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Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization

Giorgio Vallortigara
Department of Psychology and B.R.A.I.N. Centre for Neuroscience, University of Trieste, 34123 Trieste, Italy.
vallorti@univ.trieste.it **http://psico.univ.trieste.it/labs/acn-lab/**

Lesley J. Rogers
Centre for Neuroscience and Animal Behaviour, School of Biological, Biomedical and Molecular Sciences, University of New England, Armidale, NSW 2351, Australia.
lrogers@une.edu.au
http://www.sciences.une.edu.au/zoology/lesleyrogers.asp

Abstract: Recent evidence in natural and semi-natural settings has revealed a variety of left-right perceptual asymmetries among vertebrates. These include preferential use of the left or right visual hemifield during activities such as searching for food, agonistic responses, or escape from predators in animals as different as fish, amphibians, reptiles, birds, and mammals. There are obvious disadvantages in showing such directional asymmetries because relevant stimuli may be located to the animal's left or right at random; there is no a priori association between the meaning of a stimulus (e.g., its being a predator or a food item) and its being located to the animal's left or right. Moreover, other organisms (e.g., predators) could exploit the predictability of behavior that arises from population-level lateral biases. It might be argued that lateralization of function enhances cognitive capacity and efficiency of the brain, thus counteracting the ecological disadvantages of lateral biases in behavior. However, such an increase in brain efficiency could be obtained by each individual being lateralized without any need to align the direction of the asymmetry in the majority of the individuals of the population. Here we argue that the alignment of the direction of behavioral asymmetries at the population level arises as an "evolutionarily stable strategy" under "social" pressures occurring when individually asymmetrical organisms must coordinate their behavior with the behavior of other asymmetrical organisms of the same or different species.

Keywords: asymmetry; brain evolution; brain lateralization; development; evolution of lateralization; evolutionarily stable strategy; hemispheric specialization; laterality; lateralization of behavior; social behavior; theory of games

1. The rise of a neuroethology of the dual brain

Research on the topic of cerebral lateralization has been characterized by periodic peaks and troughs in level of interest. For instance, the early wave of excitement raised by Broca's discoveries in the 1860s waned after the turn of the century. Similarly, the renaissance of interest induced by Sperry's discoveries with split-brain patients in the 1960s has shown signs of decline in recent years (Efron 1990). It should be noted that, until very recently, virtually all research on cerebral lateralization had been confined to the laboratories of experimental psychologists and neuropsychologists and was largely centered on the human species. Even after the evidence for the existence of cerebral lateralization in nonhuman species had become impressive, extending from fish to primates (for recent reviews see Rogers 2002a; 2002b; 2002c; Rogers & Andrew 2002; Vallortigara 2000; Vallortigara et al. 1999), the subject remained largely outside the realm of biology on account of a focus on the causal mechanisms rather than on its function. In the past few years, however, something really new has appeared: namely, evidence for lateral biases affecting everyday behavior in the natural environment of a variety of species. Though this has gone largely unnoticed among neuropsychologists who study humans, we believe that such evidence is going to force all of us to rethink some of the basic issues on the evolution of cerebral lateralization; most important, it can also provide a bridge between the (once-believed) disparate disciplines of neuropsychology and evolutionary biology, as well as between neuropsychology and developmental biology.

Before considering why we should care about lateral biases exhibited in naturalistic settings, let us describe some examples. Consider first the response to predators. A variety of species of different classes (see Vallortigara et al. 1999 and Rogers 2002b, for extensive reviews) appear to be more reactive to predators seen in their left, rather than right, hemifield. Toads, for instance, are more likely to react, most often by jumping away, when a simulated predator is introduced into their left monocular field than when it is introduced into their right monocular field (Lippolis et al. 2002), and recently the same result has been obtained in dunnarts, *Sminthopsis macroura* (Lippolis et al. 2005) and chicks (Lippolis & Rogers, in preparation). These findings suggest

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that predator-escape and associated fear responses are controlled by the right side of the brain. Some evidence indicates that also in rats the right hemisphere controls fear responses: lesions of various types, including infarcts, in the right hemisphere elevate activity in the open field (Robinson 1985), presumably because the fear response of freezing is suppressed. Robinson and Downhill (1995) have drawn attention to the similarity between these effects of right hemisphere infarct in rats and the heightened anxiety that occurs in humans following damage to the right hemisphere. Neurochemical changes, apparently associated with long-term alterations of neurotransmission, are also induced in the right, but not the left, hemisphere by predator stress, as shown in rats and cats (Adamec et al. 2003).

