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ABSTRACT: Why do the left and right sides of the vertebrate brain play different functions? Having a lateralized brain, in which each hemisphere carries out different functions, is ubiquitous among vertebrates. The different specialization of the left and right side of the brain may increase brain efficiency—and some evidence for that is reported here. However, lateral biases due to brain lateralization (such as preferences in the use of a limb or, in animals with laterally placed eyes, of a visual hemifield) usually occur at the population level, with most individuals showing similar direction of bias. Individual brain efficiency does not require the alignment of lateralization in the population. Why then are not left- and right-type individuals equally common? Not only humans, but most vertebrates show a similar pattern. For instance, in the paper I report evidence that most toads, chickens, and fish react faster when a predator approaches from the left. I argue that invoking individual brain efficiency (lateralization may increase fitness), evolutionary chance or direct genetic mechanisms cannot explain this widespread pattern. Instead, using concepts from mathematical theory of games, I show that alignment of lateralization at the population level may arise as an “evolutionarily stable strategy” when individually asymmetrical organisms must coordinate their behavior with that of other asymmetrical organisms. Thus, the population structure of lateralization may result from genes specifying the direction of asymmetries which have been selected under “social” pressures. © 2006 Wiley Periodicals, Inc. Dev Psychobiol 48: 418–427, 2006.

Keywords: lateralization; hemispheric specialization; evolution of lateralization; handedness; brain asymmetry

BEHAVIORAL AND BRAIN LATERALIZATION IN NATURAL CONTEXT

Research on brain lateralization was used to be the province of psychologists and neuropsychologists studying the human brain. This quite exclusive focus on the human species has prevented consideration of behavioral lateralization as an evolutionary problem, that is, in terms of costs and benefits associated with possession of asymmetric brains. Of course, several researches have been devoted to the investigation of the advantages of lateralization (e.g., Levy, 1977), but, in my view, they failed to recognize the hard problem, for they considered the advantages of having an asymmetric brain without considering the riddle of the alignment of the direction of asymmetries at the population level. The reason why the problem was not apparent is, I believe, a lack of ecological evidence, that is, evidence that left–right asymmetries are ubiquitous in the behavior of organisms in their natural environments, and that such asymmetries convey costs and benefits. Now evidence for lateral biases affecting everyday behavior in the natural environment of a variety of species is widespread. However, because of increased specialization in the different scientific fields, it has gone
largely unnoticed among human neuropsychologists. Thus, I will start with briefly reviewing some of this evidence. However, my aim here is not to provide a complete review (see for recent reviews Rogers & Andrew, 2002; Vallortigara, 2005; Vallortigara, Rogers, & Bisazza, 1999). Rather I will use some selected examples (mostly from work in my own laboratory) to pave the way to some theoretical arguments.

Let us consider some cases in which behavioral lateralization can affect in a quite direct way the biological fitness of animals, that is, prey caching and agonistic behavior. Some years ago we performed some experiments showing that toads attack conspecifics to the left and strike preferentially at prey on the right (Robins, Lippolis, Bisazza, Vallortigara, & Rogers, 1998; Vallortigara, Rogers, Bisazza, Lippolis, & Robins, 1998). In the experiments a preferred prey was moved mechanically in a horizontal plane around the toad, entering first either its right or its left monocular visual field depending on the direction of rotation. We found that when the prey moved clockwise, and thus entered first the left and then the binocular field of vision, almost all of the tongue-strikes occurred in the right half of the binocular field. When the prey moved anticlockwise, and thus entered first the right and then the binocular field of vision, a more symmetrical distribution of strikes in the left and right halves of the binocular fields occurred. Thus, it seemed necessary that a prey entered the right half of the binocular visual field in order to evoke predatory behavior. Functionally, it was as if the toads’ left hemifield showed a form of stimulus-specific visual “hemineglect.”

