social withdrawal.

It is not known whether control of predator-escape responses is a specialization of the Rhemi in primates but it is a possibility worth investigating. The evidence discussed earlier makes Rhemi involvement highly likely.

IV. Spatial Maps and Attention

Perhaps in association with its specialization for attending to novel stimuli and in controlling escape responses, the Rhemi is specialized to process spatial information using a topographical map. These abilities might be linked because there is a functional need to attend to the spatial location of a novel stimulus and to use spatial information to escape effectively from attack by a predator.

A. Birds

The first evidence for use of the Rhemi to assess topographical cues and to utilize spatial memory was provided by Rashid and Andrew (1989), who tested chicks in a search task requiring them to find food buried under sawdust. The chicks were able to locate the buried food using two types of topographical cues, both distant cues from outside the testing arena (i.e., structures within the room and mainly overhead) and local cues inside the arena (two cylinders placed next to the buried food during training). The chicks were trained binocularly and tested monocularly. During testing either the walls of the arena were rotated relative to the distal cues in the testing room or the local cues were shifted. To prevent new learning during testing, no food was buried under the sawdust. The site(s) where the chicks scratched in their attempts to uncover food were recorded. The results showed that the chicks used the distal cues to locate the expected food site when they were using their LE (Rhemi) and they used the local cues when they were using their RE (Lhemi).
Evidence that chicks using the LE attend to spatial cues is also shown by the fact that the response to a colored bead dishabituates when the bead is introduced into their cage from a different angle, whereas chicks using the RE ignore this change (Andrew, 1991). The spatial information is taken into account only when the Rhemi is used.

Although it would be simpler to think of the Rhemi as processing spatial information and the Lhemi as being unable to do so, such an absolute division of function is not correct. In fact, both eyes and hemispheres are able to use spatial information of very different kinds. The LE and Rhemi use a topographical map taking into account the distal cues, whereas the RE and Lhemi use location relative to nearby features. Both types of information are available to chicks tested in the binocular condition, but the topographical cues take precedence over the local cues, as Tommasi and Vallortigara (2000) were able to show. They trained chicks to find buried food in the center of an arena and then tested them in arenas of different sizes, the chicks being able to use both eyes in training and testing. When the chicks were tested in a smaller arena, they searched in the center, showing that they were using topographical cues. When they were tested in a larger arena, they focused their searching in two locations, in the center and, to a lesser extent, at distances from the walls equivalent to the distance at which the center had been located in the smaller, training arena. Most of their searching relied on a concept of the center, but relative distance from the walls was also used.

Further tests by Tommasi and Vallortigara (2000) showed that the chicks were using angular estimates of the height of the walls to specify the center rather than a detailed topographical map, but, in their tests, a screen placed over the arena prevented the chicks from seeing any features of the room. Angular estimation of height would, in fact, be a basis on which to construct a topographical map if more features were available for the chick to view. Such a topographical map would be constructed using rules, and it would encode spatial information in a more global and adaptable form than the other kind of spatial information that relies on measuring relative distance from conspicuous, local features.

Subsequent experiments by Tommasi, Vallortigara, and colleagues have shown that the Rhemi can operate on rules that use spatial information to construct a topographical map, whereas the Lhemi cannot. If chicks are trained to search for buried food in the center of an arena, they choose to search in the center of distorted versions of the arena when they use their LE but not when they use their RE (Tommasi et al., 1997; summarized in Vallortigara, 2000). When using their RE they simply search at a distance from the walls equal to where the center was in the training arena (i.e., they search in a strip around the walls at this distance). The chicks using their RE rely on local, object-specific cues, instead of on a spatial map plus a rule specifying the topographical location of food.
In another task, chicks were trained binocularly to find buried food in the center of a square arena and then tested monocularly in a larger arena, also square (Tommasi and Vallortigara, 2001). Chicks using the LE during testing searched in the center of the enlarged arena and chicks using the RE searched at a distance from the walls equivalent to the distance to the center in the training arena (Tommasi and Vallortigara, 2001). When the testing arena was made smaller than the training arena, LE chicks again searched at the center, whereas RE chicks searched erratically and in a dispersed manner, presumably because they could no longer specify the distance from the walls to the center. When the location of the food was marked by a vertical rod inserted into the sawdust during training and then placed in a corner during testing, LE chicks were able to ignore it and search at the center but RE chicks searched next to the shifted landmark. All of these tests show that the Rhemi uses relational spatial information to build a map, whereas the Lhemi uses absolute measurement of distance specified by local cues (Tommasi and Vallortigara, 2001).

The hen’s preferential use of the LE to monitor overhead for an aerial predator (Evans et al., 1993; discussed earlier) may make use of the spatial abilities of the Rhemi since the position in the visual field of a potential predator is important information for the bird to take into account. Indeed, the LE is expected to dominate in tasks requiring the bird to monitor topographical information. This specialization may also explain the observation that kookaburras (Dacelo gigas) tilt their head to use the LE when monitoring the ground beneath them for moving prey. Almost two-thirds of wild kookaburras (total of 90 birds) spotted sitting on telegraph wires while searching for prey on the ground were recorded as using the LE to look downward, the remainder mostly used both eyes (Rogers, 2001). Such a preference for the LE and Rhemi enables use of spatial information and it also ensures that the bird responds rapidly. A limited number of observations suggest that the kookaburra looks briefly with its RE just before it swoops to capture the prey. If the latter is confirmed by more observations, this shift to the RE would reflect use of Lhemi in object-related tasks and therefore feeding (discussed earlier).

Spatial learning and memory is highly developed in marsh tits (Parus palustris) and lateralized in similar ways to that shown in the chick (Clayton, 1993; Clayton and Krebs, 1993). Lateralization is shown during recovery of cached food items, when the birds are tested with one or the other eye covered (Clayton and Krebs, 1994). When the RE is in use, for retrieval just after food has been cached, the marsh tits make use of the local cues associated with the hole used for storing the food. When the LE is in use, spatial position relative to the test room is used instead to locate the cache. Hence the Rhemi is specialized to use and to store spatial information in this species also.
Successful foraging for food may require use of spatial cues (Rhemi) in some circumstances and local cues (Lhemi) in other circumstances. Tommasi et al. (2000) have shown that parallel processing of information in the two hemispheres allows competition leading to choice of the hemisphere more suited to carry out the task at hand. They trained and tested chicks binocularly in a task requiring the chick to find a dish of food in one arm of a cross-shaped arena, and there were two different conditions of searching. One condition required the chick to use spatial cues of conspicuous objects in the testing room because all arms of the arena had dishes that looked the same but the dish in one arm was baited and always in the same position. In this case, the chicks began to search by making a series of turns to the left, indicating that the Rhemi was in control. In the other condition, the dish with food was distinguished by colored stripes and it was moved between the arms of the maze on each trial. Hence the chick had to use the local cues (stripes) to locate the food dish and, in this case, searching began with a series of right turns, indicating control by the Lhemi. Therefore, task demands had set the bias for which of the hemispheres would assume control.

B. AMPHIBIANS

No research has been conducted to see whether spatial processing is lateralized in amphibia. It is known that toads update the position of their escape routes each time they move and that this guides their escape leaps (Ingle and Hoff, 1990). Furthermore, toads are more likely to respond to a predator on their left side (see earlier discussion). On the basis of this result, one would predict that the Rhemi has an advantage processing topographical information, but this remains to be investigated.

C. FISH

Little can be said about the processing of spatial information in fish. Preferential use of the LE and Rhemi to view familiar scenes and objects when no specific response has to be given may depend on diffuse attention (Mikløsi et al., 1998), and this function of the Rhemi may be an aspect of processing spatial information. At least, it could be argued that diffuse attention would allow detection of stimulus change anywhere in the visual field and effective response would require processing of spatial cues.

As mentioned previously, schooling fish approach a predator more closely when they swim with their mirror image on their left side (Bisazza et al., 1999), and, even in the absence of a predator, they prefer to swim with their mirror image on their left side (De Santi et al., 2001). This preference for having a “conspecific” on the left side might affect the structure of a school. Since fish space themselves at rather precise distances from each other when
they are in a school, the preference for swimming with a conspecific on the left could reflect a need to monitor the position of that fish precisely. The need to monitor spatial information to maintain the species-typical spacing between fish in a school may explain the preference for having a conspecific on the left side, since it would allow use of the LE and Rhemi.

Escape responses inevitably involve processing of topographical cues to monitor the position of the predator and to enable effective movement away from the predator to a safer location. In fact, in teleost fish the direction of escape C-turns, driven by one of the Mauthner cells, is influenced by obstacles around the fish (Eaton and Emberly, 1991). Given the rapidity of the C-turn, it is likely that the spatial information used by the escaping fish has been acquired during regular monitoring of the topography before turning is elicited. There is no evidence associating this monitoring of topography to either one of the hemispheres, but it may be relevant to note that the preferential right-side turning of *Girardinus falcatus* as it approaches a predator (Cantalupo *et al.*, 1995) permits monitoring of the spatial location of the predator relative to obstacles with the LE and Rhemi.

D. Nonprimate Mammals

Studies on rats have indicated that the Rhemi is involved in processing spatial information. Bianki (1981) tested rats on a discrimination task requiring them to locate the position of a spot of light using depth cues and found that this performance was impaired by causing spreading depression in the Rhemi but not in the Lhemi. In other words, the rat can determine depth provided that the Rhemi is functioning.

Perhaps the best demonstration of the Rhemi specialization for spatial learning has been obtained by testing rats monocularly in the Morris water maze. This task requires a swimming rat to locate an escape platform submerged beneath the water’s surface using spatial cues only. These spatial cues are features in the testing room (i.e., distal to the water maze). Cowell *et al.* (1997) found that rats with the RE occluded, and so using their Rhemi, were able to find the hidden escape platform but those with the LE occluded had great difficulty doing so. However, this lateralization was present only in rats that had been handled in early life. Handling involved taking each pup away from its mother and placing it in isolation for 3 min/day from birth to day 20 of life. Rats that had not received such handling in early life showed no difference between performance with the LE or the RE. When tested using their LE, nonhandled rats were unable to perform the task as well as handled rats, and, when tested using their RE, nonhandled rats performed better than handled rats. Hence, handling in early life unmasks the superior ability of the Rhemi for spatial navigation and, at the same time, decreases the ability of the Lhemi to use this information. Handling in early life also
unmasks other forms of lateralization in rats (summarized in Bradshaw and Rogers, 1993), including lateralization in direction of moving off in open-field tests (handled rats have a population bias to move leftward from their starting position; Sherman et al., 1980) and emotional behavior (Maier and Crowne, 1993).

E. Primates

In humans the Rhemi, it seems, subserves a broader area of hemispace than does the Lhemi (Posner et al., 1987). Lesions of either hemisphere cause inattention to the contralateral side of the body, but inattention to the ipsilateral side of the body sometimes occurs and it is more frequent following a lesion of the Rhemi (Heilman, 1995). Thus, inattention to one side of the body or even to one-half of any object (i.e., hemineglect syndrome) is more likely to occur after damage to the Rhemi than to the Lhemi (Heilman et al., 1985). The Rhemi is said to direct attention to visual extrapersonal space, whereas the Lhemi directs attention to within the person’s body space (Heilman, 1995). These observations may reflect the role of the Rhemi in processing spatial information using distal cues.

Some evidence indicates that primates may, likewise, have specialization of the Rhemi for spatial performance. For example, capuchins have a stronger left-hand preference when tested on haptic-visual tasks than they do on simple reaching tasks (Lacreuse and Fragaszy, 1999). This may be because the former task requires the integration of spatial and sensorimotor components of the task. Gorillas (Gorilla gorilla) and baboons (Papio papio) also have been found to use the left hand preferentially on spatial tasks requiring them to align transparent doors to obtain a food reward (Fagot and Vauclair, 1988a,b).

Specialization of the Rhemi for spatial processing might be the reason why Rigamonti et al. (1998) found that left-handed pigtail macaques (Macaca nemestrina) have a higher speed of performance than right-handed ones on a task requiring them to search for small food rewards from a vertical array.

Other indirect evidence points to specialization of the Rhemi for spatial processing. “Global processing” is an ability that may reflect spatial processing and it is a function of the Rhemi: Deruelle and Fagot (1997) tested baboons in an operant task in which they had to respond to a letter of the alphabet composed of smaller letters, which could be the same as, or different from, the larger letter. Attention to the larger letter was interpreted as “global precedence,” and this was associated with use of the Rhemi. Attention to the smaller letters indicated local attention and was associated with use of the Lhemi.

Chimpanzees have a Rhemi advantage for locating a short line contained within a geometric figure (Hopkins and Morris, 1989), which suggests
specialization of the Rhemi for spatial processing. The important feature of the task was the location of the line, not merely attention to the line itself. Extrapolating from the more extensive data on the processing of spatial information in the chick, the Rhemi is used for processing information about distant cues and the Lhemi for local cues. It is difficult to say whether the preceding experiments required the primates to use distant or local cues, but, where an operant task was used that required the subjects to judge the distance between a line and a dot displayed on the same key (short vs. long distance discrimination), they can only have relied on local cues. As predicted, baboons and humans performed such a task better with the Lhemi (Dépy et al., 1998).

V. Aggressive Responses

Intraspecific agonistic displays and aggressive interactions are lateralized, as shown in a number of species, and direction of bias is to the left side. The Rhemi is, therefore, specialized for control of aggressive interactions and this may be associated with, or a manifestation of, its specialization for expressing intense emotions. It is a clear example of the specialization of the Rhemi for controlling species-typical patterns of behavior given rapidly in response to specific releasing stimuli.

A. Birds

The first evidence for lateralized control of aggressive responses came from studies of chicks with glutamate injected into the left or right hemisphere on day 2 posthatching. Subsequent to this treatment, the chicks treated in the left hemisphere had elevated levels of attack, as well as copulation, responses when tested with standard hand-thrust tests (Howard et al., 1980). In fact, these chicks responded just as if they had been treated with testosterone (Andrew, 1966), whereas the chicks treated with glutamate in the right hemisphere showed no such elevation of attack or copulation.

Although it was likely that the elevation of aggressive behavior reflected control by the Rhemi, resulting from impaired function of the Lhemi following the glutamate treatment, this was not certain until chicks were tested monocularly. First the chicks were administered testosterone to elevate their attack and copulation behavior, and then they were tested monocularly. Provided that they were tested using the LE, the chicks showed elevated attack and copulation, but, when using the RE, they had levels of attack and copulation no different from those of untreated controls (Rogers et al., 1985).
The same lateralization of agonistic interactions has been found in adult hens (Rogers, 1991). The hens were tested with partial occlusion of the left or right eye (the frontal field and at least half of the lateral field was occluded). Social interactions in groups were scored and it was found that the agonistic interactions of hens with an unoccluded LE were elevated above control levels (hens with no occlusion of the eyes), whereas hens with an unoccluded RE had fewer agonistic interactions than controls. It is apparent, therefore, that elevated aggressive and sexual responses occur when the Rhemi is processing visual inputs and controlling responses, whereas control by the Lhemi suppresses the aggressive behavior.

An experiment by Vallortigara et al. (2001) has found that agonistic interactions in chicks are directed leftward even in the binocular condition. Social pecking between pairs of chicks unfamiliar with each other was recorded on videotape and the angle of fixation used by each chick just before it delivered a peck to the other was determined using frame-by-frame analysis of the videotape. It is typical for the chick to turn its head to fixate its opponent briefly, using its lateral monocular field of vision, before pecking, mostly at a region of the head. Comparison of fixations in which the chick used its left versus its right monocular field revealed a bias to use the LE in the majority of chicks (Fig. 5). Therefore, consistent with control of aggression by the Rhemi, aggressive pecks are delivered with a bias for LE use even in chicks not treated with testosterone and tested monocularly. Nonaggressive pecks, given to features in the cage, showed no such lateral bias (Vallortigara et al., 2001), a result which demonstrates that the bias is not simply a lateralized motor response and that it relates specifically to aggressive pecks.

Preferential use of the LE to direct aggressive pecks at a conspecific occurs in chicks exposed to light before hatching and in chicks hatched from eggs incubated in the dark but the latter group also has lateralized use of the frontal binocular field (Vallortigara et al., 2001). Chicks hatched from eggs incubated in the dark show a significant bias to use the right half of the frontal field in preference to the left half of the frontal field. In other words, they have complementary specialization of the left lateral field and right frontal field for controlling aggressive pecking. This complementary specialization is not seen in chicks exposed to light during incubation.

This finding leads us to reexamine earlier work showing that light exposure of the embryo is essential for establishing lateralization for attack, copulation, and feeding responses. For reasons that are outlined later, exposure of the chick embryo to light for as little as 2 h during the last few days before hatching establishes the lateralization seen in monocular tests of pecking at grains against a background of pebbles (Rogers, 1997). Such light exposure also establishes the lateralization of attack and copulation responses revealed by treatment of the left or right hemisphere with glutamate (Rogers, 1982, 1990). However, we can now see that this result
LATERALIZATION IN VERTEBRATES

Fig. 5. The preferred eye (or side) for chicks and toads attacking a conspecific is illustrated. LE and RE indicate the left and right eyes (or sides), respectively. The data for chicks (*Gallus gallus domesticus*) were collected in tests with pairs of birds that had not seen each other previously. A bird was said to attack with its LE if it delivered more pecks to a conspecific after fixating it with its left lateral field of vision, and vice versa for being right eyed. Note that the majority of chicks were left eyed. (Data from Vallortigara *et al.*, 2001.) The same method was used to collect the data shown for toads (*Bufo marinus*). (Data from Robins *et al.*, 1998.)

may be due to the complementary specialization of the left lateral and right frontal visual fields in chicks hatched from eggs incubated in the dark. Hence light exposure of the embryo influences the development of lateralization, but lateralization still develops even when the eggs are not exposed to light.

It is difficult to say what the natural condition might be in *Gallus gallus*, but, since as little as 2 h of light exposure is sufficient to alter lateralization (Rogers, 1982), it is likely that the eggs receive an equivalent exposure to light in the natural environment. At this stage of incubation, the hen frequently leaves the nest to feed and stands to move the eggs (discussed in Rogers, 1995). Whether or not this is the case, and it may vary between clutches, the left lateral visual field would be used preferentially for aggressive pecking since this bias is independent of the amount of light exposure received by the embryos.

B. AMPHIBIANS

Toads direct more aggressive responses to conspecifics on their left side than on their right side, as do chicks. Robins *et al.* (1998) scored strikes at
conspecifics given by *Bufo marinus* toads when feeding in a group. A tongue strike at another toad, often at its eye, was recorded as being left or right according to whether the point at which the tongue contacted the other toad’s body was in the attacker’s left or right visual hemifield. Individual toads were followed to allow comparison between them, and the bias in the group was also noted (Vallortigara et al., 1998). There was a significant bias to strike in the left hemifield (of 22 toads tested, 17 had a left bias, 4 had a right bias, and 1 had no bias; Fig. 5). This is clear evidence for the control of attack strikes by the Rhemi, and it is in contrast to control of feeding strikes by the Lhemi of the toad (see earlier discussion).

In addition to being more common, the leftward attack strikes by *Bufo marinus* have a more focused target than the rightward attack strikes. The leftward strikes hit one of the opponent’s eyes two to three times more often than do the rightward strikes (Robins et al., 1998). Rightward strikes hit a number of sites on the opponent’s body and appear to be directed away from the eyes. This result indicates that the leftward strikes may be more aggressive than the rightward strikes.

C. REPTILES

For the first time in this review, it is possible to mention lateralization in a reptilian species. Deckel (1995, 1998) has shown that lizards (*Anolis* spp.) tend to direct their agonistic encounters leftward. Nonaggressive encounters show no such bias. Aggressive responses are, therefore, controlled by the Rhemi in lizards.

The aggressive behavior of *Anolis* includes bobbing of the head, extension of the colored dewlap under the throat of males, changes in body posture, biting, and a lightening of skin color. Deckel and Jevitts (1997) reported the lightening of skin color as “greening,” compared to a brown skin color when aggression is low. Since the lizards have their eyes on the sides of their heads and because their snouts occlude the frontal visual field, they view each other by using the left or right monocular field. This means that they orient with the head, and often the body also, positioned sideways to the lizard at which they are directing their agonistic displays. Hence, from video recordings, Deckel could score which eye was used in agonistic displays. Not only was a LE preference found for such interactions but also the leftward-directed aggressive responses of *Anolis* were accompanied by a greening of the lizard’s skin color. Nonaggressive, and nonlateralized, assertion displays were accompanied by a darker skin color. Since serotonin is known to darken the skin color of lizards (Deckel, 1995), the Rhemi of the lizard apparently has control of the neurochemical system involved in changing skin color, as well as behavioral responses associated with aggression.
D. Fish

Siamese fighting fish (*Betta splendens*) are the obvious choice for investigating lateralized aggressive displays in fish. Cantalupo *et al.* (1996) scored the number and duration of lateral threat displays given by male Siamese fighting fish to their image in a mirror. They found individual biases for both of these scores but no population bias. These same fish were tested 2 months later, but this time their lateral displays toward a female conspecific, not a mirror, were scored. Individual fish retained their same side bias for displaying and there was still no bias in the population. It seems, therefore, that the side bias for an individual is consistent over time and context but that there is no indication of Rhemi control of these aspects of agonistic (or sexual) displays. Further investigation measuring the viewing eye preferences of fish during agonistic displays might be more revealing.

E. Nonprimate Mammals

Jarman (1972) reported that more scars are found on the right side of the pelts of impalas than on the left side. These scars are most common in the neck and shoulder region and are most likely a reflection of lateralized intraspecies interactions than of interspecies attempts at predation. In fact, it is reasonable to assume that the injuries are inflicted during agonistic encounters in which the aggressor launches an attack to its left side.

F. Primates

Casperd and Dunbar (1996) found that gelada baboons (*Theropithecus gelada*) direct more agonistic responses toward conspecifics on their left side than on their right side. In other words, they were more likely to respond rapidly to direct aggression at a conspecific sighted in the left peripheral field of vision, indicating control by the Rhemi.

Here it is interesting to note the observation of Drews (1996) that pelts of wild savanna baboon, *Papio cynocephalus*, have more scars on the right side of the head region than on the left side. This is similar to Jarman’s earlier report of more scars on the right side of the pelts of impalas. In baboons also, the lateralized distribution of scars may result from intraspecies agonistic encounters and the bias is likely to reflect leftward-directed attacks by the aggressor.

The inhibition of emotions by the Lhemi is sometimes suggested in the case of humans (e.g., Nestor and Safer, 1990) and, therefore, impairment of the Lhemi’s inhibition results in the expression of more intense emotions (discussed earlier) and, sometimes, in aggression. Subjects with epileptic seizures focused in the left temporal lobe (and so causing impaired Lhemi
function) have been reported to express higher than average levels of hostile feelings (Devinsky et al., 1994). Also, reduced activity in posterior regions of the Lhemi has been associated with suicidal and aggressive behavior (Graae et al., 1996). These suggested associations between the activity of the Rhemi and aggression in humans are interesting in light of the data for other species showing the same association but they are made cautiously here. Considerably more research is needed to confirm these initial observations.

VI. Advantages and Disadvantages of Being Lateralized

The examples given earlier demonstrate that vertebrates share a common pattern of lateralization that is present in the central nervous system and frequently manifested as side biases in responding. These side biases in responding could be disadvantageous as, for example, in the case of an animal that tends to respond to prey on its right side but to ignore them on its left side. An animal that is more likely to attack an opponent on its left side but ignore one on its right side may also be at a disadvantage. In fact, the disadvantage of being lateralized at a population level seems most evident in the left-side bias of responding to predators. Animals that may be symmetrical in physical features have, for some reason, retained consistent lateralization of behavior, and this is the case for vertebrates from fish to humans, although some species may diverge from the rule at least in some forms of lateralization.

The persistence of lateralization across vertebrate species and, presumably, over time leads one to conclude that brain lateralization has advantages (Rogers, 2000) even in cases in which the animal has to adopt particular behavior patterns to counteract centrally controlled side biases. The kookaburra, for example, turns its head to position its LE for scanning directly below its perch. Nevertheless, toads, chicks, fish, and primates tested in semi-natural conditions display side biases that might be to their detriment unless additional benefits are conferred by having a lateralized brain. A number of potential advantages of being lateralized are discussed later, beginning with the hypothesis that differential specialization of the hemispheres enhances cognitive capacity.

A. Enhanced Cognitive Capacity and Efficiency

One way to increase a brain’s capacity to carry out simultaneous processing is to channel or filter the different types of input and/or output so that processing takes place in parallel in different regions of the brain (Deng and Rogers, 1998a). Neurophysiologists have concentrated on how this takes place in a vertical sense, from one level of brain organization to another,
but mostly they have ignored filtering that occurs laterally at the same levels of neural organization. Generally, it has been assumed that differential specialization of the hemispheres enhances neural and cognitive capacity (Dunaif-Hattis, 1984; Gazzaniga and Le Doux, 1978) but little evidence in support of this hypothesis has, so far, been provided.

There is an obvious way to conduct behavioral tests to assess the potential advantage of being lateralized at an individual level. This is to compare the performance of strongly lateralized individuals with that of weakly lateralized individuals. The chick presents itself as a model for such experimentation since it is possible to produce chicks that are weakly or strongly lateralized for attack, copulation, and feeding responses (see later), although they are still strongly lateralized for other responses in the visual as well as the other sensory modalities (Rogers, 1982, 1997; Rogers et al., 1998).

As mentioned earlier, chicks hatched from eggs exposed to light just prior to hatching are strongly lateralized for attack and feeding responses, but chicks hatched from eggs incubated in the dark are not lateralized for control of feeding responses and the specialization of their left lateral visual field for aggressive pecking is balanced by specialization of their right frontal field for aggressive pecking. Light exposure affects the development of lateralization because the embryo is turned in the egg so that it occludes its left eye, whereas light entering through the shell can stimulate the right eye (Rogers, 1990). The light stimulation enhances the development of visual pathways receiving input from the right eye and projecting to the forebrain (Rogers, 1996) and, as a consequence, the thalamofugal visual projections that cross the midline of the brain become asymmetrical (Rogers and Deng, 1999). There are more projections from the left side of the thalamus to the forebrain than from the right side to the forebrain (Fig. 2). Following incubation in the dark, no asymmetry develops in these visual projections (Rogers and Bolden, 1991), and, after hatching, the chicks show no lateralization of attack or feeding responses as revealed by treatment of the left or right hemisphere with glutamate (Rogers, 1990, 1997). However, dark-incubated chicks tested without treatment still direct more pecks at an unfamiliar conspecific in the left visual field compared to the right (Vallortigara et al., 2001). The data for feeding responses show clearly that, after incubation in the dark, there is no lateralization at either the group or the individual level (Rogers, 1997). Hence, dark-incubated chicks are less lateralized than light-incubated ones but the difference is a matter of degree, rather than being absolute, and it is limited to certain visual functions. Despite this qualification, it has still been fruitful to test the hypothesis relating lateralization to enhanced cognitive capacity by comparing dark-incubated and light-exposed chicks.