In some circumstances, an approach towards, rather than avoidance of, a potential predator is needed. Some fish leave their school in groups of two or three to approach a predator and examine it more closely. By placing a mirror on the left or right side of a tank, Bisazza et al. (1999) found that the test fish approached a predator more closely in order to inspect it when the mirror was on its left side than when the mirror was on its right side. 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 eight different species of teleosts (Sovrano et al. 1999; 2001; see also Sovrano 2004). Similarly, the preference for a fish to position itself so that the image of a predator being inspected is on its right side has been observed in the absence of other conspecifics in several species of teleosts (De Santi et al. 2000; 2001). Even tadpoles have been shown to prefer to position themselves so that the image of a conspecific is on their left side (Bisazza et al. 2002; Dadda et al. 2003).

Giorgio Vallortigara, Professor of Behavioural Neuroscience and Animal Cognition at the University of Trieste, Italy, is the author of over 150 scientific papers, most in the area of animal cognition and comparative neuroscience. He discovered the first evidence of functional brain lateralization in the so-called "lower" vertebrate species (fish, amphibians); he also worked on recognition of partly occluded objects, spatial cognition and geometric modularity in animals. Vallortigara served in the editorial boards of several psychobiology and neuroscientific journals and has been the recipient of grant awards from, among others, the Association for the Study of Animal Behaviour and the Universities Federation for Animal Welfare.

Lesley J. Rogers, Professor of Neuroscience and Animal Behaviour at the University of New England, Australia, is the author of fourteen books and over 200 scientific papers and book chapters, most in the area of brain development and lateralization of brain and behaviour. She obtained her first degree (with Honours in zoology) at Adelaide University and her D.Phil. at Sussex University. Subsequently, Sussex University awarded her a Doctor of Science. Rogers is a Fellow of the Australian Academy of Science. Her other awards include Australian Research Council Special Investigator, Clarke Medal from the Royal Society of NSW, and Centenary Medal awarded for service to neuroscience and Australian society.

In contrast to their leftward responses to predators, toads strike preferentially at prey to their right side (Vallortigara et al. 1998). The rightward bias for feeding responses has also been documented in a variety of species of birds (chicks: Andrew et al. 1982; Mench & Andrew 1986; Rogers 1997; Vallortigara et al. 1996; pigeons: Güntürkün 1997; Güntürkün & Kesch 1987; parids and corvids: Clayton & Krebs 1994; zebrafinch: Alonso 1988; quails: Valenti et al. 2003; black-winged stilts: Ventolini et al. 2005) and has been traced back to an appearance during evolution as early as teleost fish (Miklosi & Andrew 1999; Miklosi et al. 1998). These rightward biases for prey catching and foraging responses are apparent when the prey or food has to be discriminated from similar targets: for example, toads show a right hemifield preference for directing tongue strikes at prey that has to be recognized precisely and "handled" with care (e.g., crickets) but not for simplified prey models, such as a rectangular silhouette moving along its longitudinal axis (Robins & Rogers 2004). Similarly, chicks show the rightward bias for pecking at grain (controlled by inputs from the right eye) that has to be discriminated against a distracting background or uncovered by removing a lid from a bowl (Andrew et al. 2000). These findings indicate that the left hemisphere, which primarily processes input from the right eye, controls responses that require considered discrimination between stimuli and manipulation of objects. To some degree this particular specialization of the left hemisphere is manifested in hand preferences in primates (discussed later). As the left hemisphere controls the right hand, planned use of the right hand for fine manipulation of objects, as in writing by humans, may have arisen from this ancient evolutionary specialization.