Prompted by these observations, more recently we carried out some work with birds. It is well-known that humans primarily attend to objects in the left side of space, as shown in cancellation tasks routinely used during neuropsychological testing (Uttl & Pilkenton-Taylor, 2001). This asymmetry is thought to arise from a right hemispheric superiority in the control of spatial attentional resources (Nobre et al., 2004). Following right hemisphere damage, many patients display indifference to the left side of the world, attending primarily to the right hemisphere (“spatial hemineglect”); Brain, 1941; Halligan, Fink, Marshall, & Vallar, 2003). The syndrome has attracted considerable interest as it may shed light on the neural mechanisms underlying the spatial allocation of attention. A related phenomenon in healthy subjects is “pseudoneglect” (Albert, 1973; Jewell & McCourt, 2000): the slight systematic leftward bias in the allocation of attention in tasks, such as the cancellation task, in which subjects are asked to “cancel” visual targets on a sheet of paper placed midline in front of them. This is one of the tests used to diagnose visuospatial attention deficits in human patients. In this test, normal subjects show right lateralized inattention (Vingiano, 1991). We devised an adapted version of this task and administered it to two model bird species: the domestic chick (Gallus gallus) and the pigeon (Columba livia). The birds were given a free choice to orient towards and peck at grains spread evenly over an area in front of them. They could freely move their head, while their body was restrained and aligned centrally in front of the search area. Chicks and pigeons both showed a strong and significant leftward bias, spread uniformly across the left hemispace (Diekamp, Regolin, Güntürkün, & Vallortigara, 2005).

Spatial hemineglect is more frequent and severe after damage to the right hemisphere in right-handed humans; this asymmetry is usually explained assuming that neural circuits in the right hemisphere are capable of attending to and representing both sides of space, while the left hemisphere would be concerned only with the contralateral right side (Weintraub & Mesulam, 1987). Our results suggest that a similar asymmetry is present in the bird’s brain. Here, however, I would not concentrate on the cognitive and neural mechanisms mediating attentional asymmetries, but rather on the functional (in the biological sense) implications of these findings. Why do birds should show such a striking bias in spite of obvious ecological disadvantages? Grains of food are unlikely to be located systematically to the left of an animal’s midline in a natural environment!

Obviously, a reason why the right eye system seems to be not as good as the left eye system at finding targets in rapid search is likely to be that the right eye system is specialized for something else1. In search tasks, this has been shown to be approach to the selected target (pursuit if the target is alive) and its seizure (Tommasi & Andrew, 2002; Tommasi, Andrew, & Vallortigara, 2000). But this leaves us somewhat hungry for more: Is there any reason why all (actually, most) of the animals should show such a splitting of functions? Would it not be possible for each individual animal to gather the very same advantages, but with a different (mirror-image) organization of its brain (i.e., with a left hemisphere specialized at finding targets in rapid search and a right hemisphere specialized in approaching to selected targets and their seizure)? And, if so, would not we expect a random (50:50) distribution of the direction of lateralization in the overall population (with some animals choosing left for rapid search and

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1In birds with laterally placed eyes there is a virtually complete decussation at the optic chiasm (the fibers of the avian optic nerve cross over nearly completely). In the optic nerves less than 0.1% of the fibers proceed to the ipsilateral side (Weidner, Reperant, Miceli, Haby, & Rio, 1985), and only a limited number of axons recross via the mesencephalic and thalamic commissures. This means that information entering each eye is largely, though not completely (see Rogers, 2002a; Rogers & Deng, 1999), processed by the contralateral side of the brain. Thus, by simply temporarily occluding one eye we can gather insights on lateralized functions of the avian brain.
other choosing right)? Before trying an answer let us consider some more evidence.

The same toads used in the prey-catching experiment were also tested for agonistic behaviors in the form of tongue-strikes at competitors during feeding (Robins et al., 1998). Toads showed a population bias to strike with the tongue at conspecifics when these were occupying their left visual field. Thus, toads seem to be more likely to attack a prey to their right side (and ignore them to their left side) and to attack a conspecific to their left side (and ignore them to their right side).

Intriguingly, the same results have been obtained in a variety of other species, phylogenetically very disparate. For instance, a similar phenomenon has been shown to occur in birds (i.e., domestic chicks, review in Rogers, 2000). Lizards (Anolis sp.) have also been shown to have a preference to attack conspecifics on their left side by Deckel (1995). In mammals Casperd and Dunbar (1996) reported that male gelada baboons used their left visual field significantly more frequently than their right during fights, threats, and approaches of conspecifics.