Dark-incubated chicks perform less successfully than light-incubated chicks in a task requiring dual attention to entirely different categories of stimuli (Rogers, 2000). The task tested the chick’s vigilance for a simulated
aerial predator while the chick was pecking at grain and mealworms on the floor. This placed demands on two known and opposite lateralizations of the chick. The first was the use of the RE (Lhemi) for pecking to feed, and the second was use of the LE (Rhemi) to monitor overhead for an aerial predator (Evans et al., 1993; discussed earlier). Thus, a chick feeding in a situation in which it might expect a predator to appear overhead is expected to use the Rhemi to monitor overhead and the Lhemi to control feeding pecks. Dark-incubated chicks might find this channeling of tasks to the separate hemispheres more difficult, or impossible, and be less efficient at detecting the overhead predator. The results indicated that this was, in fact, the case: When the predator approached from the chick’s left side, light-exposed chicks detected it sooner than did dark-incubated chicks (Rogers, 2000).

The chicks were tested in the second week posthatching and after several hours of food deprivation (Rogers, 2000). Once a chick had started to peck at grains and mealworms, a model predator, shaped to resemble a raptor, was passed overhead. The latency to detect the predator stimulus was scored, as indicated by the chick ceasing to peck and, usually, giving a startle trill and a twitch of the head. The light-exposed chicks detected the simulated predator after a very short latency when it advanced on their left side (LE) and with a significantly longer latency when it advanced on their right side (RE). This lateralization was expected. The dark-incubated chicks showed no such lateralization and their latency scores were between those of the LE and RE scores for the lateralized group of chicks. Their latency scores were both more variable and longer than those of the light-incubated chicks using their LE. Therefore, in the dark-incubated chicks, the Rhemi fails to show an advantage in detecting the stimulus. Controls showed that these results were due neither to differences in the motivation to feed in dark-incubated and light-exposed chicks nor to differences in fear responses to the simulated predator (Rogers, 2000). The results demonstrate enhanced vigilance in light-incubated chicks, and this could confer an advantage in the natural environment, even though it is limited to the LE only.

A somewhat similar result has been found for cats tested on a task requiring them to track a moving spot of light using one or the other forepaw. Fabre-Thorpe et al. (1993) compared the reaction times of cats with and without a preference to use one paw over the other when performing the task and found that those with lateralization of paw preference had a shorter reaction time to commence tracking than those without such lateralization. The enhanced ability of the lateralized cats appears to depend on channeling responses to one or the other forelimb and paw (and thus to control by one hemisphere). In this case, it is lateralization of motor output that enhances performance, rather than perceptual input as is the case with chicks.
In the cats, enhanced ability appears to be attained by specializing each paw to perform a different function, one for tracking the moving stimulus and the other for supporting and balancing the body. A similar result has been found in capuchin monkeys (*Cebus appella*); individuals with a greater degree of hand preference were found to solve a problem with shorter latency than individuals with a lesser degree of hand preference (Fragaszy and Mitchell, 1990). Another similar result has been found in wild chimpanzees foraging for termites. Both hands are used by chimpanzees in termite fishing, one to hold the twig used as a probe and the other to act as a stabilizer across which the twig covered in termites is rubbed when the chimpanzee eats them. Some individuals always use the same hand to probe and the other to stabilize the twig, whereas others vary which hand is used for either purpose. McGrew and Marchant (1999) studied the efficiency of termite fishing by the chimpanzees (*Pan troglodytes schweinfurthii*) at Gombe and found that completely lateralized chimpanzees gathered more prey for a given amount of effort than did incompletely lateralized chimpanzees.

A correlation between efficiency of response and degree of lateralization has been shown also in the pigeon. Güntürkün (2000) tested pigeons on a task requiring them to discriminate grain from grit, a task which they perform better with the RE than the LE when tested monocularly (Güntürkün and Kesch, 1987), as do chicks in similar situations. The researchers first determined the LE–RE difference in performance for each bird and used that as an index of their degree of lateralization. They then tested the birds binocularly to see whether there was an association between their efficiency on the task and the degree of lateralization. There was a significant correlation: The stronger the lateralization, the better the visually guided foraging. This result substantiates the preceding results for chicks. It is also worth noting that in pigeons, as in chicks, visual lateralization depends on exposure of the developing embryo to light (Güntürkün, 1993), although the light-dependent asymmetry in pigeons is located in the tectofugal visual system, whereas in chicks it is in the thalamofugal visual system (Güntürkün et al., 1998).

The positive association between degree of lateralization in the avian visual system and efficiency of predator detection and foraging deserves consideration in an ecological context, especially if it extends to other avian species. In the natural environment, eggs may receive varying amounts of exposure to light and, depending on the embryo’s stage of development at the time of receiving exposure to light, individual differences in both the degree of lateralization and efficiency of performance may develop. It is known for the chick that as little as 2 h of light-exposure is sufficient to establish lateralization but it must occur during a sensitive period during the last stages before hatching (Rogers, 1982, 1990; Zappia and Rogers, 1983).
Added to this, the level of steroid hormones in the embryo influences its sensitivity to the effects of light: High levels of the sex steroids decrease the effect of the light exposure (Rajendra and Rogers, 1993; Schwarz and Rogers, 1992) and so too do high levels of corticosterone (Deng and Rogers, 2001). The level of these hormones circulating in the embryo depends not only on their secretion by the embryo itself but also on the amount that the hen deposits in the egg before it is laid (Schwabl, 1997). In fact, the order of laying affects the amount of testosterone deposited in the egg, either increasing it or decreasing it depending on the species (Schwabl, 1993, 1996, 1998; Gil et al., 1999). In addition, stress of the hen may affect the amount of corticosterone so deposited. Therefore, there are individual differences in light-sensitivity during development of the embryo and subsequent differences in the degree of visual lateralization. If so, individual differences in predator detection and foraging efficiency may depend, at least to some extent, on early developmental processes. Of course, there are direct effects of the steroid hormones on behavior after hatching (e.g., competitive or aggressive behavior; Schwabl, 1993, 1996) but, in addition to the classical effects of steroid hormones on behavior, patterns of behavior associated with lateralization of the visual pathways, at least, may be affected.

The examples discussed in this section suggest that lateralization may be beneficial for an individual, although this may be context dependent. It is conceivable that not so strongly lateralized individuals may perform better than more lateralized ones in tasks with different cognitive demands. The advantages of lateralization discussed so far, however, operate at an individual level and are just as effective regardless of the direction in which the lateralization is present. They do not, therefore, provide an explanation for population lateralization.

### B. Population Lateralization: Advantage in Social Situations?

Population lateralization is likely to exist when there is a need to maintain coordination among individuals, that is, in a social context. In populations in which the majority, if not all, of the individuals are lateralized in the same direction, each individual could rely on the predictable lateralization of other members of the group and this could be used to a social advantage. For example, an individual might lower its chances of being attacked by approaching a higher ranking conspecific on that individual’s right side. Such behavior might be particularly important for avoiding aggression and maintaining the social hierarchy.

Rogers and Workman (1989) reported that, in the first 2 weeks of life, dark-incubated chicks form less stable hierarchies than do chicks exposed to light just before hatching. Six groups of eight chicks hatched from eggs
exposed to light during the final days before hatching (i.e., lateralized at a population level for the visual functions mentioned already) were compared to six groups of chicks incubated in the dark (i.e., not lateralized at a population level for those same visual functions). A rigid (or stable) hierarchy was maintained in the groups that had received exposure to light, as indicated by the fact that the lowest ranking chicks in these groups rarely gained access to the food dish. The lowest ranking chicks in the groups hatched from eggs incubated in the dark gained access to the food dish more often than did their light-exposed counterparts, and their entry scores varied more from day to day.

Another possible advantage of population lateralization might be maintaining cohesion of a flock, a shoal, or a herd. If all members of the group have the same bias to turn, say, to the right when they see a predator, the integrity of the group will be maintained during escape avoidance. There is evidence in support of this hypothesis.

Bisazza et al. (2000) have shown that schooling in fish is associated with a population bias to turn in one direction (either left or right) when faced by a barrier of vertical bars through which the fish could see a model that simulated a predator. Each fish was tested singly and it had to swim down a corridor toward the simulated predator placed behind the barrier. On reaching the barrier, the fish turned right or left and this was recorded. Each fish was given 10 such trials and from this score an index of lateralization was calculated. Next the social behavior of the species was determined in terms of tendency to school. Groups of fish were placed in a tank together and an index of their proximity to each other was determined. Six species were found to school and all six were lateralized for turning bias at the population level. Ten species were found to be nonschooling and six of these were not lateralized at the population level. The species not lateralized at a population level were, however, composed of individuals that were lateralized.

It seems possible, therefore, that a group bias for the majority of individuals to turn in the same direction may be maintained to advantage in those species that school. A population lateralization for turning would maintain the integrity of the school on contact with predators or other features of the environment that evoke a change in the direction of swimming. This would operate effectively provided that the school is moving in one direction or, say, facing upstream so that all of the individuals are aligned in the same direction. Once the school remains stationary with the individuals facing in different directions (e.g., when the school has been cornered), this mechanism would no longer be effective and a predator might exploit this to dissipate the school, a tactic used by yellowtail (Seriola lalandei) fish when they prey on schooling jack mackerel (Trachurus symmetricus) (Dugatkin, 1997).
C. LATERALIZATION AND IMMUNE RESPONSES

Immune responses differ according to whether they are under the control of the left or the right hemisphere. Mice with a lesion in the right parieto-occipital lobe of the neocortex show depressed mitogen-induced lymphocyte proliferation and enhanced antibody production, whereas mice with an equivalent lesion placed in the left parieto-occipital lobe show no modification of these immune responses (Barnéoud et al., 1987). Another study found that lesioning of the left neocortex depressed T-cell functions, whereas right side lesioning either enhanced T-cell functions or had no effect (Nevue, 1988). Also, individual differences in turning bias have been associated with different immune responses: Rats which circle to the left have higher indices of lymphocyte stimulation than those that circle to the right (Nevue, 1988).

Paw preference in mice is also associated with immune responses, almost certainly because it reflects preferential activation of one or the other hemisphere. Nevue et al. (1991) reported that left-pawed mice (determined for reaching into a tube to obtain food) have higher mitogen-induced T-lymphocyte proliferation than right-pawed mice. Ablation of the left cortex abolished the difference in T-cell function between left- and right-pawed mice whereas ablation of the right hemisphere had no effect on this difference.

In humans also, an association between hand preference and immune reactivity has been suggested, and there is some evidence, albeit not well-substantiated, indicating that left-handers have a higher incidence of immune disorders (Geschwind and Behan, 1982). Although these data for humans need confirmation in well-controlled conditions, which are difficult to achieve in studies of humans (Peters, 1995), considered together with the research on paw-preference and immune responses, the evidence makes a reasonably strong case for an association between hand preference and immune responses.

In my opinion, it is worth speculating that in some populations and some environments, there has been direct selection of a particular type of immune response, and that limb preference and other forms of lateralization are a secondary aspect of this. Some populations might have been exposed to conditions favoring the immune responses controlled by the left hemisphere and others to conditions favoring those of the right hemisphere. Such differing immune types would be associated with differences in hemispheric activity at a population level. Hence, it is possible that some types of lateralization, including handedness, may occur because they are associated with particular types of immune response.

The association between paw/hand preference and immune responsiveness in mammals has laid a strong basis for investigating similar associations...
between preferential limb use and the immune system in birds, amphibians, and even fish. Right-pawedness has been reported in laboratory studies of three species of toads (Bisazza et al., 1996, 1997b), and Litoria spp. exhibit side biases (Fig. 4). There may be a number of reasons for the population bias but selection for a particular type of immune response presents itself as a possibility worth investigating in these and other species.

VII. SUMMARY

A pattern of hemispheric specialization common to all vertebrates has been presented (summarized in Fig. 6). It has been considered, as far as possible, in terms of behavior patterns that are important in the natural environment. Responses in foraging and prey capture are typical specializations of the left hemisphere and they are often apparent as rightward-directed responses. Responses to novel stimuli and potential predators are specializations of the right hemisphere and responses to these stimuli are directed preferentially to the animal’s left side. The right hemisphere is also specialized for the expression of fear and aggression, and to process and memorize topographical information, essential in association with predator-escape responses. The baseline differences between the hemispheres are (1) rapid and

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<td></td>
<td>Fear responses</td>
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<td>Aggressive responses</td>
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<td>Spatial maps</td>
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Fig. 6. Summary of the general pattern of lateralization of the hemispheres.
species-typical responses being under the control of the right hemisphere and
(2) responses requiring considered decision making being under control of
the left hemisphere.

Side biases in responding to prey to the right side and agonistic responses
delivered to conspecifics on the left side occur not only in species with eyes
placed on the sides of their head and with only a small binocular field of
vision, but also in species with smaller lateral fields and with a large binocular
overlap. At least in one case, that of prey striking in toads, there is clear
evidence that the side bias occurs within the binocular field and manifests
itself as a hemifield neglect of prey to the left side of the toad’s midline. Chicks
also, provided they have been hatched from eggs incubated in the dark, have
a bias within the binocular field: They show a preference to fixate with the
right half of the binocular field before delivering an aggressive peck. It should
be noted, however, that the majority of aggressive pecks made by chicks are
delivered after use of the left, monocular field of vision in dark-incubated
chicks as well as those exposed to light before hatching. Lateralized use of
the visual hemifields deserves further investigation in a range of species.

Side biases in responding are not easily associated with any evolutionary
advantage but they may be balanced against other advantages of lateral-
ization. Lateralization may enhance cognitive abilities and more efficient
responding in some species and contexts. It may also be associated with spe-
cialized functioning of the immune system selected on the basis of past expe-
rience of the species in terms of physiological demand on the immune system,
although this hypothesis has yet to be tested. Finally, population bias for the
majority of individuals to be lateralized in the same direction is considered
as a potential benefit to group cohesion, as in schooling fish, and a mecha-
nism by which individuals can interact in predictable ways within a social
group. For example, the bias for directing attack responses leftward may be
used by an approaching animal to avoid an aggressive encounter; approach
on the potential aggressor’s right side would minimize the chances of attack.

Until now, most examples of lateralization have come from experimen-
tation in the laboratory or using captive animals. There are relatively few
examples demonstrating lateralization in wild populations, despite the ob-
vious implications of lateralization for survival of species and individuals.
Those lateralizations found in species in their natural habitat have been
mentioned. They highlight the promise of gaining a better understanding of
behavior of animals in the wild if lateralization is taken into account as a
characteristic of all vertebrates.

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LATERALIZATION IN VERTEBRATES

References


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Auditory Scene Analysis in Animal Communication

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I. INTRODUCTION

It is an early spring morning, and I have decided to take a walk in the woods. Many sounds surround me. I listen to my feet in the leaves on the path and, perhaps, to the sound of a wood thrush in a tree on one side and a blue jay in some scrub on the other. A farmer’s tractor in the distance breaks the silence. So does a car on a nearby road and a jet plane flying overhead. Even an everyday walk is a journey through a multitude of natural and man-made sounds that come from all directions. Yet somehow I am able to focus on these sounds and hear each of them as a unitary, coherent whole, as if they represented functional objects—auditory objects. And this happens effortlessly even though the sounds may frequently overlap each other in time.

Although my perception of all the auditory events on my walk seems completely natural and simplicity itself, it is truly a remarkable perceptual process that parses the surrounding world of sounds, the auditory scene, into functionally significant auditory objects. All the sounds identifying an object strike my sensory system through a single common pathway—my ears. Still, I somehow perceive the objects as distinct qualitatively and spatially. Furthermore, a spectrographic analysis of the mixture of sounds I hear would be remarkably complex, especially if two, three, or more sounds overlapped each other. Yet my auditory system accomplishes this auditory scene analysis with ease. How can this be so?

Albert Bregman (1990) published a major introduction to the problem of auditory scene analysis in human auditory perception in a seminal book published some years ago, and the field has become increasingly active since then (for more summaries, see Darwin and Carlyon, 1995, and Yost, 1997). Previously, however, there has been little or no work done with nonhuman species, despite the fact that any animal that depends on sound to get along...
in the world must certainly face the problem of auditory scene analysis. A short life awaits the animal that fails to detect the sound of a predator among other benign sounds that comprise the animal’s acoustic environment. That is not to say that the problem which scene analysis tries to solve has not been recognized by students of animal behavior. Early on, Busnel (1968) noted specifically that animal communication involves the detection of a signal in biologically significant background noise produced by a crowd of social animals and identified this with the “cocktail party” phenomenon (Cherry, 1953). The cocktail party phenomenon refers to the ease with which a person’s voice can be identified in the midst of a noisy gathering.

The remainder of this chapter examines auditory scene analysis in the context of nonhuman auditory perception. The next section explains very briefly some of the general perceptual processes that govern the formation of auditory objects and the parsing of the auditory scene. Following that, I discuss some work with songbirds from my own laboratory to introduce methods for studying auditory scene analysis in animals and to provide some basic evidence for the validity of the process in nonhuman species. Remaining sections review the animal literature for data, few though they may be, that suggest auditory scene analysis at work. Finally, I discuss briefly the directions in which future research with animals might go.

II. Auditory Scene Analysis

I have observed that the prevailing auditory scene is composed of one or more auditory objects, but what does that mean in more detail?

A. Auditory Objects and the Auditory Scene

According to Bregman (1990), auditory objects are coherent, organized auditory stimuli that come from a single source and signal a functional acoustic event. Function is a key concept here; auditory objects are sounds imbued with ecological significance. Although one could analyze acoustically the complex of sounds that strike my ear on a morning walk, albeit with some technical difficulty perhaps, the starting point of a scene analysis is not an acoustic analysis, but a functional analysis based on the source of the sound, its likely identity, whether it is approaching or receding, and so on. For example, the stream of acoustic events that comprise the auditory object of a “birdsong” are the sounds uttered by that particular wood thrush, in that particular tree, in that particular location. More generally, auditory objects as the listener experiences them are not merely complex acoustic spectra (which they may well be), but the separate sounds of footsteps in the forest, birds, tractors, autos, airplanes, and the unique quality of my voice as I speak.
That is not to say that auditory objects are not amenable to acoustic analysis. Indeed, an important challenge is to identify those acoustic features and processes that assure the creation of an auditory object and its perceptual segregation from the complete auditory scene. But such an acoustic analysis will never suffice completely. The ecological significance of auditory objects necessarily derives from processes other than a formal analysis of an acoustic waveform by the auditory system.

B. Auditory Objects, Grouping Principles, and Stream Segregation

An important characteristic of all stimuli is that they change in time. A bout of birdsong as an auditory object is not a momentary event, but a flow of acoustic information through time—an auditory stream. What is it about this flow that makes it cohere into a streaming auditory object that is unique and differentiable from other objects in the auditory scene? As Bregman (1981, 1990) suggests, the answer lies in the principles of Gestalt psychology. These include the principles of grouping (proximity, similarity, etc.), closure, and belongingness. They also include the principle of exclusive allocation, which refers to the fact that the perceptual system assigns a sensory event to the perception of just one object at a time.

Visual analogies help to demonstrate some of these principles at work. For example, the familiar reversible figure shown in Fig. 1 can be seen as either a vase or two human profiles facing each other, but the figure cannot be seen as both concurrently, a demonstration of the principle of exclusive allocation. An example in the auditory domain would be that a given blob of sound can be part of a birdsong or a tractor noise, but it cannot be part of both simultaneously. The perceptual system assigns the auditory event to one auditory object or the other, but not to both at the same time.

The principles of similarity and proximity are illustrated in Fig. 2. Visually, the filled and open figures at the top are each grouped together on the basis of their similarity; like objects tend to group with like objects. At the bottom, the same figures have also been separated by their proximity; the filled objects are closer to each other in space than they are to the open objects, and so filled and open objects each hang together even more cohesively.

Note, too, that the open and filled objects are interleaved, that is, open and filled objects alternate in time. However, interleaving fails to disturb the perceptual grouping afforded by similarity and proximity.

To bring the schemas of Fig. 2 into the auditory world, observe that the open and closed figures are plotted on coordinates of frequency (pitch) and time. At the bottom of the figure, it follows from grouping principles that the objects (tones) high in frequency should cluster together into two high groups of ascending “melodies,” whereas those low in frequency should cluster into two low groups of descending “melodies.” By the principle of
Fig. 1. A familiar “reversible figure.” The figure can be seen either as a black vase or as two white faces in profile, but not both at the same time.

Fig. 2. Examples of similarity and proximity at work. At the top of the figure black figures are grouped together visually by similarity into two descending sequences while open figures group into two ascending sequences. At the bottom of the figure, grouping principles based on proximity have been added to those of similarity. The segregation of black and white figures into ascending and descending sequences has been enhanced by the combination of the two grouping principles.
exclusive allocation, one ought to be able to attend to the high, ascending melodies or to the low, descending melodies, but not both at the same time. If the frequency separation between the high and low tones and the rate at which the successive tones occur are set appropriately, that is exactly what happens.

One might think that interleaved melodies might be heard in the sense that the objects comprising the melodies alternate in time—high–low–high–low…. In fact, at low repetition rates (and at appropriate frequency separations between high and low tones), a listener does hear the tones bouncing back and forth between high and low. But as repetition rates and frequency differences increase, the alternating tones segregate and “split” to be heard as two separate auditory objects streaming through time (Miller and Heise, 1950). In fact, functions can be obtained that relate frequency separation, repetition rate, and the likelihood that tone sequences will segregate perceptually into separate streams (Rose and Moore, 2000; Van Noorden, 1975). In discussing this phenomenon, Bregman notes that Gestalt principles of visual apparent motion can also be applied to such auditory motion, in particular, Körte’s third law (Bregman and Campbell, 1971).

In addition to pitch differences, grouping and stream segregation can occur on the basis of other acoustic dimensions. Timbre, or the spectral composition of a sound, is an especially important one (Culling and Darwin, 1993; Hartmann and Johnson, 1991; Singh and Bregman, 1997). Differences in spatial location is another, albeit one that—surprisingly—may serve most importantly as a vehicle for other auditory grouping cues (Arbogast and Kidd, 2000; Bregman, 1990).

The distinction between primitive segregation and schema-based segregation (Bregman, 1990) provides another important aspect of auditory scene analysis. The former refers to innate, unlearned capacities to segregate auditory objects in the natural world and, presumably, depends primarily on bottom-up auditory processes that have evolved in many animals over time—an idea that Gestalt psychologists stressed at the outset. Schema-based principles, on the other hand, are top-down and learned through individual experience. For example, the way we hear music or our spoken language may depend in part on unlearned organizational principles, but much of our ability to perceive music (e.g., to hear distinctly the sounds of one musical instrument from another) depends on learning the harmonic structure that defines the sound of the instrument in question. As we shall see, the themes of unlearned, bottom-up principles and learned, top-down principles will recur frequently in this review.

It is impossible in this chapter to explore the field of human auditory scene analysis in any great detail; for an elegant exposition, Bregman’s (1990) book is without comparison. In it you will find many further illustrations of the
parallels between perceptual organization in the visual and auditory worlds and a far more detailed discussion of the factors that enter into auditory scene analysis. McAdams and Bigand (1993) provide another useful general source which discusses principles of auditory scene analysis (as well as memory and some other functions) in auditory cognition.

Before we move on, we should reemphasize that Bregman develops the relevance of scene analysis for the flow of auditory information characteristic of the perception of both language and music. In fact, viewing language as a stream of coherent auditory information accounts for many important phenomena in language perception. And music composers discovered the principles of scene analysis and stream segregation many centuries ago. For example, such principles underlie the construction of melodic counterpoint, and as you listen you can partition the larger sound of a symphony orchestra into the sounds of its component instruments—the strings, the brass, the woodwinds, and so on. Given that birdsong and other forms of acoustic communication by animals are, similarly, flows of acoustic information in time, the application of the principles of auditory scene analysis to acoustic communication has obvious utility.

C. The Role of Time in Scene Analysis

It is worth emphasizing that the flow of acoustic events in time is a hallmark of auditory scene analysis. I have introduced auditory scene analysis in part by drawing upon some of the basic Gestalt organizing principles. Although it is possible to do this with visual examples by using static figure–ground relations (as in Fig. 1), it is never possible to illustrate the organizing principles in auditory scene analysis unless sounds are moving in time. To be sure, many visual examples of Gestalt principles rely on time and motion for their production, but with audition this is necessarily the case. A brief glimpse at a stable visual figure can generate grouping (e.g., as in the grouping of open and filled objects in Fig. 2), but a brief burst of sound will never allow the organizing principles of auditory scene analysis to take hold. Instead, sounds must move through time for their organization to occur. Indeed, although open and filled objects in Fig. 2 group together visually, the auditory stream segregation they are designed to illustrate will appear only if the objects (now conceived as tones) move through time.

D. The Role of Attention in Scene Analysis

There is yet another aspect of scene analysis that warrants discussion, and that is the role of attention in our perception of auditory objects, especially those that overlap in time.
The familiar “cocktail party” phenomenon provides an example. Cherry (1953) wondered how we can distinguish one speaker among a multitude of others in a crowded auditory scene such as a cocktail party. He proposed that the auditory system might do so by an appropriately chosen set of auditory filters, but today we also recognize the cocktail party phenomenon as a functional auditory scene analysis. One of the critical features of the phenomenon is that it involves the process of selective attention. I can easily attend to the voice of the person with whom I am speaking directly at the party, but if I try, I can also switch my attention to the voice of the person who is chatting with someone else behind me—even though in each case both speakers are talking simultaneously and the sounds of their voices strike my ears almost simultaneously. In either instance, the voice to which I am not attending recedes into the background—much as the two opposing faces in the reversible figure (see Fig. 1) recede into the background if one attends to the vase. Also, recall my spring walk in the woods. The process of listening to the jet plane or the thrush or the auto is an active, goal-driven process of focusing on one auditory object to the exclusion of others—which recede perceptually into the background of the overall auditory scene.

Once again it is far beyond the scope of this chapter to discuss the complex factors that govern the process of selective attention. Bregman (1990), Yost (1997), and Jones and Yee (1993) have discussed the problem in the context of auditory scene analysis, but most of the work on attention has been done in the visual domain: see Pashler (1998) and Yantis (2000) for summaries. Yantis (2000) makes the general claim that selective attention is both a top-down (learned and goal directed) and a bottom-up (stimulus driven) process, which fits the emphasis of an auditory scene analysis very well. In other words, as I single out objects from the auditory scene, my attention is actively driven (goal directed) toward some functionally significant sound in particular, but my attention is also drawn by stimulus features unique to the object, such as its loudness, spectral composition, and so on. These ideas parallel Bregman’s notions of primitive and schema-driven organizational principles.

It cannot be overemphasized that selective attention among a panoply of potential auditory objects is a hallmark of auditory scene analysis.