Aggressive responses also seem to be strongly lateralized in intraspecific agonistic settings: toads (Robins & Rogers 2004; Robins et al. 1998; Vallortigara et al. 1998), lizards (Deckel 1995; 1997; Hews & Worthington 2001; Hews et al. 2004), chicks (Vallortigara et al. 2001), adult hens (Rogers 1991), and gelada baboons (Casperd & Dunbar 1996) direct more aggressive responses to conspecifics on their left side than they do to those on their right side. These findings indicate that aggressive responses are controlled by the right side of the brain, usually by the right hemisphere, as shown clearly in the chick by intrahemispheric treatment with glutamate (Deng & Rogers 1997). In fact, the expression of aggression appears to be inhibited by the left hemisphere as impaired functioning of the left hemisphere, following glutamate treatment, causes the release of aggressive responses. A similar inhibition of the right hemisphere by the left hemisphere has been shown in humans: impairment of the left hemisphere leads to the expression of more intense emotions (Nestor & Safer 1990), likely because the latter are controlled by the right hemisphere. In some cases, the increased intensity of emotion expressed is manifested as hostility and aggression. For example, epileptic seizures with their focus in the left temporal lobe increase hostile feelings (Devinsky et al. 1994), and impaired activity of the posterior regions of the left hemisphere is associated with heightened aggression (Graae et al. 1996). Damage to the frontal region of the left hemisphere, which forces the equivalent region of the right hemisphere to assume control, leads to decreased levels of interaction with other people, and brain scans have revealed elevated activity in the right hemisphere in panic-prone subjects (Davidson 1995). More recently, fMRI scans

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have added further support to this particular functional specialization of the right hemisphere in humans (e.g., Tabert et al. 2001).

Although most of these data show similarity in the directional bias of responses among the different species, there are exceptions. For instance, a study conducted on sixteen species of fish presented with a predator model behind a barrier with vertical bars revealed a population-level turning preference in ten species, but six of those species showed a rightward bias and four a leftward bias (Bisazza et al. 2000). More recently, Templeton and Gonzalez (2004) have shown that, in contrast to the right eye bias for feeding responses that require discrimination of food from background in chicks, pigeons, parids and corvids, quails and zebrafinches (cited earlier), the European starling performs discrimination tasks better when using the left eye. Similarly, species differences in lateralization have been reported in vigilance behavior in birds: Franklin and Lima (2001) observed two avian species feeding alongside a wall and recorded side preferences, which most probably reflect the eye chosen to monitor for predators; whereas juncos oriented themselves so that their right eye is looking outward away from the wall, tree sparrows favored the left eye in this regard. It is difficult to establish whether species variations in the direction of laterality reflect basic differences in laterality per se or differences in the behavioral strategies. The direction of turning to go around a barrier studied in fish must depend on when the final decision to approach is made (see Andrew 2002) and it is not surprising that different species should exhibit different strategies in this regard. The same holds for the use of object-centered and position-centered searching strategies in visual discrimination learning: it could be that some bird species (e.g., European starlings) rely more on spatial than nonspatial cues during foraging, thus favoring left-eye/right-hemisphere strategies. Clearly, understanding whether the direction of lateralization is the same in all species would be relevant to understanding the possible homology or homoplasy of cerebral lateralization among vertebrates. It is quite possible that, for example, two species have the usual general pattern of lateralization of brain function (say, the right hemisphere for spatial functions and rapid, species-typical responses versus the left hemisphere for considered responses; see Table 1) but show opposite directions of lateralization in a particular behavior on account of processing the available inputs differently because they experience different degrees of arousal/emotionality in the same context (e.g., eye preferences in birds to view certain stimuli may reflect choice of the hemisphere used to process the visual inputs, as suggested by Dharmaretnam & Andrew [1994], Tommasi & Vallortigara [2001], and Vallortigara [2000]).

Recent evidence from molecular biology, using the zebrafish model, suggests that asymmetries of the dorsal diencephalic region of the brain could be related to the highly conserved Nodal signaling pathway (Concha et al. 2000; Gamse et al. 2003; Halpern et al. 2003). In fact, the overall evidence available suggests that there is a common pattern of lateralization among vertebrates (see Table 1; for some

Table 1. *Summary of the lateralized functions discussed in the text*

Left Hemisphere	Right Hemisphere
Prey discrimination and catching (fish, toads)	Predator detection (fish, chicks)
Foraging with discrimination and/or manipulation of food items (birds)	Predator escape (frog tadpoles, fish, toads, chicks, dunnarts)
Approach and manipulation of objects (birds, monkeys, apes)	Neurochemical changes with predator stress (rats, cats)
	Avoidance/withdrawal (monkeys, apes, humans)
Inhibition of aggression (chicks, humans)	Fear (chicks, rats)
Inhibition of intense emotions, especially negative emotions (humans)	Aggression (toads, lizards, chicks, monkeys)
	Courtship and copulatory behavior (newts, birds)
	Expression of intense emotions (monkeys, apes, humans)
Recognition of categories/attention to large changes (birds, rats)	Contact/monitoring of conspecifics (fish, tadpoles)
Recognition of species-typical vocalizations (birds, mice, some monkeys, humans for speech)	Recognition/analysis of faces (sheep, monkeys, humans)
	Recognition of individual conspecifics (chicks)
Attention to landmarks (birds)	Spatial cognition (birds, rats, humans)
Attention to local cues (birds, monkeys, humans)	Attention to global cues (chicks, monkeys, humans)
Considered responses:	*Rapid, species-typical responses. Visuo-spatial analysis centered on relational properties of the spatial layout*
Able to inhibit responding while deciding between alternative responses	
Visuo-spatial analysis centered on local features	