Now consider another behavior of enormous biological significance—response to predators. In a series of experiments we presented toads with a simulated predator entering suddenly into their left or right monocular or binocular visual fields (Lippolis, Bisazza, Rogers, & Vallortigara, 2002). We found that toads were more likely to react, most often by jumping away, when a simulated predator was located in their left monocular field than when it was located in their right monocular field. Again, similar results were obtained in birds and mammals (Vallortigara & Rogers, 2005a for a review).

Complementary eye use has been observed in cognitive tasks as well. Chicks trained to discriminate food boxes on the basis of position-specific or object-specific (e.g., color) cues, used the left eye to encode position and the right eye to encode color (Vallortigara, Regolin, Bortolomiol, & Tommasi, 1996 and see also Vallortigara, Pagni, & Sovrano, 2004).

Recently, we documented complementary eye use in naturalistic settings in the black-winged stilt (Himantopus himantopus; see Ventolini et al., 2005) during predatory pecking and during courtship and mating behavior. We found that black-winged stilts have a population-level preference for using their right monocular visual field before predatory pecking; moreover, pecks that followed right hemifield detection were more likely to be successful than pecks that followed left hemifield detection, as evinced by the occurrence of swallowing and shaking head movements after pecking. In contrast, shaking behavior, exhibited as part of courtship displays, and copulatory attempts by males were more likely to occur when females were seen with the left monocular visual field.

I already mentioned that domestic chicks have higher levels of attack when tested monocularly with the left eye open. Interestingly, as the black stilts studied in natural conditions, chicks also learn to discriminate grain from pebbles better when tested with the right eye open (Andrew, 1991, 2002; Andrew, Mench, & Rainey, 1982; Rogers, 1991). Similar results have been reported for a variety of other species of birds, for example, pigeons (Güntürkün, 1997, 2002), zebra finches (Alonso, 1998), and quails (Valenti, Sovrano, Zucca, & Vallortigara, 2003).

A final example which I discuss is particularly relevant with respect to the hypothesis I am going to put forward. We found (Bisazza, De Santi, & Vallortigara, 1999; and see Vallortigara & Bisazza, 2002 for a general review) that in some species of fish that exhibit predator-inspection responses, most individuals prefer to swim with a conspecific on the left side (using the lateral field of the left eye) while monitoring a predator on the right side (using the lateral field of the right eye). Such a preference for a fish to position itself so that the image of a conspecific is on its left side has been reported even in the absence of predators in several different species of teleosts (De Santi, Sovrano, Bisazza, & Vallortigara, 2001; Sovrano, 2004; Sovrano, Rainoldi, Bisazza, & Vallortigara, 1999; Sovrano, Bisazza, & Vallortigara, 2001).

One must suppose that there would be striking disadvantages to possess a perceptual system that is asymmetrical to any substantial degree. The physical world is indifferent to left and right and any deficit on one side would leave an animal vulnerable to attack from that side or unable to attack prey or competitors appearing on that side. Note that perceptual asymmetries have been revealed in humans under very artificial conditions (i.e., tachistoscopic viewing or dichotic listening) and it has been usually maintained that they cannot be apparent in the everyday behavior. But ethological evidence shows that such asymmetries are not at all rare in the animal kingdom; instead they are quite ubiquitous in animal behavior. All this demands for an explanation.

**LATERALIZATION AT THE INDIVIDUAL LEVEL: COSTS AND BENEFITS**

A possible explanation for the existence of such pronounced left–right lateral biases in the behavior of animals in naturalistic contexts would be to argue that the advantages associated with possession of an asymmetric brain can counteract the ecological disadvantages associated with lateral biases in overt behavior.