III. DEMONSTRATIONS OF AUDITORY SCENE ANALYSIS BY SONGBIRDS

With the foregoing brief introduction to the general process of auditory scene analysis in mind, let us turn now to some examples of experiments in which auditory scene analysis has been the focus of attention in nonhuman animals. Almost all the work has been done with songbirds, especially the European starling (Sturnus vulgaris)—although as we shall see Benney and
Braaten (2000) have extended the work to zebra finches (*Taenopygia guttata*) and Bengalese finches (*Lonchura striata* var. *domestica*).

Starlings are a semicolonial species of birds that gather and roost in large flocks during the winter months, then disperse to breed in the early spring. Both males and females are adept singers with complicated, multisyllable (multimotif) songs that may last for 40 s or more (Eens, 1997). Starlings also show an ability to mimic both natural and synthetic sounds which indicates that they perceive and respond to their auditory scene with some facility. The birds are also excellent for the operant studies of auditory perception and scene analysis to which I turn now.

Thus far, experiments aimed directly at auditory scene analysis in starlings have been addressed to three issues. First, can a starling identify one species' song when that song is mixed with a song from another species? Is starling song privileged in this regard, that is, are starlings especially sensitive to conspecific as contrasted with heterospecific song as an auditory object? Second, can a starling discriminate between the songs of two other starlings, thus showing individual identification, and can that discrimination be maintained when the songs of even more starlings are added to the background auditory scene? Third, is auditory scene analysis a general perceptual process for the starling? That is, can auditory object formation and stream segregation be achieved with synthetic, nonnatural stimuli?

**A. Segregating Two Simultaneous Bird Songs into Separate Auditory Objects**

The first demonstration of auditory scene analysis was obtained in an experiment in which my colleagues and I tested starlings for their ability to single out the birdsong of one species from that of another (Hulse *et al.*, 1997). Table I shoes the scheme of the study.

<table>
<thead>
<tr>
<th>N</th>
<th>Song pairs with starling song</th>
<th>Song pairs without starling song</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>Starling + brown thrasher</td>
<td>Nightingale + mockingbird</td>
</tr>
<tr>
<td>2</td>
<td>Starling + nightingale</td>
<td>Mockingbird + brown thrasher</td>
</tr>
<tr>
<td>2</td>
<td>Starling + mockingbird</td>
<td>Nightingale + brown thrasher</td>
</tr>
</tbody>
</table>

*Note: Five exemplars from each stimulus combination were used in the experiment. From Table 1 in Hulse *et al.* (1997). Copyright © 1997 by the American Psychological Association. Adapted with permission.*
Six starlings were trained in an operant conditioning task with food as a reward to discriminate superimposed 10-s mixtures of birdsongs which combined the song of one species with that of another. One category of songs (Category A) contained many exemplars of a simultaneous mixture of a starling song with a song from one of three other species, brown thrasher (*Toxostoma rufum*), nightingale (*Luscinia megarynchos*), or mockingbird (*Mimus polyglottos*). The other category of songs (Category B) contained many exemplars of a simultaneous mixture of a brown thrasher song, say, with a nightingale or a mockingbird song, but no starling song. The birds’ task was to peck one key in an operant conditioning chamber if they heard an exemplar from Category A played through the single loud speaker in the chamber, and a second key if they heard an exemplar from Category B. Correct responses were rewarded with food; incorrect responses turned the light out in the chamber for a few seconds and led to a correction trial.

Spectrograms of a representative sample of the stimuli appear in Fig. 3. A 10-s segment of starling song appears at the top of the figure, and a 10-s segment of nightingale song appears just below the starling sample. The third line contains a spectrogram of the starling and nightingale songs when they are combined. Finally, at the bottom of the figure, the starling and nightingale songs are mixed with a sample of the dawn chorus. (I will discuss this last condition shortly).

All starlings learned the discrimination between exemplars from Category A and exemplars from Category B to a criterion of at least 85% correct in 20–35 daily sessions each lasting about 2 h. On what basis might the discrimination between the two categories have been learned?

1. Stream Segregation

The most interesting possibility is that the starlings learned the discrimination by segregating the song of one species from that of the other in the pair, perhaps attending to the song of one species on some trials and the song of the other species on other trials. This would be an example of auditory scene analysis at work. One might also imagine that exemplars containing conspecific starling song would be especially salient to the starling subjects and therefore more easily segregated, but that was not the case—at least in the sense that song mixtures that contained starling song were not discriminated more accurately than those that did not.

2. Memorization

Another possibility is that the birds were merely memorizing acoustic features that were unique to each of the stimulus exemplars. The use of many exemplars from each of the categories was designed to minimize this possibility, but it exists nevertheless. To check for memorization, the birds were
transferred to a new discrimination in which some of the stimuli were novel exemplars from the same two categories in the initial baseline discrimination. If the test starlings were simply memorizing acoustic features, then the novel stimuli should lead to an immediate drop in discrimination performance because the features would be new and, therefore, unlearned. When the transfer was undertaken, the starlings immediately transferred their accurate discrimination performance to the novel song exemplars. Posttransfer performance with the novel exemplars was virtually identical (>85%
correct) to pretransfer performance with the original baseline exemplars. One might still argue that features of the novel exemplars were similar to those of the baseline exemplars, but the feasibility of that argument becomes increasingly unlikely. Remember that the features in question would arise from combinations of the two superimposed songs, and novel exemplars reduce the likelihood that such combinations would recur.

3. Tests with Songs from Each Species Heard Alone

As a further, perhaps most critical, assay for song segregation, the starlings were tested next with novel stimuli that consisted of single-species song exemplars for the four species songs that were used in the previous experiment. The novel exemplars were introduced as occasional probe trials, that is, single-species song exemplars from each of the four species were presented amid regular baseline trials incorporating the usual song-pair mixtures. Single-species probes occurred on 10% of the trials in a session. This test is especially telling because the starling subjects had never heard these stimuli in the experiment—neither individually nor as part of song mixtures. If the starlings were in fact selectively attending to and segregating the individual songs from the mixtures, then they should maintain accurate discrimination performance with the single-species songs. However, if their baseline performance was based on stimulus features or other acoustic factors unique to the song mixtures, their accuracy should fall. This should be especially so for nightingale song exemplars because this species is native to Europe and our starling subjects, trapped in the United States, had certainly never heard nightingale song before. Fig. 4 tells the story.

Clearly, the starlings maintained above-chance performance on the single-song probe stimuli. Although there was some (statistically reliable) overall decrease in percent correct relative to performance on the baseline mixtures during the same session, mean performance was still better than 70% correct for all species. Interestingly, performance on the novel starling songs was reliably better than that for any of the other three species, showing in this case that conspecific starling song was indeed a privileged stimulus relative to songs of the other species.

4. Song Segregation from the Dawn Chorus

In a final transfer in this experiment, the starlings were returned to the original baseline discrimination of song-pair mixtures and asked to maintain the discrimination when recordings of the dawn chorus were added to all the two-species song mixtures (see Fig. 3 for a spectrogram of a representative sample of this stimulus condition). This transfer was an attempt to add additional natural distracters to the auditory scene to press the starlings’ abilities
to maintain the baseline discrimination between song pairs. Although the results showed a decline in performance relative to baseline, discrimination accuracy was still roughly 80% correct in the presence of the dawn chorus—substantially and reliably above chance. Auditory object formation and song segregation are apparently quite robust, as indeed they ought to be in nature.

5. **Summary**

This initial work firmly establishes auditory scene analysis and song segregation as principles that are at work in the natural world of songbirds. Starlings were able to single out the songs of single species from a variety of auditory mixtures including the song of a second species and an auditory mélange as complex as the dawn chorus.

**B. Individual Recognition and Auditory Scene Analysis**

A second series of experiments examined the ability of starlings to correctly identify and classify the songs of two other conspecifics and to maintain
that identification and classification in the face of an increasing number of conspecific distracters (Wisniewsky and Hulse, 1997).

The general procedures were virtually identical to those of the work described above for mixed-song pairs. Test starlings were first trained to discriminate ten 10-s song segments from Starling A from ten 10-s song segments from Starling B using food as a reward for correct responses on the corresponding keys in the operant chambers. The song segments were sampled randomly from longer complete songs. Training began with discrimination between one song segment from Starling A and one from Starling B, and when that pair was mastered to a criterion of 85% correct, a second pair was added, then a third, and so on. Of course, unlike the mixed-pair stimuli in the first series of experiments, just one song-segment exemplar was presented by itself on any given trial. Training was very rapid. When the 10th pair of song segments was added (and the starlings were now classifying 20 song segments), that final pair was mastered in less than 20 trials. In fact, the rapid classification of the A and B song segments into two classes suggests that the starlings learned to treat the song segments as separate higher order stimulus categories. That is, the test starlings had abstracted some general characteristics of the song segments from Starling A as compared with Starling B and learned to distinguish the songs of the two individuals on that general basis. Subsequent tests established that fact more firmly (see the original article by Wisniewsky and Hulse, 1997, for details).

1. Individual Recognition with an Added Distracter

Given the initial discrimination between the songs of Starling A and those of Starling B, a transfer test began in which a set of 10-s segments of song from Starling C, identical in length and loudness to those of Starlings A and B, were mixed (overlapped) by computer with both the original Starling A and Starling B song stimuli. Note that Starling C songs were not valid discriminative stimuli because they were common to both A and B stimuli. However, the C songs did serve as distracters because the test starlings had to selectively attend and segregate the relevant A and B songs from the irrelevant C songs to maintain the A versus B discrimination.

Figure 5 displays the results of this experiment. The addition of distracter C songs in the transfer test reduced discrimination accuracy initially by about 20%, but overall accuracy was still substantially (and reliably) above chance. The starlings also showed improvement as transfer sessions progressed.

2. Individual Recognition with Four Added Distracters

To press the starlings to some kind of limit, a final transfer required them to maintain the discrimination between the songs of Starling A and those of Starling B when distracter songs from four starlings—Starlings C, D, E, and F—were combined with both the A and B songs. To human ears, the
blend of four distracters with the songs of Starling A or Starling B creates a cacophony from which it is utterly impossible (for me and colleagues in the lab, at any rate) to identify either the target A or B songs—even after some practice listening to the target songs.

Not so for starlings. Although four distracters reduced discrimination accuracy for the Song A and Song B stimuli to 60–65% correct, performance remained reliably above chance (Fig. 5). This is strong testament to the species’ capacity for auditory scene analysis and object formation.

Lest too much credit be given to starlings’ ability to identify individuals in the midst of conspecific song, think of the analogous situation of the crowded cocktail party. In all likelihood, people would have little trouble identifying the voices of two familiar friends despite a substantial number of other distracting voices in the background. As far as I know, the limits on human capacity in this regard have not been determined. Neither has the capacity for starlings to identify two human voices in the midst of many human distracters.
But there can be little doubt that familiarity with target and distracter stimuli must have a substantial effect on the capacity to segregate auditory objects from noisy environments.

3. Summary

In this section I have broadened our demonstration of starlings’ accomplishments as auditory scene analyzers to include, first, the discrimination of the songs of two target starlings, and second, the maintenance of that discrimination when sets of conspecific songs from as many as four other starlings are added to the stimulus complex as distracters. As Wisniewsky and Hulse (1997) point out the first fact suggests that starlings can form abstract categories for the songs of individual conspecifics, an interesting observation in its own right (for which further discussion would take us beyond the scope of this chapter). Given that starlings are a semicolonial species that roost in large groups in the winter, it is perhaps not surprising that they are also accomplished at identifying the song of other individuals in the complex auditory scene created by the flock.

C. Scene Analysis in Zebra Finches and Bengalese Finches

Some of the observations just described for starlings have been replicated with two Estrildid finches, the zebra finch and the Bengalese finch. Benney and Braaten (2000), in an elegant experiment, used operant techniques similar to those just described for starlings to see if one finch species, say zebra finches, could hear examples of their own song when those examples were mixed with songs from two other species, a Bengalese finch and one of four unrelated species, brown thrasher (Toxostoma rufum), northern cardinal (Cardinalis cardinalis), American robin (Turdus migratorius), or song sparrow (Melospiza melodia). The operant task was a Go–NoGo task in which responses to one stimulus type were rewarded, while those to an alternative stimulus type were not. The discrimination emerged over trials as rapid responding appeared for the rewarded stimuli and slow (or no) responding appeared for the unrewarded stimulus type.

The results showed, first of all, that both zebra finches and Bengalese finches were quite adept at attending to and discriminating the target song when it was combined with two other songs. That is, the birds successfully singled out the critical song stimulus from the larger auditory scene and responded accurately to it. The results also showed that, if both finch species were trained to detect conspecific song as a rewarded target in the three-song mixture, learning proceeded faster than if the finches were trained to detect heterospecific song as a rewarded target. That is, there was a significant bias among the birds for rapid learning based on conspecific song targets in the
mixtures. Further analysis of the zebra finches and Bengalese finches taken separately showed that the zebra finches were especially sensitive in this regard. Zebra finches trained to detect zebra finch song as compared with Bengalese finch song as the target were much faster to learn the discrimination. However, for Bengalese finches, learning proceeded at about the same pace regardless of whether or not the target song was a Bengalese finch or a zebra finch. These results not only generalize the results regarding auditory scene analysis with starlings to two other songbird species, but also add to data which show that conspecific song is a privileged stimulus within the auditory scene.

D. **Auditory Scene Analysis and Stream Segregation as General Perceptual Processes**

Now that I have shown that several songbird species can perform auditory scene analyses for a naturally relevant stimulus like birdsong, I can now go a step further and ask if scene analysis is a process that can be used for sounds in general. In other words, would songbirds demonstrate auditory object formation and stream segregation for synthetic sounds that are not part of their natural environment? If so, that would suggest the songbird brain has some general mechanism for scene analysis that is independent of any avian-specific auditory stimulus.

To this end, my students and I (MacDougall-Shackleton et al., 1998) studied the effect of pitch separation on auditory stream segregation (Bregman and Campbell, 1971; Rose and Moore, 2000; Van Noorden, 1975). We trained starlings initially to discriminate sequences of sine (pure) tones that varied in their temporal structure. The scheme of the experiment appears in Fig. 6.

Each object in the figure represents a time–amplitude plot of a sine tone of one frequency (e.g., 1000 Hz) that is 100 ms in duration. The objects are organized into one of three stimuli used in baseline training: a “galloping” sequence (so-called because the temporal spacing makes the sequence sound like the hoof beats of a horse, especially at quicker tempos), and two isochronous sequences in which the 1000-Hz objects are spaced at equal temporal intervals, but the interval length differs between the two sequences. Starlings were taught in baseline to peck one key when they heard the galloping sequence and another key when they heard either of the two isochronous sequences. The birds were first trained with sine-tone stimuli of one frequency, say 1000 Hz, then trained in later sessions with frequencies of 1050, 1710, and 4538 Hz. Within any training session, however, the stimuli were all of just one frequency.

After the starlings were responding to baseline stimuli to a criterion of 85% correct within daily training sessions, *probe stimuli* were introduced on
Fig. 6. Scheme of the test for generalized stream segregation in starlings. Birds were trained to discriminate the “galloping” pattern from either of the two “isochronous” patterns. Then they were tested with an interleaved pattern (bottom) in which a galloping structure was used, but tones were separated by two different pitches. If stream segregation occurs the probe stimuli should be heard as one or the other of the isochronous patterns and should be so classified by the birds. (Based on Figure 1 from MacDougall-Shackleton et al., 1998.)

10–20% of the trials in a session. The probe stimuli, schematized at the bottom of Fig. 6, had the temporal structure of the galloping baseline stimulus. However, the frequency of sine tones changed within the stimulus sequence (denoted by the upward displacement of some of the tone-objects in the figure). The more frequently occurring frequency was 1000 Hz, but on a random one-third of the probe trials, the displaced frequency was either 1050, 1710, or 4538 Hz (the same frequencies with which the starlings had been accustomed in different segments of baseline training). This created frequency separations of 50 (near threshold for starlings), 710, and 3538 Hz.

If the starlings were able to segregate the probe sequences on the basis of pitch differences, they would peck the key correlated with isochronous sequences because the low-pitched sequence (correlated with 1000-Hz tones) had a temporal structure identical to the Isochronous 1 sequence in baseline training (see Fig. 6), and the high-pitched sequence (correlated with higher frequency tones) had a temporal structure equivalent to the Isochronous 2 sequence in baseline training. If, however, stream segregation failed to
Fig. 7. Results of the test for generalized stream segregation. The left two pairs of bars show discrimination performance between galloping and isochronous patterns during initial training and during the test sessions when probes were introduced. The bars at the right show the probability that the birds classified the probes as isochronous. The tendency to do so increases with the frequency separation among tones in the galloping probe patterns. Error bars are standard errors. (Figure 3 from MacDougall-Shackleton et al., 1998.)

occur on the basis of pitch differences, then the birds should peck the key correlated with the galloping sequence because the probe sequences had the galloping temporal structure of baseline stimuli. Figure 7 shows the results.

The bars on the left of the figure show a high probability of pecking the key correlated with isochronous sequences when isochronous sequences occurred during initial baseline training and on trials with baseline stimuli during sessions that included probe trials, and they show a corresponding low probability of pecking the isochronous key when galloping sequences occurred. The bars on the right of the figure show a low probability of pecking the key correlated with isochronous stimuli when the frequency difference
on probe trials was just 50 Hz. However, the probability of an isochronous-key response increases sharply as the frequency difference increases to 710 and 3538 Hz. Clearly, as humans do in comparable situations (Van Noorden, 1975), the starlings segregated the galloping probe sequences into two isochronous auditory streams on the basis of pitch differences among the tones in the sequences.

1. Summary

The foregoing results establish that stream segregation with synthetic stimuli occurs in at least one species of songbird. There is every reason to believe that such segregation would be found in other species as well. Apparently, stream segregation (based on pitch differences, at any rate) is a general process that does not depend in some fashion on avian-specific auditory stimuli.

E. Overview

To this point, I have shown that starlings (a) can identify a target song when it is mixed with the songs of conspecifics and other species, (b) can do so even when the target song is from an unfamiliar species (e.g., nightingales; though there is a distinct bias favoring a conspecific target song), and (c) can maintain starling target song identification when distracting songs are added from several additional conspecifics. We also know that scene analysis is not limited to the perception of birdsong—starlings were able to segregate streams of synthetic sounds (sine tones) when the streams differed in pitch. Moreover, data (Benney and Braaten, 2000) show that many of these observations are not limited to starlings, but generalize to Estrildid finches.

It is worth noting that there is at least a functional parallel between segments of overlapping birdsong and sequences of synthetic sine tones. Both are acoustic events moving in time, and both offer an opportunity for the formation of segregated auditory streams. Overlapping songs, say, from two or more individuals, differ from moment to moment in pitch, spectral structure (timbre), and loudness. Any one or a combination of these acoustic cues could be used to afford the perceptual segregation of the aggregated sound into separate auditory streams—the voices of individual conspecifics in this case. Although we have focused on pitch as a cue to produce segregation of synthetic auditory streams, work with human observers has shown that people can also segregate on the basis of synthesized spectral structure (Iverson, 1995; Vliegen et al., 1999) and loudness changes (Bregman and Dannenbring, 1977), among other possible cues. Without doubt, further use of human perception as a heuristic tool for work with nonhuman animals would be worthwhile.
IV. Further Possibilities for Research on Auditory Scene Analysis in Nonhuman Animals

Because so little work has been done directly on auditory scene analysis in nonhuman animals, very little literature bears directly on the problem. There are many studies that have been done on acoustic interactions (especially among conspecifics) that would lend themselves nicely to auditory scene analysis, however, and in this section I want to draw attention to a few of them. It is not my purpose to review this literature in detail. Instead, I wish merely to suggest possibilities for future research if a scene analytic approach were to be adopted.

Scene analysis arises only when there are mélange of sound from which a functionally significant acoustic signal must be perceptually isolated. At first glance, this suggests the signal-in-noise problem of classical auditory psychophysics, and there are, of course, a plethora of studies on both humans and nonhuman animals examining an observer’s capacity for identifying an acoustic signal in noise—especially white noise. However, although examinations of signals in white noise are useful for establishing basic auditory functions such as critical ratios, for example, auditory signals in the psychophysical laboratory rarely have functional significance, and white noise rarely occurs in nature.

A. What Is Natural Noise?

So, then, what characterizes “natural” noise? For the purposes of scene analysis it is useful to identify three classes of noise that occur in nature. The classification is quite arbitrary in the sense, for example, that a given acoustic event, such as a birdsong, can be a signal on one occasion and part of a noisy environment (the sound of a flock) on another. Remember that the function of a sound is an essential part of auditory scene analysis, and this holds true for identifying classes of noise in the auditory scene.

1. Chorusing among Conspecifics

The acoustic chatter, or chorus, generated by individuals of the same species interacting simultaneously in groups provides one class of natural noise. The cacophony produced by large flocks of birds, such as European starlings in a winter roost, is a case in point in the avian world. The chorus of amphibians such as frogs in the neighborhood of a mating resource such as a breeding pond is another. In each instance, from the vantage point of a single perceiver in the group, the complex auditory scene must be analyzed to identify the output from a single significant sender, such as a potential breeding mate or territorial competitor. But in all cases, functionally significant interactions arise through acoustic interactions among members of the same
species, and the task of the perceiver is to identify important signals in the midst of a simultaneous mixture of signals with which the perceiver is highly familiar and highly engaged.

2. *Heterospecific Noise*

   Potentially, sounds from other species within the same taxonomic group provide a functionally significant background from which important signals might have to be perceptually isolated. In the case of songbirds, the dawn chorus is a case in point. Certainly, the dawn chorus constitutes a natural noise from which conspecifics must isolate sounds that are functionally relevant for purposes of mating and territorial defense. To my knowledge, however, we know relatively little about the extent to which a given individual attends to the sounds of heterospecific species in that chorus. Of course the sounds of any potential predators (birds or otherwise) that might occur along with the dawn chorus is an interesting special case in its own right.

3. *Other Environmental Sounds*

   Finally, there are sounds, possibly distinct from the foregoing, that occur in nature but which have no clear functional significance for the listener. The farmer’s tractor in his field, the airplane flying overhead, or the wind in the trees are probably of little import for the songbird singing in the hedgerow nearby, and to that end, and at any given moment, they would appear to have little significance for a functional auditory scene analysis. Instead, they merely add to the general environmental noise in which all animals live. That is not to say that such noise has no consequences; clearly it has masking effects in the psychoacoustic sense on all the sounds an animal hears. And, of course, something may happen within the general acoustic background that suddenly creates a functionally significant auditory object—the cry of a hawk overhead, for example.

4. *Selective Attention—Again*

   At this point a reminder about the importance of selective attention in auditory scene analysis seems in order. The process of identifying important auditory objects in noise—no matter what the nature of the noise may be—includes the process of selective attention. Whether that process is bottom-up, depending on low-level identification of stimulus features, or top-down, depending on some goal-driven process, auditory scene analysis implies a search of the auditory scene for functionally significant signals.

B. SCENE ANALYSIS UNDER THE SEA

   Because sound travels so well under water, life under the surface of the sea occurs in an environment that is even noisier than the environment
on land. Granted that the underwater world is different acoustically (e.g.,
the speed of sound in water is about five times greater than the speed in
air), all the same necessities for auditory scene analysis exist nevertheless.
Underwater creatures must presumably sort their auditory world into the
functionally significant sounds that mark their own species, that identify
potential predators, and so on.

1. Fish

Fay (1998, 2000), using classical conditioning techniques, has undertaken
a psychophysical analysis of the goldfish’s (*Carassius auratus*) capacity for
stream segregation of two pulse trains with different repetition rates (19 and
85 pps) and spectral envelopes (centered at 238 and 625 Hz, respectively). In
one experiment (Fay, 1998), the fish were trained initially with simultaneous
mixtures of the two sound types and then tested for stimulus generalization
for pulse rate at each of the two spectral envelopes separately. The data
showed that generalization was greatest as the pulse rates approached those
associated with the particular spectrum used in initial training. This indicates
that the fish had learned initially to perceptually segregate the two pulse
streams on the basis of their spectral composition. Fay also found that if
one stream began 500 ms before the other (onset asynchrony), it facilitated
stream segregation—just as it does in humans. In a later experiment, Fay
(2000) extended these results to show that if sounds of different spectra were
interleaved, then stream segregation was a function of the center frequency
differences between the interleaved sounds. Again, this replicates similar
results with humans (e.g., Miller and Heise, 1950; Van Noorden, 1975).

2. Underwater Mammals

It is far beyond the scope of this chapter to review the vast amount of
auditory research that has been undertaken with marine mammals—from
whales to dolphins (especially the humpbacked whale, *Megaptera novaeangi-
lae*, and the bottlenose dolphin, *Tursiops truncatus*). Tyack (1998) has pro-
vided an elegant review of this fascinating world. He describes, for example,
the sound interactions between humpbacked whales as they sing extremely
long songs when by themselves—which may be advertisement displays to
attract females—and shorter social sounds, which occur when males fight in
groups. Songs are also used for individual recognition among whales, and
dolphins, too, have their individual acoustic signatures.

I am unaware, however, of any research on underwater communication
from a scene analytic point of view. That is true despite the fact that
the sounds of underwater creatures are extremely varied and often very
loud. Furthermore—given the transmission characteristics of sound in
water—sounds disperse rapidly over very long distances. This must make the underwater auditory scene immensely more complicated—at least potentially—than that above the sea. I believe underwater communication systems may be especially fruitful scenarios for studies of stream segregation and auditory grouping. Perhaps, for example, the long, loud, individually distinctive songs of humpback whales have evolved in part because they are especially easy signals for a listener to segregate from the surrounding acoustic clutter. Interesting questions abound.

C. Scene Analysis in Anurans

In this section I want to touch very briefly on a few of the data obtained from anurans that speak to the process of auditory scene analysis. A very large body of research exists with anurans, especially frogs, and my review will seek merely to draw attention to the data from this new perspective. Among all research with nonhuman animals, the work on frogs probably constitutes the best example of an attempt to understand conspecific interactions in terms of scene analysis—without actually using that term. Essentially, the research has been aimed at understanding how frogs detect important signals such as advertisement calls and other mating signals in the midst of a complicated chorus of conspecifics and other environmental sounds.

Frogs have evolved to use just about all possible spectral, loudness, and temporal features of an acoustic signal to communicate with one another. As a general strategy they seek “spaces” in the acoustic characteristics of a chorus in which to place their own species-typical acoustic signals. These include nonoverlapping spectral frequencies, temporal adjustments in call rates (e.g., which can be exquisitely fine-tuned to avoid overlap with other individuals), and, of course, adjustments in call amplitude. Narins and his co-workers (e.g., Brush and Narins, 1989; Narins and Zelick, 1988) have recognized that the problem is one of detecting a signal in functional noise. A great many other researchers have identified in great detail the acoustic features to which anurans are sensitive in detecting, discriminating, and interacting with conspecifics, although their focus is only infrequently based on the environmental noise problem (e.g., a brief list includes Gerhardt, 1988, 1989, 1991; Gerhardt and Klump, 1988; Klump and Gerhardt, 1992; Littlejohn, 1969; Ryan, 1988; Simmons et al., 1992; Wells, 1988; Wilczynski et al., 1995; Xu et al., 1994).