Note: This table serves to support our text and is not a comprehensive summary of all of the research showing lateralized behavior in animals, nor of all of the species in which these lateralizations have been shown. Cases in which a particular form of lateralized behavior has been shown in several related species are noted generically (e.g., birds) and cases in which it has been reported in only one species so far are noted specifically (e.g., chicks, referring to the domestic chick).

The columns represent the left and right hemispheres. Similar types of behavior occur in the same grouping of rows. The bottom grouping of rows is a general summary of the functional differences between the hemispheres. Note that some of the left and right hemisphere differences are not absolute but relative biases.

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general reviews see also Andrew 2002; Güntürkün 2003b; Malaschichev & Wassersug 2004; Rogers 2002b; Vallortigara 2000; Vallortigara et al. 1999), and, although species differences may occur in the expression of lateralization at one level of neural organization or in one type of behavior and not another, the overall similarities across species strongly support the hypothesis of an early common origin of lateralization in vertebrates. However, it is not our particular interest to discuss this issue here, since our arguments to follow are totally indifferent as to whether lateralization in, say, fish and primates, is the result of homology or evolutionary convergence.

2. Disadvantages of lateral biases in behavior

On purely theoretical grounds, there appear to be obvious disadvantages to possessing a perceptual system that is asymmetrical to any substantial degree. This point has been stressed by Corballis (1998). The physical world is indifferent to left and right, and any lateralized deficit might leave an animal vulnerable to attack on one side or unable to attack prey or competitors appearing on one side.

Note that, because perceptual asymmetries have usually been revealed in humans under very artificial conditions (i.e., tachistoscopic viewing or dichotic listening), it was probably not unreasonable to maintain that asymmetries cannot be apparent in everyday behavior. Now we are learning from ethologists that such asymmetries in behavior are not rare but are in fact quite ubiquitous in animals (and it now seems likely that they may be ubiquitous in humans too; see e.g., Güntürkün [2003a] and Bracha et al. [1987] for turning biases in humans).

The existence of population-level, lateral biases in behavior of the types described above is puzzling from a biological point of view, because it provides the organisms expressing such asymmetries with obvious disadvantages. Consider the case of toads. As we have mentioned, these animals are more likely to react when a predator appears on their left side than on their right side, but predators, in principle, can appear on either side at random. Hence, lateralization would obviously be disadvantageous to the toads. On the other hand, a prey species might avoid predation if it can predict the strategy of its predator (e.g., a right-side bias for the predator to strike at its prey; see Hori 1993), and under this condition population-level lateralized behavior of a predator would be advantageous for the prey though not for the predator itself. In other words, a dynamic relationship might be established between lateralized behavior in interacting asymmetric organisms. To anticipate the key argument of this paper, we shall argue that the population structure of lateralization (i.e., the alignment of the direction of lateral biases in most individuals in a population) may have evolved as an "evolutionarily stable strategy" (Maynard-Smith 1982) to coordinate behavior among asymmetric individuals. Before considering our hypothesis, however, let us consider some alternative views.

A possible explanation for the maintenance of population-level lateral biases would be to argue that the advantages associated with possession of an asymmetric brain counteract ecological disadvantages associated with lateral biases in overt behavior. But what sort of advantages might cerebral lateralization offer?