An advantage that lateralization may offer is to increase neural capacity, because specializing one hemisphere for a particular function leaves the other hemisphere free to perform other additional functions.
for brain lateralization to be present in individuals without for vigilance against predation? Would it not be simpler efficiency is unrelated to how other individuals are explain the alignment in the direction of lateralization at the existence of individual lateralization, but it does not hard problem of lateralization. It may explain the increased brain efficiency did not provide an answer to the Iacoviello, Buonavoglia, & Vallortigara, 2006). However, & Vallortigara, 2004; Quaranta, Siniscalchi, Frate, (for instance, we did not discuss here the issue of presenting the model predator had no difficulty in learning lateralized chicks tested on the pebble-floor test without those incubated in the dark, since the light exposure aligns with lateralization of the brain is probably not complete and strengthens visual lateralization on a number of tasks (see Rogers, 1982, 1990, 1991, 2002a,b). Previously, it was shown that strongly lateralized (light-exposed) chicks detected a model predator sooner than the weakly lateralized (dark-incubated) ones, at least with the left eye (i.e., when the right hemisphere was attending to the stimulus, see Rogers, 2000). This result was confirmed by scoring not only the response to the model predator but also the chick’s ability to learn to peck at grain versus pebbles. Strongly lateralized chicks learnt pecking at grains of food (and to avoid pecking at pebbles) far better than weakly lateralized chicks and they were also more responsive to the model predator. In fact, the weakly lateralized chicks frequently failed to detect the model predator as it passed overhead: they were unable to attend to the two separate tasks simultaneously (weakly lateralized chicks tested on the pebble-floor test without presenting the model predator had no difficulty in learning to discriminate grain from pebbles).

The list of the “computational” advantages associated with lateralization of the brain is probably not complete (for instance, we did not discuss here the issue of the relationships between brain lateralization and immune function, see e.g., Quaranta, Siniscalchi, Frate, & Vallortigara, 2004; Quaranta, Siniscalchi, Frate, Iacoviello, Buonavoglia, & Vallortigara, 2006). However, increased brain efficiency did not provide an answer to the hard problem of lateralization. It may explain the existence of individual lateralization, but it does not explain the alignment in the direction of lateralization at the population level. This is because individual brain efficiency is unrelated to how other individuals are lateralized. Why do most animals of a species should possess a left eye (or hemifield) better suited than the right for vigilance against predation? Would it not be simpler for brain lateralization to be present in individuals without any specification of its direction (i.e., with a 50:50 distribution of the left- and right-forms in the population)?

## LATERALIZATION AT THE POPULATION LEVEL: COSTS AND BENEFITS

Obviously one can argue that the alignment of the direction of lateralization at the population level is a mere by-product of genetic expression. However, this cannot be so because it has been proved that selection for the strength (without direction) of lateralization is possible. This has been shown for instance by Collins (1985) with mice. Moreover, apart from this empirical issue, there is another aspect, a mostly theoretical one, which requires lateralization at the population level to be accounted for in biological terms. The puzzle is that any alignment in the direction of the asymmetries in most individuals of a species may be disadvantageous, as it makes individual behavior more predictable to other organisms. Let’s imagine that some species of animals react to the view of a predator by turning preferentially leftward or rightward (see Heuts, 1999 for evidence in fish). If the predator is facing individually asymmetric prey, then it cannot do any prediction about the possible behavior of a particular prey: the prey certainly would behave asymmetrically, but there would be exactly the same probability of its being left- or right-preferent. On the other hand, if prey are lateralized at the population level, then that would mean that the predator can learn, from experience arising from several encounters, that there is a higher probability that these particular type of prey escape, say, to the left rather than to the right. Thus, predators could exploit the regularity and predictability of behavior that arises from population-level lateralization. Such a condition seems to be not very good for the prey. In evolutionary terms, this is equivalent to say that there should have been important selective pressures to maintain directional asymmetry in the face of its potential disadvantage. It is simply unlikely that directional asymmetries would be maintained by mere accident. Individual-level asymmetries would confer all the advantages that individual brains need in terms of efficiency, and aligning the direction of the asymmetries would confer only disadvantages. Thus, why did directional asymmetries evolve at all?

Obviously, there is something missing in the example of prey–predator interaction that I discussed above. And what is missing is the possibility that left–right lateral biases are important not just for the individual, but also for the other individuals of the group. If our hypothetical animal would be entirely solitary, then our analysis would be correct and complete: individual lateralization should be expected. But (some) animals live in groups. For
instance, some species of fish form shoals. The structure and size of shoals is likely to have been selected for antipredatory purposes. Each individual fish maximizes its individual fitness by staying in the shoal (not because of cooperation, but just because shoaling behavior increases the probability that someone else would be the target of a predator). Individuals within a shoal should exhibit coordinated activity and it is obvious that, in order to maintain the shoal structure, each individual should also coordinate its lateral biases with the lateral biases of the other individuals.