The interesting characteristic of all this work is that it has essentially mapped out the correlates of auditory streaming for the frog communication system. For example, by making advertisement calls with highly specific spectral characteristics (relative to the chorus in which the call occurs), the male...
frog has evolved to assure that his call will segregate as a streaming auditory object from the larger environmental surround. Add temporal structure and interactive timing to the spectral structure, and streaming is greatly enhanced. Frogs even have a system in the inferior colliculus that represents the direction of a sound at the single-neuron level (Xu et al., 1994), and the direction from which a sound comes is a relevant feature for stream segregation. It remains to be seen if the specific application of a scene analysis approach to this work will add new information to what we know about the anuran communication system in general, but the approach certainly suggests that much more attention should be paid to the characteristics of auditory streams in segregating significant auditory objects from a frog chorus.

I have stressed the importance of selective attention in scene analysis, and this raises the interesting question of whether or not anurans are capable of selectively attending to auditory objects in their environment. Given the probable capacity limitations of the anuran central nervous system, it is doubtful that selective attention occurs as a top-down process in which the listener actively searches in a goal-driven way for important environmental auditory objects. The information suggests, instead, that selective attention—if it occurs at all—must be a bottom-up activity that has evolved to filter highly specific information at low levels in the nervous system. Early work by Capranica (e.g., Capranica, 1966; Rose and Capranica, 1983, 1985) describes activity in the frog peripheral nervous system that would have to serve for that analysis. For the future, anuran auditory perception could serve as an ideal model for studying bottom-up processes in scene analysis and vertebrate hearing.

D. SCENE ANALYSIS IN BIRDS

Oddly enough, apart from the work discussed earlier, studies that would fit the scheme of auditory scene analysis are much less common among avian species than among anurans. There has been emphasis on dyadic interactions through playback studies and so on that have examined territorial and mating strategies based on one-on-one interactions between individual birds or between a bird and song playback from an audio speaker. And Marler (1959) identified the potential significance of “background noise” in animal communication. There are interesting data that can be interpreted from a scene analytic viewpoint, however, and we turn to a brief survey of some of them now.

1. The Dawn Chorus

Just as frogs chorus around a mating pool, songbirds chorus in their natural habitat, chiefly at dawn. The dawn chorus fosters mating behavior and territorial defense, signalers advertise their sexual attractiveness and defend
their territories, and perceivers react accordingly. The properties of the dawn chorus and its function have attracted a relatively small measure of research attention. The dawn chorus is, of course, a mixture of conspecific and heterospecific noise, and offers an extraordinarily complex environment for scene analysis. Henwood and Fabrick (1979), for example, did a quantitative analysis of the acoustic properties of the dawn chorus, especially from the point of view of sound transmission. They concluded that the chorus may have evolved to occur at dawn because atmospheric conditions are most conducive to sound transmissions over long distances at that time of day. Staicer, Spector, and Horn (1996) provide a detailed discussion of why singing may occur at dawn from an ecological and functional perspective. To my knowledge, however, only Hulse et al. (1997) have studied the ability of a songbird, the European starling, to detect specific birdsong signals in the midst of the dawn chorus, and that work was done in a laboratory setting not in the field. Clearly, the ability of listeners to segregate significant auditory streams in the dawn chorus and the conditions which foster that segregation deserve more attention than they have received. The extent to which evolution has encouraged the use of easily segregated acoustic channels for communication in the background of the dawn chorus must be as important in songbirds as it is in the chorusing of frogs.

2. Flocking Birds and Colonial Species

If the dawn chorus provides an example of multiple species creating an auditory scene, a related example occurs when conspecifics interact vocally in flocks or groups. Anyone who has heard a winter roost of European starlings, for example, knows that information is presumably being exchanged among individuals in the midst of a true cacophony of conspecific song. Again, some, but not much, work has been done to study how individuals distinguish themselves in such a situation or what information can, in fact, be transmitted and perceived. Wiley (1976) studied communication among a colony of grackles (Quiscalus quiscula). He found that wide-spectrum sounds were characteristic of the species and noted that they would be especially useful for individual identification at close quarters. He even mentioned the cocktail party effect and the solutions it affords for communication among individuals at close range. As with anurans, this work fits the scene analysis model because frequency spectrum is a very potent variable for stream segregation (Bregman and Pinker, 1978; Darwin and Carlyon, 1995).

Another example comes from Beecher’s work with cliff swallows (Beecher et al., 1986, 1989). Here, parents easily identify the signature call of their own chicks, and this takes place among large colonies of breeding birds. The evolutionary benefits of segregating the calls of one’s own chicks from the auditory scene in which many chicks are begging are clearly obvious.
Auditory scene analysis suggests cues that ought to facilitate such segregation, for example, spectral cues and amplitude modulation. Temporal effects such as call repetition and the spacing of calls with respect to other chicks might be especially promising cues to examine for further information, given the importance of a flow of acoustic information in scene analysis.

Finally, there is evidence for a cocktail party effect in colonial king penguins (Aubin and Jouventin, 1998). Penguin chicks can identify the calls of their parents at sound levels which are less than the general sound level of the background colony noise. This ability has obvious adaptive significance.

3. Environmental Noise

In the larger auditory scene provided by multitudes of mixed natural sounds, some research has focused on the abilities of perceivers to detect important signals in that environment. Part of the work has dealt primarily with the acoustic filters provided by the environment that modulate the transmission of functional signals (e.g., Dabelsteen et al., 1993; Holland et al., 1998; Wiley and Richards, 1982). This research has often emphasized the degradation of signals as a ranging cue and the establishment of the distances in various environments over which functional signals can be transmitted and identified. Other research has adopted a more psychophysical model to determine thresholds and critical ratios for the detection of auditory objects (e.g., birdsong) in background noises, including white noise (for a review see, e.g., Klump, 1996; see Langemann et al., 1998, for a specific application to the great tit, Parus major). Klump makes the point that estimates of masked thresholds, rather than absolute thresholds, are important for estimating the properties of functional signals in a larger, noisy environment. I would simply add that we need to know more about the aspects of masking that facilitate (or hinder) the identification of auditory objects in the larger, noisy environment. It is possible, for example, that stream segregation and the cues that facilitate it will work to overcome the general effects of masking that are reflected in critical ratios based on signal detection in noise. Klump has spoken to this issue, and we shall return to it in due course.

4. Song Timing and Communication Networks

There is another aspect of birdsong structure that may be especially interesting from a scene analytic point of view. I refer to duetting, song overlapping, and other scenarios where two or more birds are engaged in acoustic interaction. There is evidence, for example, that the timing of an overlap (onset asynchrony) in the song of two interacting conspecifics can indicate the intended receiver and escalate behavioral arousal (e.g., Dabelsteen et al., 1997; Hultsch and Todt, 1982; Naguib, 1999; Naguib and Todt, 1997; for an especially good review, see Todt and Naguib, 2000). From a scene analytic
point of view, this may be because an auditory stream that leads in time compared to another auditory stream will capture attention first (Bregman, 1990). Especially interesting is the fact that nightingales who are merely listening to a dyadic interaction between two other nightingales also respond to such timing effects (Naguib and Todt, 1997). Similar effects in duetting may occur where the timing of the interaction between the duetting individuals may facilitate segregation of the duet from the larger auditory scene (Todt and Naguib, 2000).

There is another possible form of interaction among conspecifics that, if true, may involve scene analysis in an especially interesting way. I refer to the form of acoustic interaction that occurs potentially between conspecifics interacting in networks that are larger than simple dyads (for example, Dabelsteen, 1992; McGregor, 1993; McGregor and Dabelsteen, 1996; Todt and Naguib, 2000). The idea that conspecifics may "eavesdrop" on an ongoing acoustic interaction and gain useful information that way is an interesting possibility that comes from this work. Birds might assess the fitness of a conspecific by listening to the bird's interaction with some third bird, for example. Also, networks of signalers might be involved in the spread of alarm calls. In each case, any auditory cue that can specify individuals and their location in the network is especially important, and scene analysis suggests where to look for relevant processes. In particular, the timing of interactions in networks and the function of timing in segregating the auditory objects represented by the sound of each interacting participant ought to be especially important. That would also be true for any eavesdropper listening in on the auditory scene. There is evidence that onset asynchrony facilitates the salience of an auditory object in perception. In particular, sounds that lead others in time tend to dominate in perception (e.g., Darwin and Ciocca, 1992; Grafe, 1996).

E. SCENE ANALYSIS IN PRIMATES

Virtually all primates use auditory means for communication, especially for social communication in groups. By the same token, primates live in the same noisy environments that other animals do, environments that for some species of primates become noisier all the time. (As I write this, there is a large construction machine operating not 6 ft outside my window—an unwelcome object in my auditory scene.) Apart from the current interest in human auditory scene analysis, however, there is little, if any, comparable work that I am aware of that has been done with nonhuman primates.

That is not to say, of course, that systems of auditory communication among nonhuman primates have not received their due share of attention. There have been many studies, in numbers too far beyond the scope of
this chapter to mention, dealing with vocal interactions for many species of nonhuman primates. These studies range from analyses of the acoustic features of vocalizations that are used for communication to studies of the interactions that in fact take place within and between social groups. Hauser (1996) has provided an elegant summary and discussion of this work, and the reader is encouraged to turn to that resource for further information. But despite this plethora of information, the fact remains that there is virtually no work on auditory scene analysis in nonhuman primates designed with that particular process in mind. Snowdon (personal communication, 2001) has observed that only a few species of primates produce highly elaborate calls similar to song in birds (titi monkeys, gibbons, possibly long calls of marmosets and tamarins): such species are rarely found sympatrically and, when they are found together, may be likely to call at different times of day or in different strata. In this case, it may be that evolution has solved the scene analysis problem by assuring that the relevant communication signals rarely interfere with one another. Still, one must be on the lookout for scene analysis at work—if frequency differences between simultaneous calls are used by primates in the same habitat, that would be a clear example of stream segregation and auditory scene analysis. Sometimes scene analysis is so obvious it is overlooked.

In any case, further work with primates should be useful. Research with humans provides a general heuristic tool to guide research, and my discussion of anurans and birds defines situations, especially social situations, that ought to be especially apt for work with nonhuman primates. Given that primates have central auditory systems that are far more developed than those of, say, frogs, nonhuman primates also ought to be especially worthy candidates for studies of the top-down, goal-driven, selective-attention aspects of auditory scene analysis. One wonders, for example, if dominant members of a group have learned to use onset asynchrony in communication to establish primary auditory streams and, thus, dominance hierarchies. Do dominant males establish a salient auditory stream by speaking first? The possibilities are intriguing.

Fishman, Reser, Arezzo and Steinschneider (2001) have reported measurements of neurological evidence for auditory scene analysis in rhesus monkeys (*Macaca fascicularis*). They recorded from area A1 in primary auditory cortex with arrays of 14 microelectrodes. Recordings were made while awake monkeys listened to sequences of A and B tones that alternated between two frequencies at 5-, 10-, 20-, or 40-Hz pulse rates. At fast pulse rates (i.e., 20 or 40 Hz) they found suppression of neural responding to the B tone such that responding to the A tone was half the stimulus pulse rate. Furthermore, the degree of suppression grew as the frequency difference between A and B increased. They attribute the change in suppression to forward
masking. To my knowledge, this is the first report of a neurological process that clearly mimics the psychophysical data that appear with stream segregation based on changes in frequency and pulse rate (Bregman and Campbell, 1971; Hulse et al., 1997; MacDougall-Shackleton et al., 1998). This is also an important result because it suggests, among other things, that the neural representation of stream segregation exists in nonhuman primates, at least in part, at a fairly high level in the auditory system.

V. Theory

I turn finally to a brief presentation of theoretical schemes that have been suggested to draw together the empirical processes that define auditory scene analysis. There are three tacks to be mentioned: top-down, goal-driven approaches; bottom-up peripheral explanations; and, finally, theories based on mathematical modeling. All of these involve an appreciation of the physics and mathematics of acoustical analysis and are, therefore, formally quite complex. In the interests of brevity and simplicity, I attempt to convey the essence of the theories rather than their details. At the same time, I suggest resources to which the interested reader may turn for further information.

A. Top-Down, Goal-Driven Theory

Perhaps the best example of a top-down approach to auditory scene analysis comes from the seminal book by Bregman (1990). The initial portions of this chapter describe the essence of his theory. The theory is not mathematical, nor is it based for the most part on a complex analysis of the waveforms and formal structure of auditory signals. It does, however, draw heavily upon the principles of Gestalt psychology, the principles of grouping, proximity, similarity, apparent motion, and so on, that describe functionally the way auditory scene analysis seems to work. We have discussed the most salient organizing principles at the outset of this chapter, stressing the idea of functional auditory objects. The theory also draws upon the ideas of primitive and schema-driven processes, as we have also discussed earlier. Though the distinction is sometimes hard to make, primitive principles of organization are unlearned and independent of experience, while schema-driven principles are learned and goal-(object-)directed, leading to the formation of functional auditory objects.

Bregman is by no means alone in adopting this Gestalt approach. McAdams and his colleagues (e.g., McAdams and Bigand, 1993) have also worked within the top-down approach, identifying the acoustic conditions that produce auditory objects (McAdams uses the term auditory
images)—even in young children (McAdams et al., 1990). Similarly, Warren (1999) has drawn heavily upon top-down principles in his treatment of auditory perception. Jones and her colleagues (e.g., Boltz, 1994; Jones and Yee, 1993) have studied the role of the temporal organization of sound patterns in establishing auditory objects.

And when it comes to selective attention—which is always of potential importance in scene analysis—the distinction by Yantis (2000) between top-down, goal-directed and bottom-up attention should always be borne in mind.

B. BOTTOM-UP THEORIES

Bottom-up theories of scene analysis stress the idea that there is sufficient information in the acoustic properties of the auditory signal itself to produce stream segregation and scene analysis. In Bregman’s terms, this approach refers to primitive principles in scene analysis, that is, principles that are unlearned.

I. Peripheral Channeling

Hartmann and Johnson (1991) have reported a series of experiments and a theoretical analysis that is virtually a pure bottom-up description of scene analysis. They stress the proposition that stream segregation can be accounted for by the acoustic information contained in peripheral channels. By a peripheral channel they mean basic acoustic modes such as those based on frequency (tonotopic cues), spectrum, and ear presentation (lateralization cues). They studied the situation where two interleaved melodies were varied in pitch, location, temporal structure, and spectrum. Their experiments show that, indeed, if such peripheral channels are manipulated either to foster stream segregation or to work against it, then a peripheral channeling model describes most (but not all) of the data quite well. Acoustic cues which did not involve peripheral channeling, such as intensity and stimulus duration, could lead to stream segregation, but always to a lesser extent than if peripheral channels were involved. As Hartmann and Johnson themselves put it (1991, p. 175), “The results of the experiments lead to the practical conclusion that if a composer, or orchestrator, or gambler needs to make a prediction as to whether two melodies will be segregated or not, then the best strategy is to base the prediction on whether the two melodies excite different peripheral channels or not.” It is important to recognize, however, that stream segregation was obtained if cues that did not involve peripheral channels were used, so this bottom-up approach cannot provide the entire story—as Hartmann and Johnson freely acknowledge.
2. **Comodulation Masking Release**

Klump and his associates (Klump, 1996; Klump and Langemann, 1995; Langemann et al., 1998) have studied another low-level system based on principles of auditory masking that could well be involved in auditory scene analysis. They note that animals in the field are able to detect signals in noise at a lower signal-to-noise ratio than if masking levels are obtained in the quiet conditions of the laboratory. This leads to the possibility that natural fluctuations in the levels of the background noise and the signal may facilitate perception of the signal. This could happen in at least three ways. First, assume that signal and noise are broken into different frequency channels (remember Hartmann and Johnson’s approach earlier). Assume further that amplitude fluctuations in the frequency channels of the noise are correlated. Then if an introduced signal reduces that correlation, the change in correlation could be detected by the auditory system. This approach emphasizes cross talk between frequency channels. Second, assume that a signal is detected because the auditory system can detect a change in the modulation pattern of the envelope of the combined masker and signal when the signal is introduced. This emphasizes events in a single frequency channel. Third, assume that the frequency channels of a noise are amplitude modulated in coherent fashion. When this happens, there will be large fluctuations in the amplitude envelope of the masker; the masker will be more effective at large amplitudes, but less effective at low amplitudes. During periods of low amplitude, the likelihood that an added signal will be detected will be increased—in contrast to the condition in which the masker is not amplitude modulated. This approach emphasizes temporal factors in detection.

Klump and Langemann (1995; Langemann et al., 1998) studied comodulation masking release in starlings and great tits and found substantial release from masking for variations in the bandwidth of the masker and the rate of envelope fluctuations in the masker. As Klump (1996) points out, the data from the laboratory on birds appears to compare quite well with those obtained from humans.

There is no question that the natural habitat of animals is full of noise, and sometimes the interaction of signal and noise can work in fact to facilitate detection of the signal. Wiley and Richards (1982), for example, found that there was a 15 dB improvement in signal detection during exposure to (fluctuating) sounds from the birds’ natural habitat. Fluctuation of the noise may serve to facilitate the segregation of song.

There are some data from humans that seem especially relevant here. Oh and Lutfi (1999) found, contrary to what one would expect from our discussion, that people were no more skillful in identifying a 1 kHz signal in maskers of everyday sounds (such as a dog barking, a car horn, a baby crying)
than they were in white noise. However, there was less masking by everyday sounds than by noise on occasions when the observers reported that they easily recognized the sounds. One would like to know how the converse of this experiment would work, that is, the extent to which the detection of familiar sounds, as distinct from sine tones, in noise would be facilitated. Arbogast and Kidd (2000) have shown that informational masking is a factor when people are asked to identify where in space a target signal was emanating—accuracy and response times were improved when the target came from an expected location.

Regardless of the particular bottom-up approach that one favors, the important point is that there are large amounts of auditory information in mixtures of signals and noise that co-occur and interact with each other. This information is based on things that happen in the auditory periphery at the level of frequency analysis, spatial location, and the interactions of information in peripheral acoustic channels. There is little reason to doubt, as Hartmann and Johnson (1991) show so clearly, that this information can be used in auditory scene analysis. The question remains whether or not peripheral mechanisms are entirely adequate for a full account of auditory scene analysis. The idea that auditory perception is guided by learning and by a functional analysis of the objects in the auditory scene certainly suggests that bottom-up mechanisms are, in and of themselves, not sufficient for all species.

C. Formal Models of Auditory Scene Analysis

We should not be surprised to find that the phenomena associated with auditory scene analysis have been studied closely by those who build formal, mathematically oriented models of perceptual phenomena. This is a large literature growing at a rapid rate, and it would be far beyond our perspective to do more than mention a few articles that will outline the ideas involved and lead the interested reader to places where further information can be found.

Beauvois and Meddis (1991, 1996) have developed a model which describes auditory stream segregation phrased in terms of known properties of the peripheral auditory nervous system. The model is based on the idea that mechanisms may exist in the nervous system that will render one of two overlapping sounds as accentuated over the other; both sounds are heard, but one has salience, and hence captures attention. The claim is that this process arises because of the stochastic nature of nervous system activity in the periphery. The model is appropriately complex but, in brief, comprises bandpass filters that provide an initial frequency analysis, simulations of inner-hair-cell/auditory-nerve synapses (Meddis, 1990), a series of three excitation-level pathways, a comparator that selects the dominant channel in the excitation-level pathways, and an attenuator that reduces the excitation
in the nondominant pathways. Stream segregation is determined by the relative amplitudes in the dominant and attenuated nondominant paths. The model works surprisingly well in accounting for some of the basic phenomena of scene analysis, for example, the frequency and rate boundaries which determine whether or not stream segregation will occur. The theory has received confirmation by Rose and Moore (2000) who also find that their data support Hartmann and Johnson’s peripheral channeling model described earlier (Hartmann and Johnson, 1991). McCabe and Denham (1997) have also developed a model that accounts for stream segregation and selective attention.

For further reading about the application of formal modeling to auditory scene analysis, Rosenthal and Okuno (1998) have provided an excellent collection of papers by a number of researchers, and that volume will lead the interested reader to many other resources.

VI. Final Comments

After reading the material in this chapter, I hope the reader will have a basic appreciation of the fundamental principles of auditory scene analysis. Even more, I hope the reader will see how those principles can be applied to further our understanding of auditory communication in animals. There has not been very much research with nonhuman animals aimed directly at auditory scene analysis, but I have tried to show that there are many facets of such communication that are amenable to study with the scene analytic approach. Over the years some researchers have noted, usually in passing, that animals live in a noisy environment, and animal communication must somehow deal with this noise if it is to succeed. The principles offered by scene analysis can be a tool to guide investigations of this problem.

Work with animals can be especially important because research can use evolutionary principles as a tool to analyze the capacity for auditory scene analysis. Where in evolution did scene analysis arise, and what were the anatomical and physiological structures that enabled it to take place? We know from Fay’s work (Fay, 1998) that scene analysis exists in fish, and my descriptions of our work with starlings establishes the process in songbirds. The work of Fishman et al. (2001) established the process in nonhuman primates at the neurological level. But what are the true roots in phylogeny for auditory scene analysis? My suspicion is that the roots are very old because, as I have noted before, there is an enormous adaptive advantage for any creature that parses the auditory world into objects which have significance for survival: the sounds of environmental dangers, predators, rivals, and potential mates.
In all likelihood, early scene analysis was based on bottom-up processes which depended extensively on organizing principles contained in the structure of the stimulus itself. If that is so, when did top-down, learned, goal-directed processes emerge? These almost certainly involved selective attention among auditory objects. When did that capacity first appear? These are fundamental questions in the study of perception. It seems to me that auditory scene analysis provides an arena in which these questions can be studied with profit.

VII. Summary

In this chapter, I first introduced the concept of auditory scene analysis, the principle that the auditory perceptual system somehow parses a noisy world into individual auditory components—auditory objects—that often occur simultaneously but are attended to selectively. I then discussed some initial studies which demonstrated for the first time that auditory scene analysis occurs in nonhuman animals, European starlings in particular. I turned next to studies of other taxa (e.g., other songbirds, fish, nonhuman primates, and especially anurans) which suggest that auditory scene analysis may be an important principle helping to organize the perception of auditory events. Finally, I discussed two classes of theory—top-down and bottom-up—that have been developed to account for auditory scene analysis. Throughout, I have tried to identify situations in which it may be especially profitable to pursue further research on auditory scene analysis in nonhuman species.

References


Electric Signals: Predation, Sex, and Environmental Constraints

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I. INTRODUCTION

Animal signals have adapted to the environment in ways both obvious and subtle. Signals of many animals show spectral and temporal adaptations to improve transmission, to circumvent environmental noise, and to avoid predators (reviews by Dusenbery, 1992; Bradbury and Vehrencamp, 1998). Not surprisingly, as animals move to new habitats with different conditions, their signals must evolve as well. We are familiar with the idea that habitat use can guide or constrain signal evolution, but what about the converse? Is the relationship between signal and habitat strong enough that preexisting signal traits with limited plasticity can constrain an animal’s movements between habitats or into new habitats?

This question is probably not best addressed in the oscine songbirds because of their extreme evolutionary plasticity. Territorial song of Emberizine sparrows illustrates this point: white-throated sparrows (Zonotrichia albicollis) sing a simple song of two or three pure-toned whistles whereas white-crowned sparrows (Z. leucophrys) sing complex songs consisting of buzzes, FM transients, and pure-toned whistles. In electric fish, however, a picture is emerging that signal adaptations to particular habitats may constrain further habitat choices. This story is at the model stage, synthesized from ecological studies in the field and physiology studies in the laboratory. Significant portions of these models need further testing, particularly in the field. I hope this chapter focuses future research efforts along these lines.

The electric organ discharge is known universally by the acronym EOD. The same EODs used for active electrolocation can double as communication signals. Thus, it is easy to see how adaptations driven by one function (i.e., electrolocation) would have significant consequences for the other function
In this chapter I explore how the external forces of electrostatic law, predation, and aquatic environment interact with internal constraints to shape the evolution of electric communication signals. The key internal constraints I address are, of course, the need to electrolocate and communicate, but also the neural substrates these fish had before their divergent radiation, as revealed by structures common to extant members of their clades.

A. A FORK IN THE ROAD: PULSE VERSUS WAVE EODS

Weakly electric fish have evolved at least four times: in the Neotropical knifefish, order Gymnotiformes; in the West African elephant noses and allies, superfamily Mormyroidae; and in isolated species within two families of African catfish, order Siluriformes (Fig. 1) (Fink and Fink, 1981; Finger et al., 1986; Baron, 1994; Baron et al., 1994). In this chapter, I focus on the

Fig. 1. Phylogeny of the teleost bony fishes (after Lauder and Liem, 1983), showing the families with electoreception (∗) and electrogenesis (◦). A few individual genera and species have evolved electrogenesis independently (indicated in parentheses).
Fig. 2. Phylogeny of the neotropical electric fish order Gymnotiformes (after Albert and Campos-da-Paz, 1998) showing representative EOD waveforms. Arrows represent likely independent origins of the multiphasic EODs. The independent origin of biphasy in the Apteronotidae is inferred from its novel electric organ. The site of independent origin within the pulse clade is more speculative. An alternative scenario is that the family Gymnotidae evolved a multiphasic EOD independently from its sister clades, although it shares with them the mechanism for generation of the large negative phase. Most of the EODs shown here have equal amounts of energy above and below 0 V (dashed line), which nulls the dc in the EOD spectrum and reduces energy that may be too detectable by predators with low-frequency electroreception such as catfish. These EODs came from the following species: Electrophoridae (*Electrophorus electricus*) electric eel, Gymnotidae (*Gymnotus cf. carapo*), Rhamphichthyidae (*Steatogenys* sp.), Hypopomidae (*Brachyhypopomus pinnicaudatus*) feathertail knifefish, Sternopygidae (*Eigenmannia virescens*) glass knifefish, and Apteronotidae (*Apteronotus leptorhynchus*) brown ghost.

gymnotiform electric fish of the New World, but I draw some parallels to their mormyroid counterparts. The most recent phylogeny of the Gymnotiformes (Albert and Campos-da-Paz, 1998) divides these electric fish into two clades—those with continuous EODs (“wave fish”) and those with discontinuous EODs (“pulse fish”) (Fig. 2). Because electromotor and electrosensory systems are so tightly connected through the two functions of electric sense, the evolutionary split of Gymnotiformes into two signal strategies has had profound consequences for every aspect of electroreception and electric communication. The divergence of pulse and wave fish lets us explore how gymnotiform electric fish were forced to evolve two sets of solutions to the same problems. In the rest of this chapter, I look at how these problems have been addressed differently by pulse and wave signalers:
1. Avoiding predation—Electric signals should attract electroreceptive predators. Most of these predators are endowed with ampullary electroreceptors sensitive to the lower frequencies present in the ancestral EOD spectrum. Pulse and wave fish have evolved different tricks to shift their electric spectra upward.