3. Possible advantages of cerebral lateralization

A crucial 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 (Levy 1977). This would allow brain evolution to avoid useless duplication of functions in the two hemispheres, thus saving on neural circuitry. Recent evidence in support of this hypothesis has come from research on an invertebrate species, the fruitfly: Pascual et al. (2004) have discovered that, compared to fruitflies with symmetrical brain structure, fruitflies with asymmetrical brain structure have superior ability to form long-term memory. More generally, by enabling separate and parallel processing to take place in the two hemispheres, lateralization could be one way of increasing the brain's capacity to carry out simultaneous processing. We have argued elsewhere, for instance, that incompatibility of function, other than competition for space, may have contributed to the evolution of cognitive lateralization (Vallortigara et al. 1999). Some recent evidence supports this hypothesis. For example, Rogers (2000) tested chicks on a dual task, one involving the left hemisphere in control of pecking responses and the other involving the right hemisphere in monitoring overhead to detect a model predator. Chicks exposed to light before hatching were compared to those incubated in the dark, as the light exposure aligns and strengthens visual lateralization on a number of tasks (Rogers 1990; 1997; also discussed in sect. 8). The strongly lateralized (light-exposed) chicks detected the model predator sooner than did the weakly lateralized (dark-incubated) ones, at least with the left eye (i.e., when the right hemisphere was attending to the stimulus). This suggests that lateralization of these two types of processing into the separate hemispheres enhances performance, and this result has been confirmed recently by scoring not only the response to the model predator but also the chick's ability to learn to peck at grain versus pebbles (Rogers et al. 2004). Strongly lateralized chicks learned to avoid pecking at pebbles far better than did 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 and they were less and less able to discriminate grain from pebbles as the task progressed; they were unable to attend to the two separate tasks simultaneously. As a control, we tested the weakly lateralized chicks on the pebble-grain task without presenting the model predator and found that they had less difficulty in learning to discriminate grain from pebbles (also found in another study by Rogers 1997). Hence, the weakly lateralized chicks had their greatest difficulties when they were tested in the dual-task paradigm.

A second advantage of lateralization is that dominance by one hemisphere (or in general by one side of the brain) is likely to be a convenient way of preventing the simultaneous initiation of incompatible responses in organisms with laterally placed eyes (Andrew 1991; Vallortigara 2000). This problem is particularly acute in vertebrates that lack a mobile neck, as in most species of fish. As we have seen above, the left and right hemifields of fish and birds exhibit a large degree of independence, and it is not infrequent that, because of independent scanning by the two eyes, the left and right halves of the world seen by these animals are completely different. In fact, the two eyes can scan independently in a number of species distributed throughout the

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vertebrate classes of birds, reptiles and fish (Andrew 1991; Wallman & Pettigrew 1985). Clearly, in such circumstances, dominance by one side of the brain – for example, through inhibitory connections with the other side – would be the only way to guarantee a proper course of action for the "unitary" organism. Ingle (1973) found that frogs could select between prey objects seen in the lateral fields of both eyes, and suggested that interhemispheric communication must play a crucial role in reducing potential competition of response emission. It is also possible that this occurs with a consistent lateral bias of one hemisphere over the other.

The problem with all these views, however, is that, although the hypothesis of a computational advantage may explain individual lateralization, it does not in itself explain the alignment in the direction of lateralization at the population level. In fact, individual brain efficiency is unrelated to how other individuals are lateralized. Why, therefore, do most animals (usually 65–90%) possess a left eye (or hemifield) better suited than the right eye 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)?

4. Individual-level and population-level lateralization

A crucial aspect of the lateral biases in natural behavior that we described in section 1 is that these left-right asymmetries are population- or species-level asymmetries, that is, asymmetries showing a similar direction in more than 50% of the population (see also Denenberg 1981). In biological terms these are "directional" asymmetries, quite distinct from "fluctuating" asymmetries or, for that matter, from antisymmetry, which is asymmetry at the individual but not the population level (Palmer 1996b; also see Fig. 1). In the main, it