This is of course a quite specific example of a more general idea. Sometimes what is better to do for an (asymmetrical) individual depends on what the other (asymmetrical) individuals of the group do. More technically, the hypothesis that I want to discuss is that the alignment of the direction of behavioral asymmetries in a population can arise as an evolutionarily stable strategy (ESS, a concept introduced in evolutionary biology by Maynard-Smith, 1982), when individually asymmetrical organisms must coordinate their behavior with that of other asymmetrical organisms (see Vallortigara & Rogers, 2005a,b for an extended discussion, with commentary, of the hypothesis).

We formalized a simple game-theory model showing that population-level lateralization can indeed be evolutionarily stable (Ghirlanda & Vallortigara, 2004). The model was framed in the context of prey–predator interactions, but it can be extended to other scenarios. Consider prey–predator interaction. Prey lateralized in the same direction have a greater chance of keeping together as a group. On the other hand, predators may learn to anticipate prey escape movements, or to approach prey from a given direction. So there will be some benefit to learn to anticipate prey escape movements, or to approach together as a group. On the other hand, predators may the same direction have a greater chance of keeping together, each individual should also coordinate its lateral biases with the lateral biases of the other individuals.

The meaning of such a situation is that the majority of prey get protection by keeping together, but pay a cost because predators are better at handling them. A minority of prey manages to enjoy the same escape probability by trading-off protection from the group with an advantage in the face of predators. (Note that since the model does not assume any intrinsic benefit of left or right lateralization, there are always two specular solutions, one with a majority of left-type prey and one with a majority of right-type prey).

In summary, game-theory models show that populations consisting of left- and right-type individuals in unequal numbers—the most common situation among vertebrates—can be evolutionarily stable if being lateralized in one or the other direction has frequency-dependent costs and benefits. A very interesting convergence of results in a similar direction arises from studies of population genetics of human handedness. As it is well known humans exhibit hand preference for most manual activities with left-handers being a minority in all human populations (McManus, 2002). The persistence of such a polymorphism of handedness is a puzzle, because this trait is heritable (though its underlying genetic mechanisms are still obscure) and severe fitness costs are associated with left-handedness (actually it is becoming more and more clear that to be nonright-handed, or to be poorly left-handed, see Gerardin et al. (2006), this issue; Leconte & Fagard (2006), this issue). Thus, some sort of benefit should exist to counteract these costs and to maintain the polymorphism. Quite interestingly, left-handers have an advantage in sports involving dual confrontations, such as fencing, tennis, and baseball, but not in noninteractive sports, such as gymnastics (Raymond, Pontier, Dufour, & Moller, 1996). Hence, the advantage does not arise from the well-known association between use of the left hand and direct control of it by the more visuospatially talented right-hemisphere. The advantage is a frequency-dependent one: left-handers are relatively uncommon, as both left- and right-handers are less familiar with this category of competitor. Analyses of cricket have shown that the frequency of left-handers in this sport is best explained by a negative frequency-dependent selection mechanism (Brooks, Bussière, Jennions, & Hunt, 2004).

Faurie and Raymond (2004) have recently shown that the frequency of left-handers is strongly and positively correlated with the rate of homicides across traditional societies: ranging from 3% in the most pacific societies to 27% in the most violent and warlike. The interpretation of this finding would be that the advantage of being left-handed should be greater in a more violent context, which should result in a higher frequency of left-handers. In the absence of any selection pressure, the resulting equilibrium should be a 1:1 ratio of right-/left-handers.
LATERALIZATION AN ESS?