2. Risky sex—The power spectra of ancestral gymnotiform signals included more low-frequency energy (0–100 Hz) than signals of most modern gymnotiforms. When predators drove gymnotiforms to evolve signals with a higher frequency spectrum, female gymnotiforms may not have lost their preference for low-frequency courtship signals. Males in modern pulse and wave groups have different mechanisms for inserting low-frequency energy back into their courtship signals and for keeping this energy transitory.

3. Limits imposed by signal strategy—The bifurcation of gymnotiforms into wave and pulse clades has strong implications for the versatility of these animals. Models indicate that the higher discharge rates of wave fish might impose severe constraints on other aspects of behavior and life history. I suggest that the wave signal strategy may constrain options for communication, interfere with energy conservation strategies, and lock these fish out of productive habitat with variable dissolved oxygen or daily temperature cycles.

II. A GYMNOTIFORM PRIMER

For those not familiar with the gymnotiform electric fish, I include the background information needed to follow the main inquiries. More complete coverage of these issues can be found in excellent reviews (Bullock and Heiligenberg, 1986; Hopkins, 1988; Heiligenberg, 1991; Kramer, 1995; Moller, 1995; Hopkins, 1999b).

Gymnotiforms are generally referred to by scientific names, most often by the genus name, though a few have common names from the aquarium trade. Gymnotiforms currently constitute six families with about 150 species, though both numbers could increase with further taxonomic work. The interesting comparisons made in this chapter hinge on distinctions between the clades. I list these in Table I along with the type of EOD (pulse or wave) and the approximate range of discharge rates. The remainder of the background section is divided between the electromotor system that produces electric signals and the electrosensory system that detects electric signals.

Electric signals and electric sense serve two key functions: electrolocation and communication. Electroreception can be passive or active. In passive electroreception, fish use ampullary electroreceptors in their skin to sense
TABLE I

<table>
<thead>
<tr>
<th>Family</th>
<th>Well-known genus</th>
<th>Common name</th>
<th>EOD</th>
<th>Rates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Electrophorida</td>
<td><em>Electrophorus</em></td>
<td>Electric eel</td>
<td>Pulse</td>
<td>0–8</td>
</tr>
<tr>
<td>Gymnotidae</td>
<td><em>Gymnotus</em></td>
<td>Banded knife</td>
<td>Pulse</td>
<td>15–85</td>
</tr>
<tr>
<td>Hypopomidae</td>
<td><em>Brachyhypopomus</em></td>
<td>Pintail knife</td>
<td>Pulse</td>
<td>4–115</td>
</tr>
<tr>
<td>Rhamphichthyida</td>
<td><em>Steatogenys</em></td>
<td>Leaf knife</td>
<td>Pulse</td>
<td>30–120</td>
</tr>
<tr>
<td>Sternopygidae</td>
<td><em>Sternopygus</em></td>
<td>Black knife, Golden-line knife</td>
<td>Wave</td>
<td>60–230</td>
</tr>
<tr>
<td></td>
<td><em>Eigenmannia</em></td>
<td>Glass knife</td>
<td>Wave</td>
<td>200–630</td>
</tr>
<tr>
<td>Apterontidae</td>
<td><em>Apterontus</em></td>
<td>Ghost</td>
<td>Fast wave</td>
<td>500–1800</td>
</tr>
<tr>
<td></td>
<td><em>Sternarchorhynchus</em></td>
<td>Elephant nose knife</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*b Common names derive from the aquarium trade.
*c EOD discharge rates given are typical.

weak electric fields of prey or the electric signals of other fish. With active electrorception, fish emit a weak electrostatic field then sense the distortion of that field caused by nearby objects that differ in complex impedance from the surrounding water (Fig. 3). Active electric sense enables these fish to navigate dense tangles of vegetation under nocturnal conditions where vision is useless. Gymnotiforms can detect objects through active electrolocation at distances of about half a body length. The range of passive electrolocation is harder to characterize because it depends not only on the spectrum and electric field intensity of the external signal but also on how that signal sums with the fish’s own EOD.

Gymnotiforms inhabit freshwater ponds, streams, and rivers of the Neotropical lowlands where some member of this order has evolved to eat just about any sort of animal material available. Small invertebrates constitute the majority of diets, but species have been found that subsist on fish, plankton, freshwater sponges, and even tails of other gymnotiforms (Lundberg et al., 1987; Marrero and Winemiller, 1993; Crampton, 1996; Lundberg et al., 1996).

A. ELECTROMOTOR SYSTEM

The EOD makes an electrostatic field around the fish, much in the way a dry-cell battery would if dipped briefly into water. Current flows out of the fish, through the water, and back into the fish. The EOD produces no significant electromagnetic emission and does not propagate. At a distance, the electric field resembles that emanating from an electric dipole, attenuating at the reciprocal of the cube of the distance—this in contrast to sound
intensity which attenuates with the square of the distance (Knudsen, 1975; Brenowitz, 1986). Electric field strengths within a body length are significantly stronger than predicted by the inverse cube law. Close to the body, electric fields of most gymnotiforms are far from an ideal dipole, displaying remarkable spatial and temporal heterogeneity (Rasnow and Bower, 1996; Assad et al., 1998; Stoddard et al., 1999).

EODs are the composite action potentials of electrocytes, excitable cells comprising bilateral electric organs (Fig. 4). Individual EOD pulses last 0.5–5.0 ms depending on the species. Electrocytes are arrayed in series within an insulated tube, much like batteries in a flashlight. The serial arrangement of electrocytes increases the EOD source voltage. The serial arrays of electrocytes are often arranged in parallel to magnify the source current. Tropical soils are noted for their low ionic concentration and, as a consequence, tropical freshwaters have low conductivity. Low water conductivity enables a small electric fish to generate a wide enough electric field to serve some useful purpose. The small electric organs of gymnotiforms would short-circuit in salt water.
FIG. 4. Electric fish generate electricity with a bilateral pair of electric organs. In fish of the genus *Brachyhypomus* shown here, electrogenic cells (electrocytes) are arrayed in series within insulating tubes, an arrangement that increases voltage. Tubes of electrocytes are arranged in parallel, a mechanism to increase current. Spinal motoneurons trigger action potentials in the posterior face of the electrocyte, creating a net-forward flux of positively charged sodium. Summation of these currents throughout the electric organ make the initial, head-positive phase of the EOD. The action potential in the posterior face triggers a second action potential in the anterior face, resulting in a tailward flux of sodium and the second, head-negative phase of the EOD.
The command signal for an EOD originates in the pacemaker nucleus of the medulla (Fig. 5). Pacemaker neurons discharge spontaneously, setting a regular rhythm for the EOD. The baseline rate of pacemaker neurons is set by the inward leak of sodium and calcium ions (Smith and Zakon, 2000). Action potentials in the pacemaker cells trigger action potentials in the adjoining relay cells. Relay cells in turn project long axons down the spinal cord where they make electrotonic synapses onto a subpopulation of spinal motoneurons called electromotoneurons. Electromotoneurons form nicotinic (cholinergic) synapses onto electrocytes, giant excitable cells derived embryonically from muscle cells. In development, future electrocytes lose the contractile apparatus of muscle and take on a nervelike function, generating enormous action potentials through the rapid influx of sodium ions (Ferrari and Zakon, 1993; Unguez and Zakon, 1998; Zakon and Unguez, 1999).

Wave fish generate EODs with onset intervals lasting one to two times the duration of the EOD waveform (Fig. 2). The even duty cycle results in a near sinusoidal discharge. Played through an audiospeaker, a wave discharge sounds tonal. Fish with longer intervals between EODs are called “pulse fish.” Played through a speaker, EOD trains of pulse fish sound like a nasal buzz. In general, discharge rates of wave fish are faster than those of pulse fish, although wave fish such as *Sternopygus* may discharge slower than some pulse fish such as *Microsternarchus*. Gymnotiforms of the family Apteronotidae produce high-frequency wave EODs at discharge rates ranging from 600 to 1800 Hz (Hopkins and Heiligenberg, 1978; Crampton, 1998b). In Apteronotids, the electromotoneurons themselves generate the EOD (Bennett, 1961). Myogenic electrocytes appear during
development, function briefly, then regress (Kirschbaum, 1995). Apteronotid electromotoneurons oscillate freely if severed from the pacemaker (Schaefer and Zakon, 1996). Both the oscillatory properties and the loss of a chemical synapse enable the apteronotids to achieve higher discharge rates than are possible with myogenic electric organs. The neurogenic organ does impose other constraints on signal performance that will be discussed later.

Wave EODs have a narrow power spectrum centered about the discharge frequency, with energy peaks appearing at the various harmonic intervals (Bullock et al., 1975; Hopkins and Heiligenberg, 1978; Crampton, 1998b). These harmonics are not caused by resonance in the electric organ, but by the imperfect fit of the EOD to a pure sine wave. EODs of pulse fish have much broader power spectra than those of wave fish, and their discharge rate has much less relation to the peak power frequency (Heiligenberg, 1977; Hopkins and Heiligenberg, 1978). Unlike in wave EODs, where peak power frequency is a critical metric, peak power frequency of pulse EODs tells relatively little about the shape of their EOD or energy distribution in their power spectrum.

Information for communication can be encoded either within the EOD waveform or in modulations of the discharge rate. When a gymnotiform discharges at a constant rate, the EOD waveform still conveys information about the signaler. EOD waveforms can identify the signaler’s family, genus, species, and in some cases age, sex, social status, or individual identity (Hopkins, 1988). Electric fish have become specialists in the control and modulation of the action potential waveforms that make up their EODs (Zakon, 1996; Zakon et al., 1999). Individual electric fish can vary EOD waveforms over three distinct time courses: (1) organizational changes over the lifetime of the individual, (2) activational changes over the course of the day, and (3) instantaneous changes from one EOD to the next (~10 ms). I illustrate these with examples from the hypopomid genus, Brachyhypopomus, a widely distributed pulse fish with a biphasic EOD.

During development, the EOD begins as a monophasic pulse, then becomes biphasic as more myocytes convert to electrocytes (Franchina, 1997). Once the development of the electric organ is complete, the second phase of the EOD continues to change (Fig. 6). In juveniles, the second phase is shorter than the first phase and greater in magnitude. In adult females the second phase is about the same shape as the first phase. In adult males the second phase is longer than the first phase and lower in magnitude. Juveniles and females can be induced to produce masculine EODs by injecting or implanting them with androgens (Hagedorn and Carr, 1985; Silva et al., 1999, unpublished data).

Two sexually dimorphic characters, EOD duration and amplitude, are surprisingly plastic. Males change their EOD between day and night, enhancing
the sexual dimorphism during the early evening when spawning occurs and decreasing sexual dimorphism at other times (Hagedorn, 1995; Franchina and Stoddard, 1998). Social isolation decreases the degree of sexual dimorphism over the course of several days and social stimulation restores males’ EOD traits, the time course of recovery depending on the stimulation and the EOD trait (Franchina et al., 2001). Capture stress can decrease sexual dimorphism in minutes and release from confinement restores it equally fast (Franchina and Stoddard, 1998). The neural and hormonal bases of these rapid changes are currently under investigation.

*Brachyhypopomus* produces instantaneous alterations in the EOD waveform in the context of reproduction. During courtship, these fish produce a series of stereotypic rate modulations, the more dramatic of which alter...
Figs. 7. Acceleration and chirp, two of the complex courtship signals of male *Brachyhypopomus pinnicaudatus*. The acceleration signal is given early in courtship, most often while the male runs his nose into the female’s midsection. The female’s discharge is also visible in the upper trace as the smaller EODs amid the larger ones of the male. Seen in expanded view, the male’s EODs are unchanged from normal. The slight diminution in amplitude is due to the male’s movement with respect to the recording electrodes. The chirp signal is given later in courtship, immediately before and during spawning. EOD amplitudes are reduced during the chirps and the EOD waveform loses much of its second phase.

briefly the EOD itself by causing EODs to fail partially, reducing briefly the EOD amplitude (Fig. 7).

Pulse fish appear to engage in more subtle, dyadic interactions, involving interactions between the EODs of the two participants. Members of courting pairs of *Brachyhypopomus* track each other’s discharge rates in what appear to be rate duets (Fig. 8). During such interchanges, discharge rates can be different but highly correlated. If either member of the pair changes its rate, then the other member changes in the same direction. This rate correlation could be a form of courtship communication, or it could be an artifact of jamming avoidance in which the leader changes its discharge rate for some reason and the follower shifts its rate to avoid electric interference. Detailed analyses of rate and phase to evaluate these possibilities are in progress.
In the first study of gymnotiform ecology, Lissmann (1958) proposed that wave fish were adapted to faster waters than pulse fish, their higher discharge rates serving the faster pace of life in a moving medium. Presumably, the higher the EOD rate, the shorter the potential latency to detect novel features in the aquatic environment. The correlation between water flow and signal strategy is good but not absolute; both wave fish and pulse fish live in slow streams, and a few wave fish are found in still waters (Hopkins and Heiligenberg, 1978; Crampton, 1998a,b). Key environmental differences between fast and slow waters include not only flow rate itself but also oxygen availability and predator distribution (Marrero and Taphorn, 1991; Crampton, 1998a), all of which appear to affect gymnotiform distribution and signal strategies.

B. Electric Sense

Animals that sense electricity have specialized electoreceptive cells in the skin called electoreceptors, similar to mechanosensory hair cells in derivation. Electoreceptors are divided into two broad classes, ampullary and tuberous (Fig. 9).

Ampullary electoreceptors are tuned to low-frequency electric fields (∼0–100 Hz) and can sense electric field intensities on the order of a microvolt per centimeter, such as the weak electric fields generated by the muscle action of nearby animals (e.g., wiggling worms, locomoting daphnia, ventilating fish). Ampullary electoreceptors are useful for detecting prey under conditions of poor visibility and, potentially, for listening to or eavesdropping on EODs of other individuals.
Fig. 9. Ampullary and tuberous electroreceptors from gymnotiforms (drawn from Szamier and Wachtel, 1970; Szabo, 1974) and their respective tuning curves. Gymnotiform ampullary electroreceptors are very sensitive to low-frequency energy. Tuberous electroreceptors are less sensitive but are tuned to the spectrum of the EOD. Both sets of tuning curves shown here are from pulse fish. The ampullary electroreceptor threshold was measured in Gymnotus cf. carapo (adapted from Dunning, 1973). Three representative threshold curves of tuberous receptors were recorded in the pulse fish Brachyhypopomus occidentalis (adapted from Shumway and Zelick, 1988). Tuning curves take on three shapes: narrow bandpass, broad bandpass, and lowpass. Tuberous receptors of wave fish resemble the more narrow of these.

Ampullary electroreceptors are found in the Gymnotiformes (New World electric knifefish) and in their sister order the Siluriformes (catfish) (Fink and Fink, 1981). Catfish use olfactory whiskers to locate prey, then they guide the final strike with passive electrolocation (Atema, 1969; Roth, 1972). An acute electric sense gives large piscivorous catfish the potential ability to detect the EODs of tasty little electric fish at significant distances. Ampullary electroreceptors are found in all primitive fish, including those that gave
rise to the tetrapods (Northcutt, 1986). Ampullary electoreceptors were
lost in the early teleost fish then reevolved in two teleost lineages (Fig. 1)
(Finger et al., 1986). Until someone sequences the genes for electoreceptors,
we can only guess whether their appearance in electoreceptive teleosts
represents complete evolutionary novelty or some reexpression of an ances-
tral developmental program.

Tuberous electoreceptors are derived specialties of the teleost electric
fish. In gymnotiforms, tuberous electoreceptors code either the amplitude
or the time of the EOD. Most of an individual’s tuberous electoreceptors
are tuned to its own EOD rather than to that of fish it may need to listen
to (Hopkins, 1976) such as members the opposite sex which may have a
different EOD spectrum (Hopkins, 1974a,b; Meyer, 1983). The amplitude
coding receptors have a narrow dynamic range (∼10–12 dB), approximately
centered around the individual’s own EOD.

If tuberous electoreceptors of the gymnotiforms were adapted for elec-
tric communication, we would expect broader tuning and more extreme
sensitivity to EODs than they display. African mormyrid electric fish have
evolved a unique type of electoreceptor, the Knollenorgan, with precisely
those characteristics. Knollenorgans are broadly tuned to the entire EOD
spectrum, they are extremely sensitive, and their afferent signals to the brain
are gated off during the listener’s own EOD (Bell and Grant, 1989).

Based on the evidence presented earlier, it is probably safe to assume that
tuberous electoreceptors in gymnotiforms evolved for active electroloca-
tion rather than communication. I am less certain that the gymnotiform
EOD evolved for active electrolocation, as has been assumed (Lissmann,
1958). The source of my hesitation is an unrelated group of electric fish, the
saltwater skates. Skates possess ampullary electoreceptors (the ampullae
of Lorenzini) and an electric organ in their tail, a location more conducive
to communication than electrolocation (Bass, 1986). In the breeding sea-
son, androgens shift the spectral sensitivity of the electoreceptors in male
stingrays to better match the ventilation signal, a shift which presumably
helps them locate females at the expense of prey detection (Tricas et al., 1995;
Sisneros and Tricas, 2000). Based on the skate and stingray, one can envision
an alternate scenario in which early gymnotiforms evolved low-frequency
electric signals to stimulate the ampullary electoreceptors of prospective
mates. These early gymnotiforms might have shifted their EOD spectrum
to higher frequencies to facilitate active electoreception with their newly
evolving tuberous electoreceptors.

Sensory information from the electoreceptors is gathered by afferent gan-
glion neurons of the anterior lateral line nerve (ALLn). The ALLn projects
to an enormously hypertrophied region of the brainstem called the elec-
trosensory lateral-line lobe (ELL) (Maler et al., 1981; Carr and Maler, 1986).
Information from the different electoreceptor classes (ampullary, tuberous
time coders, tuberous amplitude coders) remains segregated throughout the hindbrain and much of the midbrain, undergoing extensive parallel processing (Carr et al., 1981; Shumway, 1989a,b) before converging in the upper layers of the torus semicircularis (Metzner and Heiligenberg, 1991). Unlike the electroreceptive periphery, the electrosensory regions of the gymnotiform brain shows significant specialization for communication. The key feature of the gymnotiform brain, however, is its specialization for detecting distortion of the fish’s own EOD. In particular, amplitude distortion is detected in the ELL, and phase distortion is detected in the torus.

Neural networks of the ELL and associated structures filter the input stream to delete predictable information, thus revealing and enhancing novelty in the fish’s electric world (Bell et al., 1997). The ELL is a cortical structure bearing four somatotopic maps of the electroreceptive periphery (Carr and Maler, 1986). The medial map segment receives afferent input from the ampullary receptors, and the outer-three map segments process information from the amplitude-coding tuberous receptors in parallel (Heiligenberg and Dye, 1982). Each tuberous map segment performs a unique optimization of the trade-off in spatiotemporal acuity. Pyramidal cells of the innermost map segment have the smallest receptive fields and display the best spatial resolution, whereas pyramidal cells of the outermost segment have the largest receptive fields and the fastest temporal resolution (Shumway, 1989a,b). Different map segments appear specialized for different electrosensory tasks as well. Fish with lesions of the innermost map segments cannot perform the jamming avoidance response necessary for electrolocation whereas those with lesions of the outermost map segments can shift their discharge rate to avoid jamming but cease to emit aggressive chirps in response to conspecific signals (Metzner and Juranek, 1997; Juranek and Metzner, 1998).

Temporal information converges slightly in spherical neurons of ELL and then is relayed directly to the torus semicircularis of the midbrain (Maler et al., 1981). Layer 6 of the torus transforms spike time over the body surface into phase differences between the different receptive fields (Bastian and Heiligenberg, 1980; Carr et al., 1986; Rose and Heiligenberg, 1986), encoding EOD phase distortion with submicrosecond acuity (Kawasaki et al., 1988).

### III. The Perils of Predators

A catfish’s face is bespeckled with sensitive ampullary electroreceptors, ideal for locating a small prey species that gives off a robust electric signal (Roth, 1972). Large piscivorous catfish course the river channels of tropical South America and Africa, consuming electric fish when they are encountered (Marrero and Taphorn, 1991; Winemiller and Kelso-Winemiller, 1996). Many catfish of the New World family Pimelodidae hunt gymnotiforms
opportunistically whereas at least one species, *Pseudoplatystoma tigrinum*, specializes on gymnotiforms (Reid, 1983). In Africa, where mormyrid electric fish occupy the electric fish niche, clarid catfish hunt them in packs (Merron, 1993), attracted to low-frequency spectral components in the EOD (Hanika and Kramer, 1999, 2000).

Having evolved electroreceptors before their split with the Gymnotiformes, catfish have probably been a strong selective agent ever since gymnotiforms emitted their first EOD. Not surprisingly, most gymnotiforms exhibit electric adaptations that render their signals less attractive to piscivorous catfish.

The electric eel has an extra, high-voltage electric organ that can discharge hundreds of volts into any predator that fails to sever its spinal cord on the first bite (Faraday, 1839; Hagiwara et al., 1965). Even baby electric eels can deliver a painful shock (personal observation). The electric eel is itself a serious predator of gymnotiforms (Westby, 1988, M. Hagedorn, personal communication). The rest of the gymnotiforms have no high-voltage electric organ, but instead appear to rely on a suite of characters that shift their EOD spectrum upward and out of the spectral sensitivity band of the catfish’s electroreceptors (∼0–30 Hz—Peters and Buwalda, 1972). Two aspects of the EOD work to keep the spectrum high: (1) discharge rate set by the pacemaker nucleus and (2) dc balance of the remote EOD waveform. A good treatment of spectral structure is given by Bradbury and Vehrencamp (1998).

If the discharge rate falls within the spectral range of the ampullary electroreceptors, some amount of EOD energy will fall there also. Pulse gymnotiforms generally discharge at low rates (8–20 Hz) during the day but increase their discharge rate by a factor of 2–5 when the risks are higher (i.e., at night or when they are disturbed during the day). Wave fish maintain high and relatively constant discharge rates all the time. The fundamental frequencies of their EOD spectra lie far above the sensory range of the ampullary electroreceptors. Apteronotid wave fish, in particular, dominate the fish fauna of river channels where water flows quickly and large catfish are plentiful (Lundberg et al., 1987).

If the net current under the EOD curve (between the curve and 0 V) is not zero, then the EOD has a net dc component with a spectral frequency of 0 Hz. Because the ampullary electroreceptors are sensitive to very low frequencies, residual dc components in the EOD spectrum may be detected by electroreceptive predators. Gymnotiforms have evolved two mechanisms to reduce or eliminate the dc spectrum of the EOD.

The pulse fish clade and the wave fish family Apteronotidae independently evolved multiphasic waveforms that matched positive and negative energy to produce a net dc energy close to zero (Fig. 2). The wave fish
clade Sternopygidae produces head-positive monophasic EODs but offsets them with a head-negative dc (Bennett and Grundfest, 1961) that cancels the net dc in the EOD. Bennett (1971) speculated that the head-negative dc of the sternopygids evolved to maintain ionic balance in the electrocytes. I favor predation avoidance as the basis for reduction of dc energy in the EOD because it explains dc balance for all taxa whereas the ionic homeostasis hypothesis applies only to the Sternopygidae. For instance, in those *Brachyhypopomus* species with biphasic EODs, currents close to the body are extremely asymmetric with respect to 0 V dc and also have a large low-frequency spectral component (Fig. 10). Only at distances greater than a body length from the fish does the waveform assume dc symmetry and the dc component approach zero (Fig. 11) (Stoddard, 1994). Given that the asymmetry in the local EOD is reflected in the ionic conductances of individual electrocytes (Bennett, 1961), ionic flux would not be maintained by the EOD itself. In contrast, laboratory trials have shown that dc-balanced waveforms are significantly less detectable by electric eels and clariid catfish than dc-imbalanced waveforms (Hanika and Kramer, 1999, 2000; Stoddard, 1999).

At least three gymnotiforms not only produce monophasic EODs (Fig. 12), but apparently have evolved from ancestors with multiphasic EODs (Alves-Gomes et al., 1995; Sullivan, 1997; Albert and Campos-da-Paz, 1998). The reversion of the EOD to a form with a large dc component would seem to challenge any adaptive hypothesis for dc symmetry. So far, each species I have examined seems to have some scheme for reducing risk predation by electroreceptive predators. The electric eel (*Electrophorus electricus*) produces a high-voltage discharge. *Gymnotus cyllindricus* lives in streams lacking large electroreceptive predators. *Brachyhypopomus* sp. ("monophasus") appears to be an electric Batesian mimic of young electric eels with which it is sympatric, though we still need behavioral confirmation that this species deceives predators as readily as it fools field biologists (Stoddard, 1999).

Both field and lab data suggest that the modern gymnotiform weakly electric fish has not yet won the evolutionary arms race with electroreceptive predators. Catfish appear to present an ongoing source of predation. Pimelodid catfish consume gymnotiforms in the large river channels, sometimes in large numbers (Reid, 1983; D. Taphorn, personal communication). In fact, live *Gymnotus* are the preferred catfish bait of commercial fishermen in the Orinoco. Whether they use electroreception or olfaction is not known. Among electroreceptive predators, the electric eel (*Electrophorus electricus*) may present a special problem for gymnotiforms. *Electrophorus* has been observed hunting the pulse fish *Gymnotus carapo* in the field and is readily attracted to them in the lab (Westby, 1988). When *Electrophorus* get trapped in oxbow lakes with smaller gymnotiforms during the annual...
Fig. 10. EODs local to the body of female Brachyhypopomus pinnicaudatus express significant energy in the range of the ampullary electroreceptors due to dc imbalance in the local EODs. At more remote locations, the local electric fields merge to form a symmetric, biphasic EOD with much less energy in the low-frequency spectrum. In the example shown here, the remote EOD has 27 dB less energy at 10 Hz than at 1000 Hz. EOD spectra at the head and tail are nearly flat through the spectral range of both electroreceptor types. Cancellation of low-frequency energy makes the EODs less detectable by electroreceptive predators and has been proposed as the initial selective force for the evolution of multiphasic EODs (Stoddard, 1999).
Fig. 11. Electric field measurements in the midplane of a female *Brachyhypopomus beebei* show how the dc symmetry varies with distance from the body (Stoddard, 1994; Stoddard et al., 1999). For this figure, I calculated the RMS of the three-dimensional dc component of the signal across a 20 ms interval which approximates the nighttime discharge rate. At distances beyond 5 cm, the dc component of the EOD drops below the detection threshold of ampullary electroreceptors, presumably reducing risk of predation.

dry-down, the smaller gymnotiforms disappear completely (M. Hagedorn, personal communication). The electric eel is a remarkable predator and the most unusual gymnotiform by any measure. Where other gymnotiforms have a single bilateral pair of electric organs, *Electrophorus* has three morphologically distinct pairs of electric organs (Hunter, Sachs, main). The Sachs organ emits the low-amplitude EODs used for electrolocation and communication, and the Hunter and the main electric organs are used to generate high-voltage discharges for stunning prey and for defense (Coates, 1950; Keynes and Martins-Ferreira, 1953; Hagiwara et al., 1965). Other gymnotiforms emit
Fig. 12. A few gymnotiforms produce monophasic EODs with no dc offset to conceal low-frequency energy. These are the electric eel (*Electrophorus electricus*), and two species with low-voltage EODs, *Gymnotus cylindricus* of Middle America, and *Brachyhypopomus* nov. sp. *monophasus* (Sullivan, 1997). *Brachyhypopomus* nov. sp. *monophasus* may be a Batesian mimic of the sympatric electric eel. *G. cylindricus* live in streams devoid of large electoreceptive predators. Phylogenetic analysis shows secondary loss of multiple EOD phases in the latter two species (Sullivan, 1997, unpublished data).