Two theoretical points need to be stressed at this point. First, the theory outlined here should not be confused with theories arguing for a socio-cultural origins of lateralization (review in McManus, 2002). On the contrary, I am arguing here for a basically genetical theory. I am quite convinced that there are genes for left–right asymmetries and that some of them also code for direction of asymmetry (see Barth et al., 2005; Concha, Burdine, Russell, Schier, & Wilson, 2000; Halpern, Liang, & Gamse, 2003; Sovrano & Andrew, 2005, in press for very promising search of these genes using the zebrafish model). The hypothesis I outlined here concerns the “why” such directional genes should have been selected: for reasons, I believe, that have to do with the development of stable equilibria in populations in which the needs of coordination among asymmetrical individuals determine costs and benefits associated with the presence of left–right lateral biases. Second, it is also important to stress that the hypothesis holds only because asymmetries in the brain might manifest themselves in overt behavior as left–right biases. If asymmetries in the brain are without any apparent effect in the left–right behavior of organisms (and certainly this sort of asymmetries also exist), then no selection pressures for aligning the direction of asymmetries among different individuals would arise.

IS POPULATION-LEVEL LATERALIZATION AN ESS?

Though it proves mathematically conceivable that stable equilibria of left- and right-type organisms in unequal numbers can arise when the fitness of each lateralized individual depends on its aligning with the direction of bias of the majority of the individuals of the group (Ghirlanda & Vallortigara, 2004), this represents a mere theoretical possibility. Mathematically the theory is sound, but is there any empirical evidence that actually supports it? In part, empirical evidence is provided by studies on frequency-dependent effects on human left-handedness mentioned above. It is clear, however, that as an evolutionary hypothesis, that is, a hypothesis concerning a historically event, it is difficult to test it in current-living organisms. The ESS hypothesis would make the quite straightforward prediction that “social” organisms should be lateralized at the population level and “solitary” organisms at the individual level only. But this obviously refers to the conditions at the origin of a very complex evolutionary trajectory. I would envisage that the early solitary chordates with a bilaterally symmetrical organization of the body in which lateralization first appeared were lateralized at the individual level, because that would enhance their brain efficiency. As a result of the presence of lateralization in the brain (and certainly in other parts of the body) lateral biases in behavior became apparent. When these individually asymmetric animals started to interact to each other in a manner for which their lateral biases would matter, then selection pressures became at work and favored the genes that promoted the alignment of lateralization at the population level.

Now the problem is that when we are speaking of the modern, current-living vertebrates, arguing that a species would be completely solitary or completely social is very hard, at least for higher vertebrates (birds and mammals). Moreover, many current-living vertebrates that are considered today to be solitary actually derive from more social ancestors and therefore they may have retained population-level rather than individual-level asymmetries for this reason. A similar point has been raised with respect to ontogenetic development (see Vallortigara & Rogers, 2005a). For instance, anuran amphibians exhibit relatively poor sociality, except in their juvenile stages: in several species, tadpoles show aggregative behavior based on kin and familiarity, and population-level lateralization has been observed in this behavior. It is thus plausible that directional asymmetries in the relatively solitary adults are retained from the juvenile stages. Finally, it is also obvious that some forms of asymmetries that are unlikely to have been directly selected as ESS strategy in social contexts (say, limb usage in toads, e.g., Bisazza, Cantalupo, Robins, Rogers, & Vallortigara, 1996) could have evolved as population-level biases as by-product of other biases that in fact evolved as ESSs. It is likely, indeed, that when an asymmetry is stabilized as a directional one, other asymmetries that in principle would not require any alignment at the population level because irrelevant to any social interactions would organize themselves as directional as well simply because a directional organization in the two sides of the brain already exists.

Nonetheless some tests of the ESS hypothesis can be carried out on certain current-living species in which the distinction between solitary and social behavior can be defined quite clearly with respect to at least some aspects of behavior and in which it is likely that no major changes in their sociality have occurred in evolutionary terms. A case in point is antipredatory behavior of fish that shoal versus those that do not shoal. Shoaling in fish is a way of gaining protection against predators and it has been shown that this sort of grouping can arise from very simple “selfish” principles (Dawkins, 1976). We investigated whether shoaling 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 a dummy predator could be seen (Bisazza, Cantalupo,
Capocchiano, & Vallortigara, 2000). The social tendency 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. Some species were found to be gregarious (i.e., to shoal) and all of them were found to be lateralized for turning bias at the population level; some other species were found to be nongregarious (i.e., not shoaling) and most of them were found to be lateralized at the individual level. These data fit the ESS hypothesis quite well.

Further tests of the ESS hypothesis can be associated with the fact that it predicts changes in the strength of occurrence of behavioral asymmetries depending on ecological factors, such as degree of predatory pressures. Evidence for this has been provided very recently by Brown, Gardner, and Braithwaite (2004) who found that populations of a single fish species collected from high predation areas showed strongly lateralized behaviors, whereas fish from low predation areas showed no evidence of cerebral lateralization (Brown et al., 2004).

Lonsdorf and Hopkins (2005) have shown recently that when combining data across studies, chimpanzees show a population-level bias for termite fishing. Interestingly, they also showed that there is regional variation in handedness for tool use in wild chimpanzees. Moreover, offspring typically develop patterns of asymmetry that resemble their mothers. Thus, these findings somewhat support the view of a role of social systems and their influence on handedness in primates, consistent with the EES theory.

Several other issues deserve to be investigated. For instance, positive and negative mechanism of frequency-dependent selection can be contrasted in animal behavior study with respect to lateralization. Tactics of coordinated antipredator behavior provides an example of positive frequency-dependent selection, since the behavior of each individual is affected by similar behaviors displayed by the majority of individuals in the group. An individual’s fitness is thus dependent upon the animal’s ability to conform to the rest of the group. However, competition for food also increases with group size and therefore, in some circumstances, it may pay to behave differently from the rest of the group. Group foraging behavior, therefore, may provide an example of negative frequency-dependent selection. A correct balance between foraging and antipredator behavior is essential if individuals are to maximize fitness, and such a balance can predict and explain any variation in the pattern of lateralization we can observe at the population level in a wide range of species.

Finally, it should be stressed that, although it is true that in current-living organisms one cannot argue (at least in higher vertebrates) that a species is entirely social or not social, this should not prevent us from studying lateralization within a ESS framework. A case in point could be related to brain asymmetries in face processing. There is evidence that portraits are typically produced with the left side of the face overrepresented, with the head turned slightly to the sitter’s right. The leftward bias seems to be determined by the sitters and their desire to display the left side of their face, which is controlled by the emotive, right cerebral hemisphere (Nicholls, Clode, Wood, & Wood, 1999). It has been suggested that the motivation to portray emotion or, conceal it, might explain why portraits of males show a reduced leftward bias and also why portraits of scientists from the Royal Society show no leftward bias (Nicholls et al., 1999). Furthermore, since the left side of the face is more “expressive” (because of the major involvement of the right hemisphere) than the right side of the face, people (and perhaps other animals) may probably make use of this by presenting their left or right side depending on tasks and social context (e.g., showing the right side when lying). Intriguingly, semiwild orang-utans have been found to preferentially expose the left side of their face to observers, as they look sideways at the observer (Kaplan & Rogers, 2002). Of course these strategies of face-showing would work only assuming a population structure for the lateral biases. Thus, these situation can be studied using theory of games as we did with prey–predator interactions (Ghirlanda & Vallortigara, 2004). Consider expressivity of the face. On the one hand, there could be advantages in terms of predictability of behavior if in all individuals the left side of the face is more “expressive.” You can approach conspecifics on a particular side. On the other hand, animal communication quite frequently has not evolved to transmit honest information, but rather to deceive (Dawkins, 1976). From this point of view, having an unpredictable (50:50) expressive side of the face may confer advantages. However, if all individuals choose unpredictability (i.e., to be liars) then a disadvantage for every single individual would arise. Very likely the expected outcome would be a majority of individuals that behave cooperatively (aligned) and a minority (frequency-dependent) not aligned. This is an entirely new field that deserves to be explored further (see e.g., Güntürkün, 2003, for head turning biases requiring mutual coordination during social interaction in humans). In fact, I believe that whether or not the ESS hypothesis would prove correct as a general theory for the origins of (directional) lateralization (and see e.g., Corballis, 1997 for different views), it has the merit of providing a bridge for the previous disparate approaches of neuropsychology and evolutionary biology to the riddle of our lopsided brain.

NOTES

I gratefully acknowledge support by grants MIUR Cofin 2004, 2004070353_002 “Intellat,” MIPAF “Benolat,” and Waltham Foundation during preparation of this manuscript.
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