EODs continually, driven by an oscillating pacemaker nucleus, but *Electrophorus* lies silently for minutes on end, discharging only when it is active. Hopkins (1973) proposed that irregular discharges of mormyrid electric fish blend into the background of electrical noise from tropical electric storms. Perhaps the irregular discharge of the electric eel facilitates a stealthy approach upon electoreceptive prey. Most pulse gymnotiforms can gulp air when oxygen levels are low, a trait that allows them to inhabit oxygen poor waters (Crampton, 1998a), a possible refuge from large, active predatory catfish. But electric eels are obligate air breathers (Farber and Rahn, 1970; Garey and Rahn, 1970; Johansen, 1970) and they can penetrate oxygen poor waters. All these characters—multiple discharge types, facultative signaling, air breathing—equip *Electrophorus* as a formidable predator of smaller gymnotiforms. In keeping with this role, *Electrophorus* begins hunting in the late afternoon while other gymnotiforms are still inactive (Westby, 1988).

Based on his field observations, Westby (1988) speculated that *Electrophorus* uses its tuberous electoreceptors to detect smaller gymnotiforms. There is an unresolved problem with this proposal: to detect the dc-balanced EOD of a gymnotiform at any useful distance (e.g., 1 m), the eel would need tuberous electoreceptors significantly more sensitive than those of any known
ELECTRIC SIGNALS

Fig. 13. EODs of Brachyhypopomus pinnicaudatus used as playback stimuli with an electroreceptive predator, the electric eel (Electrophorus electricus). The half EOD (solid line) has about 30 dB more energy in the spectrum of the ampullary electroreceptors than does the full EOD (dashed line). The eel was significantly better at detecting the half EOD than the full EOD (Stoddard, 1999). The eel thus appears to use its ampullary electroreceptors to detect signals of prey. Signals that conceal the low-frequency spectrum will be less readily detected, even if their overall amplitude is greater.

gymnotiform. Such electroreceptors would be equivalent in sensitivity to the Knollenorgans of mormyrids or the type I gymnarchomasts of Gymnarchus niloticus (review by Zakon, 1986). So far, no evidence suggests Electrophorus is endowed with high-sensitivity tuberous receptors. Reported thresholds for the eel’s tuberous electroreceptors range from 2 to 30 mV/cm (Hagiwara et al., 1965). EOD intensities of 2 mV/cm appear between 1 and 5 cm from the tail of adult Brachyhypopomus (Stoddard et al., 1999). So tuberous electroreceptors, by themselves, do not appear sufficiently sensitive to enable electric tracking of small gymnotiform prey over significant distances.

Electric playbacks to a resting electric eel suggest the eel might have a clever solution to this problem. When we played monophasic EODs with significant energy in the spectrum of its ampullary electroreceptors (Fig. 13), it swam silently until it reached the electrode. Not surprisingly, when we played biphasic, dc-symmetric EODs expressing little energy within the spectral sensitivity of the ampullary receptors the eel generally did not react (Stoddard, 1999). But a few times the eel began to discharge rapidly as it homed in on the playback electrode. Although the eel’s tuberous electroreceptors may be too insensitive to detect the remote EOD in isolation, its gymnotiform brain is exquisitely sensitive to distortion of its own EOD. By discharging rapidly and continually, the eel can create a carrier signal that biases the weak, remote EOD up into the active range of its tuberous electroreceptors. The eel thus could use its active electrolocation system to track the remote EOD to the source, a variant of the “scan sampling hypothesis”
Fig. 14. (A) Complex social signals of three gymnotiform species. The two recordings from *Brachyhypopomus pinnicaudatus* include both male and female EODs. The female EODs remain at constant amplitude and rate throughout, but their coincidences with the male EOD constitute the unusually high and low traces. Because of their dc symmetry, the female EODs do not contribute to the low-frequency components in the recording. The chirp of *Eigenmannia virescens* was resynthesized from an EOD and a dc-coupled chirp recording from Metzner and Heiligenberg (1991). (B) Complex electric signals used in courtship and aggression (A) contain significant energy in the spectral range of the ampullary electroreceptors. The
Fig. 14. (Continued) low-frequency components shown here are revealed by passing the digitized waveform through a digital 2-pole Butterworth low-pass filter with a corner of 8 Hz. Of the complex signals shown here, *Eigenmannia* chirps generate the greatest proportion of low-frequency energy, but even *Apteronotus leptorhynchus* produces enough low-frequency energy that it should stimulate the ampullary electroreceptors of conspecifics at close range.
(Hopkins and Westby, 1986). The eel’s electrolocation EOD is at least two orders of magnitude stronger than that of a small gymnotiform, so electrical silence could allow the eel to get close to its prey without revealing itself. Our data here are suggestive, but anecdotal. This hypothetical mechanism requires systematic investigation.

When they are not contending with predators that would swallow them whole, gymnotiforms have to contend with electroreceptive “partial-predators” vying to eat them one bite at a time. Deep channels of the Amazon harbor two apteronotids, *Magosternarchus raptor* and *M. duccis*, that, based on their stomach contents, seem to exist solely on the tails of other gymnotiforms (Lundberg et al., 1996). The blind Amazonian catfish *Pseudocetopsis* sp. has a tuberous electroreceptor with morphological similarity to the mormyrid Knollenorgan (Andres et al., 1988). The physiology of this electroreceptor is unknown, but *Pseudocetopsis* lacks an electric organ of its own and may use its novel receptor to track gymnotiforms. Andres et al. suggested that this small catfish, like *Magosternarchus*, may survive by cropping the tails of gymnotiforms. Behavioral data on the foraging habits of these two groups would be most interesting.

IV. ‘Twas Ever Thus: Sex versus Predators

Modern gymnotiforms have evolved mechanisms that avoid the production of low-frequency energy that might otherwise attract predators endowed with ampullary electroreceptors. In the sort of turnaboot we have come to expect in natural systems, male gymnotiforms have evolved secondary mechanisms to put the low-frequency energy back into their courtship signals. As with other aspects of their signal behavior, wave and pulse species have different mechanisms for resynthesizing low-frequency energy.

Courtship signals of male *Eigenmannia* consist of gaps in the continuous EOD wave train (Fig. 14). These gap signals are called “chirps” for their sound on an audio monitor (Hopkins, 1974b). As mentioned earlier, *Eigenmannia* produce monophasic EODs against a head-negative baseline. Periods without EODs are not electrically silent in *Eigenmannia*, but instead reveal continuous, head-negative dc electric fields. Thus when *Eigenmannia* chirps the net dc field goes from zero during EOD pulses, to negative during the period of silence, and back to zero when the EOD resumes. *Eigenmannia* readily discriminates between synthetic signals with and without the low-frequency spectral component (Naruse and Kawasaki, 1998).

Neurophysiological and behavioral evidence is consistent with the assumption that low-frequency energy should be attractive to female *Eigenmannia*. The pyramidal cells of the ELL are sensitive to amplitude modulation. Tuberous map segments respond to the high-frequency AM modulation and
the ampullary map segment responds to modulation of the dc component (Metzner and Heiligenberg, 1991; Naruse and Kawasaki, 1998). The different electoreceptor streams, segregated in ELL, converge in the torus semicircularis (Metzner and Heiligenberg, 1991). Some neurons found in the torus of Eigenmannia are excited only by amplitude-modulated signals that simultaneously excite both the tuberous and the ampullary electoreceptor pathways (Heiligenberg et al., 1991). Neurons in this region of the torus send projections to the preoptic area (POA), a conserved hypothalamic region that controls sexual behavior throughout the vertebrates. In keeping with the neurophysiological data, captive female Eigenmannia spawned when played chirps with the dc component intact but did not spawn when the playback was ac coupled (Hagedorn and Heiligenberg, 1985).

The idea that ampullary information is a critical component of Eigenmannia’s courtship signals has led me to look for low-frequency content in the sexual signals of other gymnotiforms. Males of the pintail knifefish Brachyhypopomus use their sexually dimorphic EOD to attract females to defended ovoposition sites then court them with a pair of complex rate and amplitude modulated signals. As with the wave fish Eigenmannia, the pulse fish Brachyhypopomus synthesizes low-frequency energy in its complex signals. But Brachyhypopomus also adds low-frequency energy to the simple EOD waveform as well. Male Brachyhypopomus enhance the sexually dimorphic characters in their EODs on a daily cycle, reaching maximum values about 1 h after sunset when nightly spawning activity begins, and reducing these characters 3 h later when spawning typically ends (Franchina and Stoddard, 1998). The EOD spectrum changes significantly between day and night, most noticeably in the spectral range of the ampullary electoreceptors (Fig. 15).

![Fig. 15. Spectra of the EODs of a reproductive male Brachyhypopomus pinnicaudatus during the day and at night. Extension of the second phase of the EOD waveform at night boosts energy in the spectral range of the ampullary electoreceptors by 15 dB (560%), presumably to attract females.](image-url)
EOD energy in the spectral range of the tuberous electroreceptors increases by about 3 dB at night, a change of 40%. More striking, energy in the range of the ampullary electroreceptors increases by 15 dB, an increase of 560%.

Early in courtship male *Brachyhypopomus* produce stereotypic rapid acceleration signals. Because a reproductive male’s EOD is net dc negative at night, increasing the EOD discharge rate increases the proportion of time the total wave train is dc negative (Fig. 14). An acceleration signal thus synthesizes a head-negative energy blip in the spectral range of the ampullary electroreceptors. As spawning begins, the male switches from acceleration signals to “chirps.” *Brachyhypopomus* chirps are a high-frequency series of small EODs in which the second EOD phase is missing or much reduced relative to the first phase. The result is a positive blip in the net dc component of the signal. Chirps given in rapid succession create a continuous low-frequency wave in the spectral range of the ampullary electroreceptor system (Fig. 14).

EODs of the wave fish *Apterontus leptorhynchus* are dc balanced, but their chirps are not. The dc component of the *A. leptorhynchus* chirp shown in Fig. 14 is 0.7% of the peak-to-peak EOD amplitude. The behavioral threshold for low-frequency signals in *A. albifrons* is 0.6–0.9 µV/cm (Knudsen, 1974). Based on electric field strength measured for a 21 cm *A. leptorhynchus* (Rasnow and Bower, 1996), the dc component in a chirp would be 1 µV/cm at a distance of 8 cm from the signaler. This distance is well within the range of courtship in this species (Hagedorn and Heiligenberg, 1985). EODs of some other apteronotids with higher frequency EODs are not dc symmetric but rather are negatively biased (Fig. 2). I have not measured the dc components of their chirps but they should be greater than that seen in *Apterontus*.

Dual-band stimulation of gymnotiform chirp signals are reminiscent of the “whine-chuck” courtship vocalizations of the Túngara frog *Physalaemus pustulosus* (Ryan, 1985). Whines focus energy in the spectral band of the amphibian papilla and “chucks” focus energy in the lower spectral band of the basilar papilla (Ryan et al., 1990). Chucks also attract the frog-eating bat *Trachops cirous* (Ryan et al., 1982, 1983). Male Túngara frogs calling in isolation produce only whine calls, but switch to whine-chucks when competing for mates with nearby males. Like Túngara frogs, the low-frequency spectrum of *Eigenmannia* is entirely transitory, appearing only during chirp signals. In contrast, male *Brachyhypopomus* produce significant low-frequency energy all the time, more energy during the spawning hours, and the most energy during the transitory courtship signals. Indirect evidence from two field studies in Venezuela suggests something in their behavior, perhaps the low frequencies in the EOD, increases their risk of predation. X rays of *B. pinnicaudatus* found that half of the sexually mature male had regenerated tails in contrast to nearly none of the females (Hopkins et al., 1990). First, during the breeding season, mature male *B. diazi* disappear from streams while
mature females survive in good numbers (P. Stoddard and E. Setteducati, unpublished data). Second, perhaps as a response to predation risk, perhaps for energy savings, male *Brachyhypopomus* reduce the energy in their EODs signals when socially isolated, particularly the low-frequency energy. They restore the low-frequency spectrum in the company of conspecifics, fastest in the company of males (Franchina *et al.*, 2001). Nobody has investigated the ampullary electrorceptive system of *Brachyhypopomus*, so I can only assume for now that it resembles that of *Gymnotus* and *Eigenmannia*, other gymnotiforms in which it has been studied.

The dual-frequency band of gymnnotiform courtship signals might have arisen for any of several reasons: sensory exploitation of a preexisting female sensory bias, phylogenetic inertia, or through female choice for a signal of male quality. I consider these in order.

### A. Sensory Bias

Several aspects of the male *Brachyhypopomus* signal fit a simple sensory bias model. During spawning hours, reproductive male *Brachyhypopomus* maximize EOD amplitude and duration (Franchina and Stoddard, 1998). Males also discharge at higher rates than females (Fig. 8). By directing energy into ampullary and tuberous spectrum bands, males increase the signal bandwidth and thus its potential conspicuousness. Higher signal amplitudes increase the active space of the signal and thus the female’s chance of detecting that signal (Brenowitz, 1986). Both greater EOD duration and higher discharge rates increase the probability that the female’s EOD will overlap with the male EOD in time. Because the gymnnotiform electroreceptive system is tuned to detect EOD distortion, temporal EOD overlap increases the sensitivity to other fish’s EODs by two orders of magnitude (Shumway and Zelick, 1988). Reproductive male *Eigenmannia* have lower frequencies than females (Hopkins, 1974b; Hagedorn and Heiligenberg, 1985) but wave fish always overlap each other’s signals, so increasing discharge rate would not enhance detection.

### B. Phylogenetic Inertia

If early gymnnotiforms courted with electric signals before the origin of high-frequency EODs and tuberous electrorceptors, they would have relied on their ampullary electrorceptors to process those signals, as Atlantic stingrays do today (Tricas *et al.*, 1995; Sisneros *et al.*, 1998). Although predation pressure acted against the low-frequency EOD spectrum, the pre-existing female attraction to the low-frequency EOD spectrum might have acted to retain low-frequency energy in the EOD even as the basic species EOD shifted upward in frequency.
C. MALE QUALITY

Females in general, and female fish in particular, are often attracted to conspicuous, expensive, and dangerous male traits, honest indicators of survival ability (Zahavi, 1977a,b; Andersson, 1994; Sargent et al., 1998). Attraction to low-frequency signals might have been selected based on their value as indicators of male quality. Low-frequency signals might indicate a “willingness” to take risks. By increasing EOD duration, male *Brachyhypopomus* increases the total energy expended on EODs. We do not yet know the costliness of EOD production so it is hard to say whether increased energy expenditure would be a reliable indicator of male condition. I can make a case, however, that total EOD amplitude could be used as a reliable indicator of male quality. EOD amplitude in *B. pinnicaudatus* depends on body size (Hopkins et al., 1990; Franchina and Stoddard, 1998). Sexually receptive females, given a choice, prefer to mate with larger males (Curtis, 1999). Under controlled lab conditions, male body size at sexual maturity depends on the amount of food we provide. Presumably body size in wild males indicates the ability to acquire food or allocate it toward growth.

Behavioral traits are often consistent with multiple mechanisms of sexual selection. Controlled mate choice studies are needed to determine whether such traits as EOD amplitude, duration, and higher discharge rate signal attractiveness per se, or whether they merely increase probability of detection by the female.

V. ELECTROSENSORY INFLUENCES ON NICHE PARTITIONING

The split into pulse and wave discharge types has further facilitated habitat partitioning by the gymnotiforms. The physiology of the electrosensory system is affected by external environment and thus has provided some novel axes for specialization and compromise. Dissolved oxygen, water flow, temperature, and water conductivity appear to be key environmental variables affecting both the physiology and spatial distribution of different gymnotiform taxa.

A. OXYGEN AND ENERGY

During the day, pulse fish lie motionless, slowing their electric discharge as much as five-fold from nighttime rates. In contrast, the elongate anal fins of the wave fish often remain in motion, and their high EOD rates remain unchanged from nighttime levels. The high activity levels of wave fish might be ideal for life in moving water, but logic dictates that such constant output must command a price. We have no data on energetic needs of gymnotiforms,
but oxygen consumption can serve as a useful proxy. Gymnotiform wave fish require high concentrations of dissolved oxygen to sustain their high output. I saw a most striking demonstration of this point when a colleague adjusted the EOD discharge frequency of an *Apteronotus* on a physiology rig merely by regulating the water flow over the fish’s gills. Crampton (1998a) studied the oxygen needs of captive gymnotiforms, recording EOD rates as he lowered oxygen content in the water. Pulse fish require less oxygen to maintain their EOD rate than wave fish. Every pulse fish Crampton studied could survive anoxic conditions for hours; most gulped air from the surface, one shut off its EOD while remaining motionless at the bottom. The only wave fish capable of surviving anoxia was *Eigenmannia virescens* which survived hypoxia by respiring at the oxygen-rich air–water interface. Other *Eigenmannia* species required high oxygen. As a rule, Crampton found that wave fish avoided Amazonian habitats with protracted or intermittent periods of low oxygen availability. Oxygen proved a better predictor of gymnotiform pulse versus wave fish distribution than water speed per se (Crampton 1996, 1998a).

It seems likely that the high oxygen demand of wave fish is a direct consequence of higher metabolic rate, possibly related to their high discharge rate. The alternative is that wave fish require no more energy, but are less efficient at extracting dissolved oxygen from the water. We need to know how much it costs an electric fish to produce its EOD and whether that portion of the energetic budget is significant relative to the cost of other activities such as locomotion.

Wave fish produce lower peak-to-peak EOD amplitudes than do pulse fish (Rasnow and Bower, 1996; Assad *et al.*, 1998; Stoddard *et al.*, 1999), perhaps as a way to conserve energy. Because their sensory tuning is narrow, a wave fish can lower the total amplitude of its EOD while concentrating the remaining energy in the narrow sensory band of its tuberous electroreceptors. Constriction of the EOD spectrum thus allows a wave fish to save energy and make its signals less conspicuous to hostile eavesdroppers without losing sensory acuity (Hopkins, 1976). Because the spectrum of a wave EOD is narrow and low in amplitude, a variety of wave fish with different frequencies should be able to coexist in the same active space without jamming their active electric sense. Noise immunity and predator avoidance thus could have been significant evolutionary advantages to the wave signal strategy.

The wave strategy may not be universally advantageous. Maintaining a wave EOD may impose some unique costs on the signaler. Narrow spectral tuning obliges the wave fish to maintain a constant discharge rate. Were a wave fish to lower its discharge rate during the day as a pulse fish does, it would also lower the fundamental frequency of the EOD spectrum out of the sensory range of its tuberous electroreceptors. The fish would be unable to sense its own EOD, and thus would become electrically blind to
much of its environment. Electric fish show no facility for rapid alteration of electroreceptor tuning. Electroreceptor tuning changes gradually, under control of sex steroids, not feedback from the EOD itself. Steroid implants retune the tuberous electroreceptors even after the EOD has been silenced surgically (Keller et al., 1986; Ferrari and Zakon, 1989). Not surprisingly, androgens masculinize the electrosensory system (electroreceptors, pacemaker, and electric organ) and estrogens feminize it (reviews by Zakon, 1993, 1996, 1998; Zakon et al., 1999).

B. Thermal Traps

Narrow receptor tuning and pure EOD frequencies may have costs beyond energetics. The tight spectral match of narrowly tuned signal and sense may trap the wave fish in a narrow thermal zone. Many neural processes are temperature dependent. Electroreceptor tuning, discharge rate, and EOD pulse width all vary with the ambient temperature (Feng, 1976; Hopkins, 1976; Dunlap et al., 2000). If these all change the same amount over the temperature range of interest, then receptor spectrum tracks the EOD spectrum and the fish can continue to electrolocate (Hopkins, 1976). If tuning of these different structures changes differently with temperature, then the fish would experience a tuning mismatch which, if extreme enough, would interfere with active electrolocation.

Subtropical Uruguay represents the southern geographic limit of the gymnnotiforms. *Brachyhypopomus pinnicaudatus* lives in the shallowest water (40–80 cm) which undergoes extreme daily temperature swings. Typical daily water temperatures during the breeding season range from 18°C at sunrise to 33°C in the late afternoon (Silva et al., 1999). *Eigenmannia virescens* inhabits deeper water in the same ponds, deeper water being notably more stable in temperature (A. Silva, personal communication). Based on published measurements of temperature effects on tuning of electric organ and electroreceptors of *Eigenmannia*, we can estimate what would happen to its electrosensory system if this wave fish were to dwell in the thermally unstable shallows.

EOD tuning in *Eigenmannia* varies with temperature following a $Q_{10}$ of 1.5 below 26°C and a $Q_{10}$ of 1.0 above 26°C (Feng, 1976). The $Q_{10}$ of tuberous electroreceptors is higher—Hopkins (1976) estimated the $Q_{10}$ for time-coding tuberous electroreceptors (T-units) in *Eigenmannia* and *Sternopygus* to be about 2.9 over the temperature range 20–22°C. In Fig. 16, I calculate best frequencies for T-units and the fundamental frequency of the EOD over the temperature range experienced by *B. pinnicaudatus* in shallow water. I use the published $Q_{10}$ values and assume the spectral match between the signal and receptor occurs at 26°C. I make several
Fig. 16. Tuning of electroreceptors and EOD discharge rates vary with ambient temperature. EOD discharge rate and electroreceptor best frequency are calculated here for the wave fish *Eigenmannia* using published Q_{10} values (Feng, 1976; Hopkins, 1976). The temperature range shown here is experienced daily by another fish, *Brachyhypopomus pinnicaudatus* in marshes of Uruguay. Based on these calculations, were *Eigenmannia* to experience the same temperature swing without retuning its electrosensory or electromotor system, the fish would lose sense of its own electric signal.

Critical assumptions here, chief among them that Q_{10} estimates and spectral width are constant for electroreceptors across the temperature range considered.

Hopkins (1976) shows that the frequency response of *Eigenmannia*’s T-units is sharp, particularly the upper shoulder. Thus at both temperature extremes, the spectral mismatch between tuberous receptors and the EOD appears sufficient to drop the response of the receptors down to the spontaneous firing rate where the fish would become deaf to its own signal.

According to this model, without a mechanism for rapid retuning of electroreceptors a wave fish should not be able electrolocate throughout the broad temperature swings of shallow water in the subtropics. As no such mechanism has been found, the wave fish may be in a thermal trap, restricted to habitat with constant temperature. EODs of pulse fish have broad spectra and electroreceptors of pulse fish are broadly tuned (Bastian, 1976, 1977; Watson and Bastian, 1979). Pulse fish thus would not have the same thermal range restrictions as wave fish, a feature which may allow them to exploit habitats with more variable temperatures. A useful set of experiments would be to explore the effects of temperature fluctuation on acuity of active electrolocation in wave and pulse gymnotiforms.
C. IMPEDANCE-MATCHING TO THE EXTERNAL ENVIRONMENT

Power transfer between two media is most efficient if the impedances of those two media are identical. The ossicles of the terrestrial vertebrate’s middle ear are an example of a structural adaptation to match the low impedance of air in the transmission environment to the high impedance of liquid in the inner ear. To transfer electric energy out of the electric organ and into the water with greatest efficiency, an electric fish needs to match the impedance of the electric organ and surrounding body tissues to the impedance of the water (Kramer and Kuhn, 1993; Caputi and Budelli, 1995). The higher the conductivity of the water, the greater is the current output of the electric organ needed to match the external impedance. Pulse fish of the genus *Brachyhypopomus* show characteristic species and racial differences in the number of parallel columns of electrocytes in their electric organ in association with the conductivity of the water in which they are naturally found. *Brachyhypopomus* species residing in high-conductivity water (~250–350 μS/cm) have five to six columns, those in medium-conductivity water (~70–100 μS/cm) have four columns, and those found in low-conductivity water (<10 μS/cm) have three columns (Sullivan et al., 1996; Hopkins, 1999a). The number of electrocyte columns is not influenced by the water conductivity in which the individual hatches and develops (Franchina, 1997). Impedance-matching by the electric organ structure may act as a mechanism for niche partitioning within a geographic region (Crampton, 1998b; Hopkins, 1999a).

D. THE PAUCITY OF MORMYROID WAVE FISH

As with the Gymnotiformes, the mormyroid electric fish of Africa split into two clades with different EOD characteristics, Mormyridae, the pulse fish, and Gymnarchidae, the wave fish (Sullivan et al., 2000). Unlike the order Gymnotiformes, which has tremendous species diversity among wave EOD taxa, the African wave family Gymnarchidae is represented by a single species, *Gymnarchus niloticus*, a large marsh-dweller that gulps air from the surface (Budgett, 1901; Svensson, 1933). Missing from Africa is the diverse radiation of small wave fish. What could be the basis for continental differences in diversity of wave species?

Evolutionary chance is always a default explanation, but given that *Gymnarchus* splits off the base of the African mormyroids (i.e., it has been around a long time) and given the enormous radiation of the mormyrid pulse fishes, it does not seem plausible that evolution has not had a chance to produce a radiation of gymnarchid wave fish. Nor should thermal fluctuation
constrain wave fish in the tropical African rivers. That would leave as possible restrictions (1) anoxia, (2) predation, and (3) niche competition:

1. Are African rivers prone to periodic oxygen depletion? Although Gymnarchus breathes air, air-breathing is most common among fish of shallow waters for whom frequent trips to the surface do not interrupt the normal course of life. Gymnarchus is the largest mormyroid electric fish, reaching lengths in excess of 1 m. Its large body size may allow air-breathing to sustain an oxygen-costly EOD in two ways. (1) large fish may be safer while traveling to the surface for the oxygen needed to sustain a continuous wave EOD. (2) Large body size may increase the relative amount of oxygen that can be banked in the blood and spent on activities other than basal metabolism.

2. Are the rivers inhabited by predators that are even more effective than those in South America? Unlike the sternopygid wave fish of South America, Gymnarchus has little or no dc offset to its monophasic EOD (Bennett, 1971).

3. Are mormyrid pulse fish such effective competitors that they excluded all the wave fish except Gymnarchus niloticus?

The scarcity of mormyroid wave fish is an interesting puzzle still to be solved.

VI. THE STORY THUS FAR

I have suggested here that the signal strategies of electric fish do in fact impose constraints on their life histories. Not surprisingly, the division of the weakly electric fish into pulse and wave strategists has forced independent solutions to the problems of communication in habitat with hostile eavesdroppers. But the division into two duty-cycle strategies has proven more significant than this. The suite of specializations that make up the wave sensory strategy appear ideally adapted for noise reduction, but it also may have imposed significant restrictions on use of habitat by fish with this signal type. Electrosensory models predict that the tight spectral match between signal and receptors imposes two critical constraints on wave fish: they may experience problems electrolocating in habitat subject to rapid temperature fluctuations, and they cannot lower their discharge rates to save energy without compromising their electrolocation sense. Further restricting the wave fish, their overall metabolic needs appear greater than those of pulse fish, as determined by their greater need for oxygen and inability to penetrate anoxic or hypoxic habitats. In spite of these restrictions, the wave strategy, however specialized, has proven extremely successful in the freshwater river systems of South America.
The pictures I have pieced together here have been synthesized from a mix of field and lab studies. They have benefited from discussions with many colleagues. Many of these ideas are explanations proposed to address unsolved questions posed by members of my lab in our weekly meetings and undoubtedly from similar discourses while I was a member of Carl Hopkins a decade earlier. I view this discourse as setting a framework for future study more than as a closed-door explanation of how the electric world came to be. Our understanding of these issues has glaring holes which should be seen as invitations for study. These gaps present exciting opportunities for young scientists looking for a field where they can make significant contributions to our understanding of animal communication. I outline below some areas in need of work.

A. **Electro sensory Predation**

- Our knowledge of electro sensory predation has been assembled from disjunct fragments. We need a good series of behavioral studies showing the foraging habits and hunting techniques of electro sensory predators and their effects on electric fish behavior and populations.

- It would be interesting to see if the electric eel engages in active tracking by using its electrolocation EOD to bias weak signals of gymnotiform prey into the dynamic range of its tuberous electroreceptors.

B. **Neuroethology of Electric Mate Choice**

- Sensory networks seem very similar among gymnotiform families (Kennedy and Heiligenberg, 1994; Heiligenberg *et al.*, 1996; Wong, 1997a,b), but it would be worth finding out whether other gymnotiforms besides *Eigenmannia* have ampullary-tuberous combination neurons that project from the torus semicircularis to the preoptic area as reported by Heiligenberg *et al.* (1991), and whether courtship signals with dc spectral components excite these circuits.

- Much work has been done on the effects of hormones on the electro sensory system (Keller *et al.*, 1986; Dulka *et al.*, 1995; Zakon, 1996) but very little is known of electro sensory influence over the endocrine system (Wong, 1997a).

- Controlled mate choice studies are needed to determine whether such traits as EOD amplitude, duration, and higher discharge rate signal attractiveness per se, or whether they merely increase probability of detection by the female.
C. ENVIRONMENTAL PHYSIOLOGY OF ELECTROLOCATION

- Is water flow a reasonable basis for evolutionary differentiation of pulse and wave strategies as originally proposed by Lissmann (1958)? We need a systematic study to determine whether discharge rate actually influences the speed of sensory integration.

- Crampton (1998a) has shown wave fish need more oxygen to maintain their EOD output than do pulse fish. Is their energetic expenditure higher, or are they simply less efficient at extracting dissolved oxygen from water? How much of their energy goes to electrogensis? My lab is currently working on this problem.

- What are the effects of temperature on electrolocation? Are wave fish really more compromised by rapid temperature swings as the model suggests? How rapidly can the electrosensory system compensate for temperature changes and by what mechanisms?

Over the past two decades, students of animal behavior have been drawn in one of two directions, toward the evolutionary track of behavioral ecology or the mechanistic track of neuroethology. The advent of molecular biology is so alluring that many young neuroethologists are failing to anchor their mechanistic studies in a firm understanding of the behavioral endpoint. On the other side of the divide, many behavior ecologists have adopted molecular techniques to answer questions of kin ship and phylogeny, but only a few have risked the learning curve involved with applying neurobiological techniques. While neuroethology has the capacity to bridge between molecular biology and behavioral ecology, I watch a further widening of the divide. In spite of this schism, or perhaps because of it, exciting potential remains for integration of the two approaches. The Holy Grail of this integrative approach is to identify every link in the chain between natural selection on behaviors and the molecular mechanisms that produce these behaviors. My heroes in this field are the scientists who have integrated studies of neural mechanisms with studies of natural behavior. Electric fish are ideal subjects for such a synthesis and the field remains wide open.

VIII. SUMMARY

Animals that depend on electric signals for navigation and communication have to balance (1) physical constraints on electrostatic conduction and detection, (2) physiological constraints on sensation and signal production, and (3) selective pressures of predation and communication. Electric fish have evolved two broad signal strategies, each with its inherent advantages and constraints with respect to these conflicting environmental demands.
Discontinuous “pulse” signals are more flexible in that their waveforms and discharge rates can be varied to suit the energetic and communication needs of the signaler. But pulse signals are also more prone to electric interference from environmental noise and other electric fish and they may be more detectable by electroreceptive predators eavesdropping on the low-frequency spectrum. Continuous “wave” signals are less prone to electric interference and are probably much less conspicuous to electroreceptive predators. But the tight match between the narrow spectrum of the wave signal and the narrow-band electroreceptors also constrains wave signalers to a narrow range of environmental conditions (high oxygen and constant temperature) that can sustain their continuous and unvarying electric output. Pulse and wave signalers have evolved various techniques for suppressing low-frequency energy in their electrolocation signals and for adding it back into their courtship signals, probably in response to mating preferences of females, but also at the peril of increased predation. Both pulse and wave strategies evolved independently in gymnotiform electric fish of the neotropics and the mormyroid electric fish of Africa. Although wave fish are abundant in the New World, they are represented by only a single species in Africa; the reason for the disparity is as yet undetermined.

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References


How to Vocally Identify Kin in a Crowd:
The Penguin Model

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I. INTRODUCTION

Sociality has several major advantages but also some disadvantages. For example, it is well known that colonial breeding improves care of offspring through communal protection (Alcock, 1972), but it is less well known that the difficulty of finding one’s own young is increased.

Marine birds and mammals breed on land but have to forage at sea. This fact is indeed the main constraint on their social behavior and their life history: seals have large fat reserves and in some species such as fur seals the adults have to alternate feeding trips at sea, a characteristic particularly striking in seabirds also (see Jouventin and Cornet, 1980, for a comparison between pinnipeds and seabirds; Bried and Jouventin, 2001, for seabirds). A wandering albatross, Diomedea exulans, may fly several thousand kilometers to find food (Jouventin and Weimerskirch, 1990) and a king penguin, Aptenodytes patagonicus, may swim several hundred kilometers on a foraging trip. As a consequence, both sexes have to cooperate to brood and rear one chick, and this heavy breeding cost explains why all of the nearly 200 species of seabirds are monogamous (Lack, 1968).

Pelagic birds have few if any predators on land, and they usually breed in colonies numbering several hundreds or thousands of pairs. After fishing for several hours, days, or weeks, one parent comes back to the crowded colony, finds its mate and takes its turn at brooding while the mate forages. Later, both parents have to forage at sea to feed the growing young. The arriving parent has to be recognized at the nest by its mate to be safe and to brood in turn and later by the large chick(s) to feed it. An
alien bird is pecked and harassed away. The ability to invest cooperatively in their own offspring (Trivers, 1972) by identifying the members of the family is thus crucial for marine animals, as it is for many other animal species.

Among seabirds where feeding trips are an ever-present feature of the breeding biology, the family of penguins is unique (1) in our knowledge of their individual recognition strategies, and (2) in the fact that they exhibit two different methods of care for eggs and chicks (some species have a nest and others do not). In a comparative study (Jouventin, 1982), we demonstrated experimentally in several species that penguins identify their mates or their chick(s) only by vocal cues, being unable to use visual cues to distinguish family members from surrounding birds: the display call is consequently the only marker used in kin recognition. Penguins are also unique because they include both nesting species as in other seabirds and nonnesting species, which walk with their egg or chick on their feet. In this group of colonial species, in which even topographical cues of nest location can be lacking (Isenmann and Jouventin, 1970), the difficulty of meeting up with mates and offspring is extreme, particularly with the latter, unusual way of breeding. So penguins, which are easy to observe, to record, to manipulate, and to test, constitute extraordinary models for studying individual recognition by acoustic means.

There are 15 species of penguins that, as in most seabirds, breed on a nest. This nest can be made with stones, as in the antarctic Adélie penguin (*Pygoscelis adeliae*) or the subantarctic macaroni penguin (*Eudyptes chryso-lophus*). Nests can also be made of grass, as in the gentoo penguin (*P. papua*), which breeds on the same subantarctic islands as the latter species, but on plateaus. Some species nest in a burrow such as the nocturnal little blue penguin (*Eudyptula minor*) which breeds along the Australian and New Zealand coasts.

Much more exceptional in seabirds, the two large (nearly 1-meter tall) nonnesting *Aptenodytes* penguins brood their single egg on their feet and usually walk around during brooding. They breed on flat and inhospitable areas such as wet subantarctic beaches in the king penguin (*A. patagonicus*) and the antarctic sea-ice in the emperor penguin (*A. forsteri*). The first of these does not move more than a few meters during the brooding phase but is much more mobile during the rearing phase when the chick waits alone for its parents to feed it (Stonehouse, 1960; Lengagne *et al.*, 1999a). The latter species moves through all of the breeding cycle because when there are blizzards blowing, brooders and chicks have to huddle in tight groups of 10 birds/m² to keep warm (Prévost and Bourlière, 1957; Prévost, 1961). During storms, the wind may blow at 350 km/h and the temperature drop
to $-34^\circ\text{C}$ (meteorological data from Terre Adélie, where our studies on antarctic penguins were conducted).

The ritualized postures and the various calls of the penguin family have been described in detail by Jouventin (1982). The biological meaning of calls and displays was determined through the observation of marked birds, often over several years, according to the ecological and social context. All genera, and for some genera several species, were studied to describe, understand, and compare their visual and vocal displays and to test by playback their use of calls in individual recognition.

Using computers, more sophisticated playback experiments have been conducted to examine the coding–decoding systems of penguins. In this chapter we summarize the acoustic constraints and behavioral adaptations described by Jouventin (1982), and we synthesize playback results to give a comparative account of the acoustic systems of six different species (Aubin and Jouventin, 1998; Jouventin et al., 1999; Lengagne et al., 1999a,b,c, 2000; Aubin et al., 2000; Jouventin and Aubin, 2000, 2001).

II. Locations and Methods

A. Subjects and Location

Six species of penguins have been studied in the past five years, at the following locations:

- The Adélie penguin and the emperor penguin were studied at the Pointe Géologie Archipelago ($66^\circ40'\text{ S}, 140^\circ01'\text{ E}$), Terre Adélie, Antarctica,
- The king, the gentoo, and the macaroni penguins were studied mainly at Possession Island ($46^\circ25'\text{ S}, 51^\circ45'\text{ E}$), Crozet Archipelago, Indian Ocean,
- The little blue penguin was studied at Phillip Island ($38^\circ31'\text{ S}, 145^\circ08'\text{ E}$), 60 km from Melbourne, Australia.

B. Recording and Playback Procedures

Calls were recorded with a Sony TCD Pro II DAT recorder (frequency response flat within the range 20–20,000 Hz) and an omnidirectional Sennheiser MKH 815T microphone (frequency response 100–20,000 Hz $\pm$ 1 dB) mounted on a 3 m pole, so that birds could be approached without disturbance. The distance between the beak of the recorded bird and the microphone was approximately 1 m for all species studied. Experimental
signals were broadcast with the same tape recorder connected to a PSP-2 E.A.A. preamplifier and a 20 W self-powered amplifier built in the laboratory, equipped with an Audax loudspeaker (frequency response 100–5600 Hz ± 2 dB). For propagation tests, signals were rerecorded by means of an omnidirectional Sennheiser MKH 815T microphone connected to another Sony TCD10 Pro II DAT. For sound pressure level measurements (SPL in dB), we used a Bruel & Kjaer Sound Level Meter type 2235 (linear scale, slow setting) equipped with a 1 in. condenser microphone type 4176 (frequency response 2.6–18,500 Hz ± 2 dB).

For propagation experiments, representative calls of each species studied were chosen. These signals were broadcast repetitively (generally 10 calls) through the colony and recorded at distances of 1 m (reference), 7 m (average distance between two birds when the incoming one started the acoustic search of the mate or the chick), and 14 m (maximum distance of recognition observed in most cases). The loudspeaker and the microphone were mounted on a tripod at the height of a penguin head (0.9 m for a king or emperor penguin, 0.7 m for an Adélie penguin, and 0.4 m for a little blue penguin). To quantify the screening effect of the bodies of birds, the recordings were compared with propagation records made at the same microphone and loudspeaker height and the same distances, but without any penguins present. The series of recorded calls were then examined in the amplitude-versus-times and the amplitude-versus-frequency domains.

In playback experiments, both chicks and adults tested were flipper-banded with a temporary plastic band to identify them. Playback experiments were conducted during clear and dry weather, with a wind speed of less than 4 m/s. The bird tested (adult or chick) was generally quiet, preening itself. The distance between the loudspeaker and the bird was on average 7 m, this corresponding to a natural calling situation between birds. Signals were played at SPL levels equivalent to those produced by the species tested. To prevent habituation, a maximum of three experimental signals per day was broadcast to any one bird. For the different birds tested, the order of presentation of the different experimental signals was randomized. In the same way, the order of presentation of signals tested was not the same for each bird from day to day. Thus, the observed responses for the whole group of individuals tested were neither the result of cumulative excitation nor dependent on playback order. For each species and for each experimental signal, from 8 to 25 individuals were tested.

In natural conditions and during the absence of the parents, chicks gathered in flocks, remaining silent and standing or lying quietly. An adult coming from the sea to feed its chick makes its way to the area of the colony where the nest (or the meeting place) is located and calls. Then, the corresponding chick in the flock holds up its head, looks around, calls in reply, and moves
toward the parent, often running (Jouventin, 1982). The other chicks in the vicinity, resting or preening themselves, exhibit no behavioral reaction to the apparently extraneous calls. The recognition process between mates is exactly the same as this except that the brooding bird does not move toward the incoming bird, but only calls in reply until the two partners meet.

On the basis of the observation of these natural meeting situations between parents and chicks or between mates a behavioral scale was used to evaluate the intensity of response of tested birds for all the different penguin species studied. The behavioral scale was ranked as follows:

−, no response;
+ , moderate response (visually inspect the environment by head-turning and calling in reply to the signal after a delay);
++ , strong response (turn to loudspeaker, immediately call in reply to the signal, and, only for the chicks, move in the direction of the loudspeaker).

C. Sound Analysis and Synthesis

Signals were digitized through 12- or 16-bit acquisition cards equipped with an antialiasing filter (low-pass filter, −120 dB/octave) at a sampling rate of 12–48 kHz (depending on the call studied) and stored on the hard disk of a computer. Calls were then analyzed and signals synthesized mainly using Syntana software built in the laboratory (Aubin, 1994). Signals were examined in the amplitude-versus-frequency domain by spectrum analysis (fast Fourier transform (FFT) calculation) and in the amplitude-versus-time domain by envelope analysis (analytic signal calculation). To follow the time evolution of the frequency we used the Hilbert (Papoulis, 1977) or zero-crossing calculations which provide a representation of the instantaneous frequency. Fundamental frequencies were detected and measured using the Cepstrum calculation defined as the power spectrum of the logarithm of the power spectrum (Noll, 1967). Experimental signals were built either by constructive synthesis (i.e., by computer synthesis starting from scratch) or by destructive synthesis (i.e., by modifying natural calls). For the constructive synthesis, the signal to be synthesized at time $t$, $S(t)$ is obtained by:

$$S(t) = \sum_{i=1}^{N(h)} \omega_i \sin[2\pi \varphi(t)t],$$

where $N(h)$ is the harmonic number, $\omega_i$ is the relative amplitude of the harmonic $i$ as determined from the power spectrum of a reference signal (a natural call taken as model). For the constructive synthesis, natural calls
were modified in the temporal, frequency, and amplitude domains. Amplitu
de and frequency modulations (respectively, AM and FM) were modified or removed using the Hilbert transform calculation (Brémond and Aubin, 1992; Mbu-Nyamsi et al., 1994). For modifications of the harmonic structure, natural calls were filtered by low-, high-, or band-pass digital filters, by applying optimal filtering with FFT (Press et al., 1988; Mbu-Nyamsi et al., 1994). The window size of the FFT was 4096 points. Natural calls were also shifted up or down in frequency by picking a data record (from a natural call) through a square window, applying short-term overlapping (50%) followed by a linear shift up or down of each spectrum, and finally by a short-term overlapping inverse FFT (Randall and Tech, 1987). As before, the window size was 4096 points. To modify call or syllable durations, we truncated the sounds. To prevent spectral artifacts arising from gaps in amplitude, an envelope was applied (by multiplication) to the data set in the time domain to smooth all the edges.

III. THE CONSTRAINTS

A. THE BIOLOGICAL PROBLEMS

Most seabirds breed in dense colonies numbering tens, hundreds, or even thousands of pairs. In penguin species, some colonies can near one or two million pairs. It is impressive to follow a king penguin leaving the sea with its stomach full and coming directly to its brooding mate or its chick on a flat area among many thousands of others in only 1 or 2 min (Lengagne et al., 1999a).

Although olfaction is well developed in petrels, another family of seabirds, penguins are not known for their abilities in olfaction and seem unable to find their partner using smell (Jouventin, 1982; Jouventin and Robin, 1984; Lequette et al., 1989; Verheyden and Jouventin, 1994). More surprisingly, penguins apparently see well, even on land, but they are unable to identify their mate or chick(s) visually. Jouventin (1982 and unpublished data) confirmed its observations by experiments consisting of obstruction of the auditory ducts or of closing the birds’ beaks by means of adhesive tape. In both these situations, partners were unable to recognize each other. The lack of visual recognition is not obvious because, after recognizing their partner vocally, penguins try to follow the bird visually in the crowd. Nevertheless, if the mate or the chick disappears completely in a group, or if the visual link is lost for some minutes, the birds cannot find each other again without calling. In fact, penguins, as with fur seals (Roux and Jouventin, 1987) and many other seabirds (Beer 1970, 1979; White and White, 1970; Charrier, 2001), find their kin using an acoustic signal. Because individual recognition is only
vocal in penguins, and the call concerned is the display call, it was possible to experiment using playback of the partner: the mate for adults or, more often, the parent for chicks.

B. THE ACOUSTIC PROBLEMS

1. The Background Noise of the Colony

In all penguin species, the display call consists of a series of sound components termed syllables, separated by pronounced amplitude declines (see Figs. 1–3). The syllable is a complex signal based on harmonic series from 250 to >5000 Hz. The call is emitted at a relatively high sound pressure level (SPL) ranging from 85–90 dB for small penguins (Jouventin and Aubin, 2001, and manuscript in preparation) to >95 dB for large ones (Robisson, 1993b; Aubin and Jouventin, 1998). As penguins breed in dense colonies, calls emitted by other individuals generate a continuous background noise in the colony. In addition, other signals, such as agonistic calls and chick calls and nonbiologically significant sounds (wind, flipper flap), increase the level of ambient noise so that it is particularly high inside the colony (see Fig. 4). Thus, for a king penguin colony numbering 40,000 pairs, we have measured an average value of 74 dB\text{SPL} during a 4-min recording period (Aubin and Jouventin, 1998). In these conditions, we hypothesized that penguins could only establish communication at short range, that is, some meters.

Penguins are large animals that are able to call loudly, an ability that is probably useful in overcoming the sound of the sea and the wind, but which cannot prevail against the signals of their equally loud neighbors. The noise generated by birds in the colony is almost continuous, and periods of relative silence are short, infrequent, and unpredictable. Thus, in a king penguin colony, periods of relative silence represent only 15% of the time and are of short (mean: 20 ms) duration (Aubin and Jouventin, 1998). In addition, the only noises that cover exactly the same frequency band as that of a penguin call, and which would thus in theory lead to a masking effect (Scharf, 1970), are the calls produced by conspecifics. The acoustic properties of the masker and those of the signaler are similar. In these conditions of competing noise, the jamming effect is very important, from an amplitude, time, and frequency point of view, and this increases the difficulty for a given bird to extract the information provided by the partner.

2. The Screening Effect of Bodies

In breeding areas of a penguin colony, the density of birds is high, for example, 2.2 breeders/m^2, measured by Barrat (1976) in a king penguin colony. Many individuals (nonbreeding adults or chicks) also gather in groups and sometimes huddle closely together. In such places, the density of birds can
Fig. 1. Sound spectrograms and oscillograms of (a) an emperor penguin, *Aptenodytes forsteri*, call; and (b) a king penguin, *Aptenodytes patagonicus*, call. Calls correspond to a succession of syllables separated by gaps in amplitude.
Fig. 2. Sound spectrograms and oscillograms of (a) a gentoo penguin, *Pygoscelis papua*, call; and (b) an Adélie penguin, *Pygoscelis adeliae*, call.
Fig. 3. Sound spectrograms and oscillograms of (a) a little blue penguin, *Eudyptula minor,* call; and (b) a macaroni penguin, *Eudyptes chrysolophus,* call.
Fig. 4. Spectra of a 4-min recording of the background noise of king and Adélie colonies (for each colony, average of 937 successive FFTs, window size = 4096 data points, sampling frequency = 16 kHz, Hamming window). Adult and chick calls represent 60 and 55% of the energy (Welch calculation method) in the spectra of king and Adélie colonies, respectively.

become twofold higher than it would be otherwise (Kodyman and Mullins, 1990; Lengagne et al., 1999b) and can even reach 10 birds/m² in an emperor penguin colony during a blizzard (Prévost, 1961). Then, the bodies of birds constitute an obstructed environment that impairs the propagation of signals. The screening effect of penguin bodies causes absorption and multiple-scattering effects. To study the modification of the call during propagation, we broadcast and recorded signals at different distances in penguin habitats. In “open field” conditions, that is, without any birds between the emitter and the receiver, the measured attenuation of the signal fitted well with the amplitude decrease that would be expected from spherical spreading: it diminishes with distance according to the inverse square law (−6 dB per doubling of distance). When the same measurements are performed with penguins between the emitter and the receiver, excess attenuation occurs because porous objects such as penguin bodies absorb sounds (Wiley and Richard, 1978; Dabelsteen, 1981; Dabelsteen et al., 1993). The greater the distance, and the greater the number of bodies in the way, the more the excess attenuation. According to our measurements, amplitude and frequency parameters of the signal showed strong degradation with increasing broadcast
distance (see the results for two penguin species in Table I). Thus, in the penguin colonies studied, after 14 m of propagation, the attenuation is so strong that the amplitude gaps that separate syllables tended to disappear and the amplitude of the signal became equal or inferior to the background noise (signal-to-noise ratio equal to or less than 1). In the frequency domain, peaks above the wavelength corresponding to the body size of a penguin (i.e., above 350 Hz for a 0.9 m high king penguin or emperor penguin and above 500 Hz for a 0.7 m Adélie penguin) are more severely attenuated and disappear in the background noise after 14 m of propagation. For little blue penguins, the same disappearance is observed, but after only 8 m of propagation, due mainly to vegetation effects (Jouventin and Aubin, 2000). For amplitude parameters, peaks tend to be embedded in the noise and to disappear in the background noise after 14 m of propagation.

According to these propagation tests, communication involving individual recognition seems possible only at a short or moderate range (<16 m). Communication in a penguin colony, and generally in seabird colonies, appears poorly adapted to transmission of individual information at long range (Robisson, 1991; Aubin and Lengagne, 1997; Aubin and Jouventin, 1998; Lengagne et al., 1999b).

### IV. The Solutions Found

A seabird colony, and particularly a penguin colony, is an extreme environment from an acoustic point of view only partly due to the loud background noise. It presents a particularly difficult problem of acoustic communication, due not only to the extraneous noises but also to propagation problems.
linked to the distance between partners or between the parent and chick and to the massive screen of birds. Faced with the problem of finding a particular individual in a penguin colony among several hundreds or thousands of conspecifics, the display call alone seems at first glance inadequate to secure communication. Nevertheless, penguins succeed, performing acoustic identification of the partner or chick usually in a few minutes (i.e., a relatively short time). How do they manage this?

A. Behavioral Solutions to Optimize Identification

Acoustic recognition is a critical process for the breeding success of seabirds (Brooke, 1978). The incoming bird arriving from the sea has to find its mate or its chick in the colony on the basis of only a few calls. If it does not succeed, the bird returns to the sea. Thus, there is a possibility that the pair will fail to reunite or that the chick will die, so demonstrating the survival value of vocal recognition. To limit the high aggressiveness and the vigorous territorial defense of other breeders (via pecking and flipper flapping), the incoming bird must limit the time it takes in the colony to identify the mate or chick. For this purpose, penguins adopt some special strategies.

1. The Meeting Place

Although colonies of penguins often number thousands of birds, an incoming adult does not have to locate its partner among all of these individuals. As described previously, the search is limited to particular meeting places (either nests or previous feeding sites for nonnesting species) that are memorized by adults and chicks. These visual cues may assist in individual recognition, but the mutual display call remains the only way to identify with certainty the partner and offspring.

For the nesting species of penguins, such as macaroni, gentoo, or Adélie, the nest is so important that, even when it is abandoned, large chicks stay close to it while waiting at the colony for their parents. The parent comes directly to the location of the old nest and utters the display call which the chick answers immediately. Sometimes several chicks answer and try to be fed but the parent pecks the alien ones, feeding and preening its own. On rare occasions, mates or parents and chicks meet on the nest without calling (Aubin and Jouventin, personal observations with little blue, Adélie, and macaroni penguins). This occurs if no confusion is possible because of other behavioral cues and the use of the nest as a meeting place.

In nonnesting penguins, the problem is more difficult because the parent has to find its partner with only vocal cues and without any landmarks. In addition, the call decreases in amplitude by half in 9 m and completely in about 15 m in this loud colony noise (Jouventin et al., 1999; Lengagne et al., 1999b). In the king penguin, during the brooding stage, the problem is not so
different from that of a nesting penguin because the brooder with its egg or small chick on its feet does not move more than 4 m (Lengagne et al., 1999a). Even if they build no nest, breeders lay in a hollow on the ground and they defend this against intruders by vigorous pecks. During the brooding stage, the mate returning from sea needed on average 5 calls and a mean of 2 min (after the first call was emitted) to meet its moving partner in the colony (data established on the basis of observation of 28 pairs of birds, Lengagne et al., 1999a). When the incoming bird starts the acoustic search for its mate, the distance between the two birds was 8 m and 70% of the incubating birds were able to discriminate the first call emitted by the mate. During the rearing stage, when the chick is too large to fit on the adult’s feet and can walk itself, it stays in the same feeding area some 10 m across and waits among many other chicks. Both parents memorize this place, termed rendezvous site by Stonehouse (1960) and attachment zone by Barrat (1976), and come directly to the edge of the chicks’ huddles to call. The awaiting chick responds, usually within 15 s of the parent’s first call (Stonehouse, 1960). Consequently, even without a nesting place, king penguins have a rendezvous site that assists their meeting considerably.

In the emperor penguin, there is no nest, feeding place, or landmark and therefore the difficulty of finding the partner or the chick is greater. Birds seem to explore the colony at random, starting more often from the center of the colony and progressively expanding their search to the edge. In this species, the time necessary for an adult to find the chick can reach more than 2 h (Robisson, 1993a). Moreover a special behavioral adaptation exists to prevent the jamming of calls: when a bird calls, a neighbor that was about to call (as we can detect by its low head position) stops and waits for the end to utter its own call. In fact, to eliminate signal jamming, two individuals less than 7 m apart abstain from calling together. This “courtesy rule” of not interrupting was proved experimentally by playing a call from a loudspeaker positioned at different distances from a calling bird (Jouventin et al., 1979; Jouventin, 1982).

2. The Signaling Posture

For efficient communication, the sender must maximize the propagation of the signal and the listener must optimize reception. Thus, in calling, penguins adopt particular body positions or “signaling postures.” King penguins, and in general all penguin species except emperor penguins, raise their beaks slowly to a vertical position, stretch their necks to their fullest extent, and call (Jouventin, 1982). This signaling posture limits signal-to-noise ratio reduction caused by the screening effect of the bodies of the birds gathered in dense flocks. The macaroni penguin holds its head up, raising the beak, and then swings its head from side to side, beaming the signal in different
directions in the colony. These calling attitudes, with the beak from 0.4 to 1 m above the ground, maximize the signal transmission distance in the colony (Robisson, 1991, 1993; Lengagne et al., 1999b). Finally, the emperor penguin remarkably directs its beak downward during calling probably to facilitate the control of the temporal pattern of this call (Jouventin, 1982). According to the measures of Robisson (1993a), another complementary explanation is that this unusual posture directs the signal forward, so that sound energy is beamed in the direction that the bird moves during the search for its partner or chick.

Concerning the receiver, different postures are observed in the colony: rising to the feet or crouching, with back bowed and head lowered between the shoulders, are characteristic of incubating birds. Finally, especially during hot weather, birds can be observed lying on the ground. This last position is not an efficient one for receipt of acoustic information: we have shown in king penguin colonies (Lengagne et al., 1999b) that, when the receiver was located 10 cm above the ground, degradation of the signal was much more pronounced in both frequency and amplitude domains than when the receiver was located either 45 or 90 cm above ground. The characteristic listening postures (with head either 90 or 45 cm up) enhance the probability that the receiver will hear the call. Birds lying on the ground are generally found to be sleeping, so acoustic communication would seem to be of no importance to them. Conversely, when the incubating bird hears the call of its mate for the first time, it leaves its incubating posture, rises to its feet, and assumes what we have shown to be the best position for signal reception.

3. The Searching Strategy

Our signal propagation tests in colonies indicated that the communication system involving the mutual recognition between either mates or parents and chicks could be established in penguin species only at short range, as predicted by Falls (1982) for seabird colonies. Our playback tests with banded chicks or adults confirms Falls’ hypothesis. To estimate the maximum distance at which a call can be recognized by the partner, natural calls were broadcast to the corresponding bird at different distances in the colony (Fig. 5). The experiment started at a distance from the bird to the loudspeaker of 8 to 20 m, depending on the species studied. The call was played back and the behavior of the bird was observed. Then, the distance was reduced by moving the loudspeaker closer. After a pause of 6 min, the call was played back again, until a detection process was observed. Birds detect, recognize, and localize the natural display call at a relatively short distance: an average distance of 11 m for the king penguin (number of birds tested: \( N = 12 \); Aubin and Jouventin, 1998) and 4 m for the little blue penguin (\( N = 7 \), Jouventin and Aubin, 2000).
When a bird comes from the sea and makes its way into the colony to find its partner, it calls regularly at different distances from the receiving bird. The farther from the receiving bird the acoustic search was initiated, the more time was necessary to complete the search and the greater the number of calls that were emitted by the incoming bird. On the other hand, we have shown in the king penguin that 70% of the birds started the acoustic search for their mate when the distance was less than or equal to the discrimination range (Lengagne et al., 1999b). So, the calling strategy adopted for finding the partner appears particularly efficient in penguins.

B. SPECIES RECOGNITION

Although we have not systematically studied species recognition in penguins, but have considered them rather a unique model for individual recognition, Jouventin (1982) did compare territorial behavior between species. We found that the display call has several biological meanings, being used by a single bird or by a pair throughout the breeding cycle to indicate both the species, the sex, and the individual. The nesting penguins are the more territorial species, particularly the burrowing genera (Spheniscus and Eudyptula). The latter is nocturnal and is strongly aggressive against intruders even if it cannot see them (Waas, 1988, 1991). Consequently this species, the little blue penguin, constitutes the best model for specific recognition in penguins. We compared it with a burrowing petrel (Jouventin and
Aubin, 2000), and tested their responses to playback experiments. The response is not tuned to a precise frequency analysis since entire calls that have been shifted strongly (200 Hz) up or down still elicit territorial responses. In fact, it appears that the little blue penguin pays attention to the lower sounds, the presence of high frequencies being unnecessary to elicit territorial responses.

It appears also that both exhaled and inhaled temporal syllables provide territorial information. With respect to the territorial function of the calls, the coding process appears very simple: a territorial call consists of a rhythmic succession of two sounds having a particular pattern of frequency modulation. The parameters which encode territorial information are those that are resistant to degradation (low frequencies, slow FM, gaps in frequency and amplitude).

To communicate the territorial message, the information represented by the patterned arrangement of the two “binary” units of sounds is highly redundant (Brackenbury, 1978), as it is based on the repetition of identical units of information at two levels. Nevertheless, it would be enough for a territorial function where the breeder has only to know that a conspecific is approaching and merely has to reply: “Keep out, this burrow is occupied!”

C. A Well-Matched Acoustic Code for Identification

1. The Cocktail-Party Effect

As mentioned earlier, the display call is transmitted in a context involving the background noise generated by the colony plus the screening effect of the birds’ bodies, both reducing the signal-to-noise ratio. In addition, the signal is masked by background noise with similar spectral and temporal characteristics. To estimate the minimal discrimination threshold of the display call in a jamming situation, a series of mixed signals was broadcast to penguin chicks (Fig. 6). The parental call was combined with five extraneous adult calls with different emergence levels, the tested signal increasing in energy ratio among the extraneous noise. The superimposition results in a mixed signal with a total lack of silences and with numerous frequencies overlapping. This jamming mimics a situation frequently observed in a penguin colony.

Chicks of three species were tested with signals of different emergence levels (i.e., the difference between the energy level of the tested call and that of the five extraneous calls) at a distance of 7 m. The emergence level was defined as 

\[ E = 20 \log \frac{A_p}{A_e} \]

where \( E \) represents the emergence level in dB of the parental call of the chick tested, \( A_p \) is the absolute amplitude of the parental call, and \( A_e \) is the absolute amplitude of the mixed extraneous
calls. Our experiments indicate that the chick can detect its parental call in an extreme jamming situation. With king penguin chicks, detection is possible even when the parental call intensity is well below (−6 dB) that of the noise of simultaneous calls produced by other adults (Aubin and Jouventin, 1998). At the same distance, the Adélie and emperor penguins are not as good at detecting calls as the king penguin chick. Nevertheless, Adélie and emperor penguin chicks have a good ability to recognize the parental call even embedded in the noise of the colony (0 dB of emergence, Jouventin and Aubin, 2001). This capacity to perceive and extract the information from an ambient noise with similar acoustic properties to that of the signal, termed the “cocktail-party effect” in speech intelligibility tests, enhances the chick’s ability to find its parents. This process of perception must be linked to an acoustic coding system adapted to the constraints of colonial life.

2. The Vocal Signature

By playing back natural calls, it has been demonstrated that individual recognition by voice exists in all the species of penguins that have been studied (Derenne et al., 1979; Jouventin et al., 1979; Jouventin, 1982; Waas, 1988; Speirs and Davis, 1991). Previous analysis of temporal and frequency parameters have shown effectively that an individual signature can also be found in the display calls of all of these species (Jouventin and Roux, 1979; Robisson et al., 1989; Brémond et al., 1990; Robisson, 1992a; Robisson et al., 1993; Lengagne et al., 1997; Jouventin and Aubin, 2000). This has mainly been done by comparing, for a given parameter, the between-individual variation and the within-individual variation (Jouventin, 1982;
By comparing the temporal and frequency patterns in the calls of two species of penguins with nests (macaroni and Adélie) with those of two species without a nests (king and emperor), a direct relationship was shown between the potential of individual coding and the difficulty of finding the partner in the colony (Lengagne et al., 1997). However, knowing that it is possible to distinguish the signals of individuals by analysis does not tell us whether the birds do it. The only way to investigate this process was to test the birds by playing back different kinds of experimental signals. These signals corresponded to natural display calls modified in different ways: modifications of amplitude and frequency modulations (AM and FM), modifications of frequency and temporal parameters, and modification of the two-voice system (Table II).

### Table II

<table>
<thead>
<tr>
<th>Signals</th>
<th>Species</th>
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<tbody>
<tr>
<td></td>
<td>EP</td>
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<tr>
<td><strong>Modulation</strong></td>
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<td>Without AM</td>
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<td>Without FM</td>
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<tr>
<td>Reversed</td>
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<td><strong>Frequency domain</strong></td>
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<td>Low Pass</td>
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<td>High Pass</td>
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<td>Shift ± 25</td>
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<td>Shift ± 50</td>
<td>++</td>
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<td>Shift ± 75</td>
<td>++</td>
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<tr>
<td>Shift ± 100</td>
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<tr>
<td><strong>Temporal domain</strong></td>
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<td>HalfCall</td>
<td>+</td>
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<tr>
<td>OneSyl</td>
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<tr>
<td>HalfSyl</td>
<td>nt</td>
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<tr>
<td>QuarterSyl</td>
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<tr>
<td><strong>Two-voices phenomenon</strong></td>
<td></td>
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<tr>
<td>One voice suppressed</td>
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</table>

*Note: ++, strong response; +, moderate response; —, no response; nt, not tested.*

EP, KP, MP, AP, GP: respectively, emperor, king, macaroni, Adélie, and gentoo penguins. (Results from: Jouventin, 1982, Aubin et al., 2000, Hildebrand, unpublished data, for the emperor penguin; Jouventin et al., 1999, Lengagne et al., 2000, for the king penguin; Jouventin and Aubin, 2001, for the Adélie and gentoo penguins; Aubin and Jouventin, unpublished data, for the macaroni penguin.)
**a. AM and FM.** Concerning the modulations, only the king penguin among the different species studied, continues to respond after the total elimination of amplitude modulation (AM) in its natural display call. This does not imply that the AM structure is without use in this species. AM is strongly degraded during propagation through the colony (Aubin and Mathévon, 1995; Aubin and Jouventin, 1998; Lengagne *et al.,* 1999b) and this is unlikely to carry a message at distance. Nevertheless, we cannot rule out the possibility that AM might transmit information which would allow estimating the distance of the emitter (Naguib, 1996) or locating the acoustic source (Konishi, 1973; Wiley and Richard, 1982), two helpful qualities for locating an individual in a crowd. Concerning frequency modulation (FM), all the species studied except the king penguin are able to identify the mate or parental call even if the natural FM is lacking. It is the same for signals where each syllable (and at the same time the FM) is reversed (Fig. 7). Thus FM appears to be a key parameter in individual recognition for the king penguin but not for the other species, where amplitude modulation is important.

**b. The Frequency Domain.** In the frequency domain, all of the species studied prefer the lower part of the sound spectrum to the higher one, probably due to the fact that high frequencies attenuate strongly during propagation in the colony (Aubin and Jouventin, 1998; Lengagne *et al.,* 1999b). Nevertheless, some species (Adélie and gentoo) pay greater attention to the spectral profile of the call than others (emperor, king, macaroni). For example, recognition occurs for low-pass calls in emperor, king, and macaroni penguins but not for Adélie and gentoo penguins. Pitch parameters reveal the same pattern of responses. Emperor, king, and macaroni penguins tolerate more change in frequency than do Adélie and gentoo penguins. To identify its partner or chick, the latter species need the right frequency values for the harmonics of the call (with an accuracy of 25 Hz), whereas the former species tolerate errors of 75–100 Hz (Fig. 8). Thus, for Adélie and gentoo penguins, the coding of identity depends on the analysis of the spectral profile and of the precise frequency values of the harmonics, that is, mainly on timbre analysis.

**c. The Temporal Domain.** In the great majority of species studied, the broadcast of only one syllable is sufficient to elicit recognition, and this recognition is not linked to any particular syllable in the call (Jouventin and Aubin, 2001; Jouventin *et al.,* 1999; Lengagne *et al.,* 2000, and unpublished data). For the king penguin, even the first half of a syllable is sufficient to elicit recognition. In this species, the basic FM structure of the syllable is always the same: an increase followed by a decrease in frequency, with the inflection point always in the first half of the syllable. This inflection point is necessary for the recognition of the signal. The small amount of information (about 200 ms) provided by the frequency modulation shape of this half of
the syllable is sufficient to provide individual information (Jouventin et al., 1999; Lengagne et al., 2000). At the opposite extreme, the display call of the emperor penguin is the only one where several successive syllables (at least three; Hildebrand, personal communication) are needed to elicit recognition. Effectively, to identify the signal, emperor penguins examine the temporal succession of syllables (Jouventin, 1972, 1982; Jouventin et al., 1979).

Display calls of penguins (emperor penguin calls included) appear to be highly redundant, consisting of more or less identical successive syllables with a repetition of the same information many times. This redundancy
Fig. 8. Responses of king and Adélie penguin chicks to parental display calls shifted in frequency (results from Jouventin et al., 1999; Jouventin and Aubin, 2001).
Fig. 9. Enhancement of the number of syllables per call emitted by king penguins as wind speed increases: in windy conditions, birds maintain the efficiency of their communication by increasing the redundancy of the signal. The circle size is proportional to the number of data (ranging from 3 to 6) and the dashed line represents least-squares piecewise linear models (data replotted from Lengagne et al., 1999b).

enhances the opportunity to find a quieter window in the continuous noisy environment of a seabird colony. In addition, in penguin colonies circum-polar winds blow strongly, generating a high level of background noise and consequently lowering the signal-to-noise ratio in the colony. In windy conditions, we have observed that birds in king penguin colonies (Lengagne et al., 1999c) maintain the efficiency of their communication by increasing the number of syllables per call, leading to an enhancement of the duration of the calls. From a wind speed of 8 m/s, the duration of the calls increases linearly as the wind speed increases (Fig. 9). Thus, penguins seem to take into account the constraints imposed by wind on their communication. This result conforms with predictions from information theory (Shannon and Weaver, 1949) that increased redundancy in signal improves the probability of receiving a message in a noisy channel.

d. The Two-Voice System. The sound-producing structure in birds is the syrinx, usually a two-part organ located at the junction of the bronchi. As each branch of the syrinx produces sound independently, many birds have two acoustic sources. The use of the two voices was first documented in the song of the brown thrasher, *Toxostoma rufum* (Potter et al., 1947), and has been actively investigated for the past fifty years. Anatomical, physiological, and acoustical evidence existed for this two-voice phenomenon
(Greenewalt, 1968) but no function for it was known (Sturdy and Mooney, 2000). In songbirds, these two voices with their respective harmonics are often not activated simultaneously but two voices are obvious in the large penguins and generate a beat pattern that varies between individuals.

Among the 17 species of penguins, only the A*pentodytes* genus employs two frequency bands (Robisson, 1992b). Both A*pentodytes* species, the emperor and the king penguins, produce a signal consisting of two simultaneous series of harmonically related bands of slightly differing frequencies (on average 65 Hz for the emperor, Aubin *et al.*, 2000, and 25 Hz for the king, Robisson, 1992b), resulting in a two-voice call that produces audible “beats.” The two-voice system appears well suited for the environment in which it is used. We have done experiments with two voice signals broadcast through the colony and recorded at different distances (1, 8, 16 m). The recorded signals were then analyzed and the amount of degradation between the amplitude modulation of the beats and the true modulation existing in the call itself were compared (Fig. 10). We found that, although the true amplitude

![Fig. 10. King penguin display call: analysis of beats generated by the “two-voice system.” Only the fundamentals of one syllable are analyzed here. The periodic amplitude fluctuations [(a) oscillographic representation] coincide with the periodic frequency discontinuities [(b) spectographic + instantaneous frequency representation] and allow quantification of the period of the beats generated by the two sources.](image-url)
modulation of the call was severely compromised by propagation, the amplitude modulation of the beats produced by the two voices remained largely unchanged.

Our experiments demonstrate that the beats generated by the interaction of these two frequency bands propagate well through obstacles, being robust to sound degradation through the medium of bodies in a penguin colony, but above all that they convey information about individual identity. To test the hypothesis that the two voices may play a key role in individual recognition in the *Aptenodytes* genus we designed a series of playback experiments.

![Sound spectrograms](image)

**Fig. 11.** Sound spectrograms (1024 points window size) of syllables of emperor (left) and king (right) penguins. (a) and (b): low-pass filtered natural syllable, with only the fundamentals and the first harmonics kept; (c): one voice removed by filtration in the emperor penguin signal; (d): synthetic signal built on the model of the low-pass filtered king penguin signal, but with only one voice. The low-pass signals with two voices are recognized but not the one-voice signals.
with signals where only one voice was kept (Aubin et al., 2000, for the emperor penguin, Lengagne et al., 2001, for the king penguin). Unfortunately, the upper frequency bands of natural calls were not spaced sufficiently to allow for removal, by simple filtration, of one of the two voices. Therefore, a preliminary playback test was performed with the two *Aptenodytes* species using only the lower frequency component of the calls as stimulus (Fig. 11).
When presented with the lower frequency component of the calls, positive responses were induced in chicks and adults for both species. When one voice in the call is experimentally suppressed, either by filtration (Aubin et al., 2000, for the emperor penguin) or by synthesizing a one-voice signal (Lengagne et al., 2001, for the king penguin), no response is observed for adults or chicks. Clearly, the acoustic contribution from two voices is required for call recognition in the genus *Aptenodytes*. This coding process, increasing the call complexity and resisting sound degradation, appears to have evolved in parallel with the loss of territoriality.

**e. Acoustic Solutions to Ecological Problems.** If we summarize the results obtained in our playback experiments with modified display calls, two acoustic code categories emerge in the penguin family (Fig. 12). The first one is elementary and concerns the nesting penguins, such as the Adélie and gentoo. These species identify the partner by analyzing the spectral profile and pitch of the call (timbre analysis). The second one is complex and concerns the two nonnesting penguins, the emperor and the king. Both these species use a vocal signature in the time domain based on an amplitude–time (AM) analysis for the emperor penguin and on a frequency–time (FM) analysis for the king penguin. This temporal analysis is complemented by another sophisticated system: the beats generated by the two-voice system. The temporal pattern of syllables associated with the two-voice system creates a huge variety of vocal signatures. This is necessary to distinguish between several thousand birds breeding without nests, that is, without visual cues. At the opposite extreme, identification by a one-dimensional parameter such as the timbre does not offer such an impressive variety of vocal signatures, and, thus, the possibility of confusion should exist with this system. Nevertheless, in nesting penguins, the nest is used as a meeting place, even when chicks have fledged, so that the probability that a bird emits the right call at the wrong place is weak. This strongly limits the possibilities for confusion.

**V. PERSPECTIVES**

**A. FUNCTIONALS**

The main perspective from these results is functional because these vocal signatures represent external markers of identity allowing the penguins to find their chicks or their parents in a crowd, that is, to find the kin-related birds with a single sound system when olfactory and, more surprisingly, visual cues are not used. During the brooding phase, the parent coming back from the sea has first to find its mate by its vocal signature if it is to find the egg.
or the small chick. Then the detection of the parent by the chick has an obvious survival value because usually parents feed only their own chick(s). The identification of the chick by the parent allows it to invest in its own chick and consequently to propagate its genes. But the general pattern is not symmetrical because, although a chick may gain from getting extra food from birds other than its parents, parents have to be cautious to give food only to their own chick(s). Consequently we have observed chicks trying to obtain “extra-feeding” from adults calling differently from their parents, sometimes with success when confusion occurs, for example, after a storm or when parents cannot find their own young (see Jouventin et al., 1995). We have also observed parents chasing away these “robbers” after hearing their call accurately.

B. Acoustics

According to the theory, to extract a signal from the background noise penguins analyze either frequency bands or temporal patterns (AM, FM, beats) of the call. The first coding–decoding system is used by nesting penguins such as the Adélie, the gentoo, and, in the first part of its call, the macaroni, and the second one is used by nonnesting penguins. The two codes seem not to be equivalent in efficiency. Frequency analysis is known to be particularly slow in a physical sense (Pimonow, 1962; Beecher, 1988) as well as physiologically (Bregman, 1978): when the duration of the analysis decreases, the uncertainty in the measurement of frequency increases. Accurate analysis of frequency is more time consuming than analysis in the time domain. The two codes seem also not to be equivalent in terms of production. Modulation in time is difficult to produce (Gaunt et al., 1973; Brackenbury, 1982): frequency or amplitude modulated calls require a high degree of control of the two sound sources of a bird. Nevertheless, this acoustic signal is particularly efficient in allowing an animal to locate the partner immediately in a noisy crowd on the move. Briefly, frequency analysis (easy to produce but costly in terms of analysis time) is enough to solve the relatively simple problem of individual recognition in nesting birds, whereas the complex temporal analysis of modulations used by the two nonnesting penguins (quick to analyze but costly to produce) appears as an adaptation to extreme acoustic and breeding conditions.

C. Comparative Approach

The case of the macaroni penguin, a nesting penguin, is perhaps intermediate between the two systems just described. Effectively, according to our first playback experiments, this species seems to identify the partner
on the basis of a simultaneous analysis of the spectral profile and of the temporal succession of syllables. However, this last parameter, again for a nesting species, seems simple involving only a rhythm fixed (= a number), whereas the emperor penguin has a more complex system using a succession of syllable-silence timings (= a “bar code”). Complementary experiments will be necessary to fully understand the coding–decoding process of the macaroni penguin and to compare with other species in this newly studied genus (*Eudyptes*).

**VI. Conclusion**

Highly vocal and colonial, penguins communicate in a particularly constraining acoustic environment to find their mate, parent, or chick. The screening effect of penguin bodies and the loud background noise prevent long-range communication and explain why some sophisticated adaptations have appeared, such as the highly developed “cocktail party effect” in the king penguin or the “courtesy rule” preventing jamming in the emperor penguin. These constraints explain the existence of complementary and visual behaviors optimizing vocal identification, such as the “head up” position when hearing or calling, particularly in the king penguin, and the memory of a feeding place in nesting penguins and in king penguins. They explain also the physical properties of the calls.

For species recognition, it seems that the penguins are not more sophisticated than other birds (see Becker, 1982, for a review). Thus, our playback experiments with the little blue penguin show that the acoustic code used for species identification is elementary. But, for individual recognition, it is surprising to find animals that are able to see nevertheless identifying their parents only by voice, in a noisy crowd, and even for some species without the help of a nest as a landmark.

In the same family, natural selection has resulted in various acoustic adaptations which are all the more sophisticated given that the problem posed was difficult to solve. In the nesting penguins where visual cues help vocal recognition, we found two main identification systems based on a single parameter, frequency, in the two species of *Pygoscelis* and on two elementary parameters, temporal and frequency patterns, in one species of *Eudyptes*. The vocal solutions found in closely related species are really different and demonstrate once more that behavior can evolve fast. It will be interesting to know what systems occur in other species of nesting penguins, not yet studied, to see if the number of acoustic identification systems is even larger.

In the nonnesting penguins, once again two closely related species have two different vocal identification systems. This dual system is much more
complex than in nesting species using topographical cues. The first identification system is based mainly on the variation of frequency in time for the king penguin and on the temporal syllable pattern in the emperor penguin. The second system relies on the two voices. It is common to the genus *Aptenodytes*, and this double-voice system is completely new because, although we have known for 30 years of the existence of this anatomical, physiological, and physical phenomenon, no function for it was known.

In fact, these new findings on a single family, although exceptional by the variety of its breeding habits, are all the more interesting since we have poor knowledge of the systems of individual identification in birds, particularly when they are not songbirds. Individual recognition playbacks are particularly difficult to carry out because to test a bird we have to present a particular call to each, whereas we need only one call type in the study of species recognition. It remains to be seen whether we can extrapolate our results to other penguins and then more widely among seabirds. We can certainly learn from this penguin study that nonsongbirds can be sophisticated in their vocal adaptations and deserve more attention, being currently relatively little studied. Enlarging upon the scope of the acoustic systems, it is also possible to study individual recognition beyond birds, for example, in mammals, where identification strategies by voice have been found in species such as fur seals (Roux and Jouventin, 1987; Charrier *et al.*, manuscript in preparation). Further studies may reveal interesting parallels in the acoustic identification systems between birds and mammals.

**VII. Summary**

In penguins, individual recognition is observed between mates and between parents and chick(s). During the past five years, their particular strategies of coding–decoding have been tested by playing back modified display calls to six species, in Australia (little penguin, *Eudyptula minor*), in Antarctica (Adélie penguin, *Pygoscelis adeliae*; emperor penguin, *Aptenodytes forsteri*), and in subantarctic islands (king penguin, *Aptenodytes patagonicus*; macaroni penguin, *Eudyptes chrysolophus*; gentoo penguin, *Pygoscelis papua*). All species use only vocal cues to identify their partner, but in territorial species the nest is used as a meeting point. In large species, such as the king and the emperor penguins, which do not have a nest, the brooder carries the egg or the small chick on the feet, while the mate, and then the chick, has to be located in the noisy colony without any topographical cue.

According to theory, to extract a signal from background calls, animals analyze either frequency bands or modulations (amplitude and frequency
modulations) of the partner’s call. The first coding–decoding system, used by nesting penguins, is easy to produce but costly in terms of analysis time. The second one, used by nonnesting penguins, is a vocal signature which is fast to analyze but costly to produce. This acoustic signal is particularly efficient as a means to locate immediately the partner on the move in a noisy crowd. Briefly, frequency analysis is enough to solve the relatively easy problem of individual recognition in nesting birds, while the complex temporal analysis of modulations of the two nonnesting penguins is an adaptation to extreme acoustic and breeding conditions.

The macaroni penguin, which we have begun to test, seems to use both a frequency code similar to that of the other nesting species and a temporal code close to the one of a nonnesting penguin species, but much simpler.

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