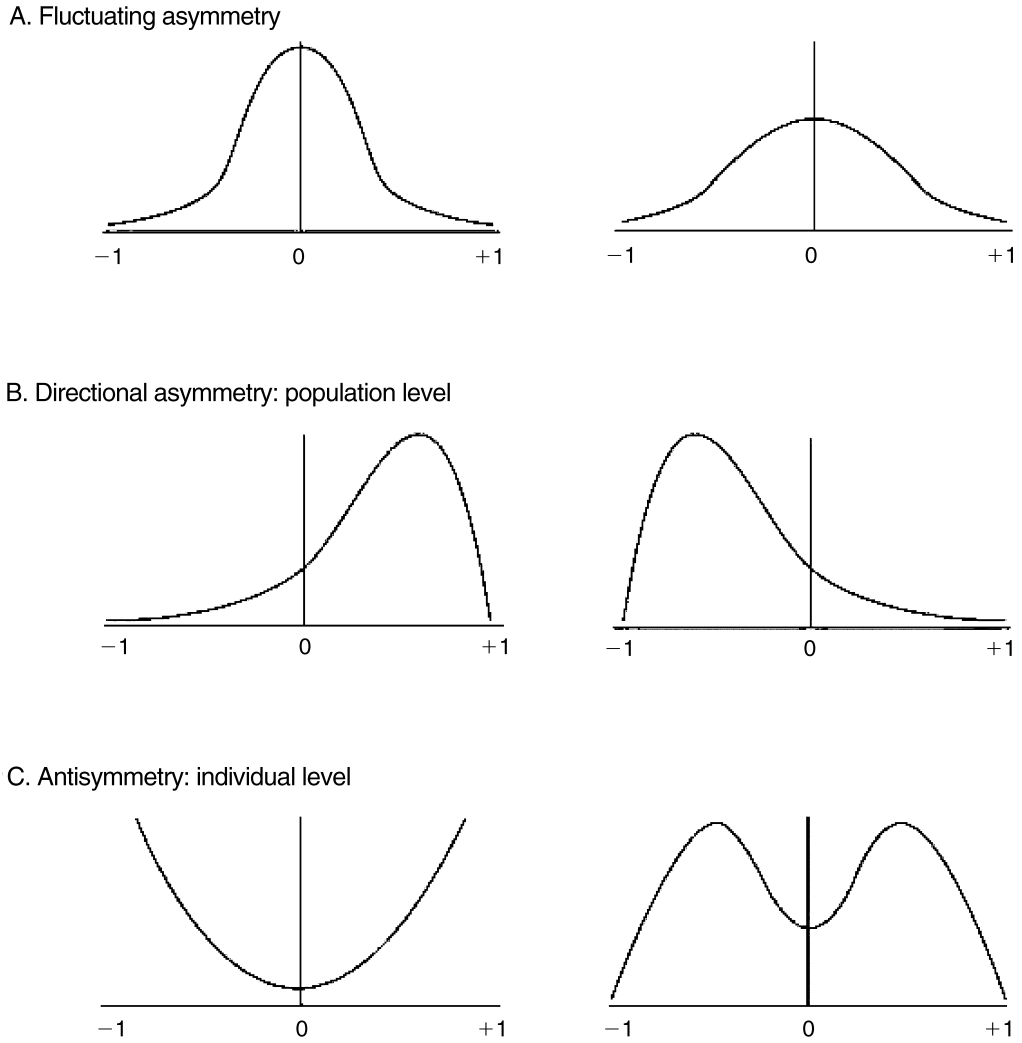


Figure 1. Frequency plots showing examples of fluctuating (**A**) and directional (**B**) asymmetry and antisymmetry (**C**). The values plotted on the x-axis are the lateralization index for each individual (right − left/right + left). In **A**, the plot on the right represents a population in which a greater number of individuals are more strongly lateralized than is the case for the population on the left. In both of these examples the direction of lateralization is at chance level. In **B**, the majority of individuals are lateralized in the same direction, causing a population bias to either the right or the left. **C** represents two typical forms of antisymmetry, in which the majority of individuals are lateralized but there are approximately equal numbers of left- and right-biased individuals in the population. Based on Palmer (1996b) and Møller and Swaddle (1997).

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is fluctuating asymmetry that has been studied by biologists.[1] This is a crucial point, since directional asymmetries may convey a specific disadvantage, which is not the case for individual asymmetries: namely, *predictability of behavior*. Let us consider again the example of toads, which are, at the population level, more responsive to predators appearing on their left side. It can be suggested that the toads are more likely to succumb to predators approaching them from their right side than from their left side. Even more important, predators might exploit this side bias, present at the population level, by preferentially approaching their prey on its right side. There is no research addressing this issue in amphibians, but let us describe a simple example related to predator-evasion responses in fish, which provides more direct empirical evidence.

It has been shown that simple, automatic responses to predators (or other threatening stimuli), which are mediated by C-Mauthner cells, are lateralized in several species of fish and amphibians (e.g., Cantalupo et al. 1995; Heuts 1999). Consider the situation from the point of view of a potential predator of these animals. If prey simply showed individual lateralization, there would be no way for the predator to make predictions about the direction of escape responses: any particular prey could be a left-biased or a right-biased individual and at first encounter there would be no possibility of the predator knowing this in advance (and the probability of making several repeated encounters with the same prey is likely to be too low to be exploited in any significant way). If, on the other hand, the prey are lateralized at the population level, then the predator can learn quite easily that there is a bias in the population of these organisms and it can exploit this regularity in prey behavior. There is clear evidence that fish can adapt lateral biases in prey-predator interactions. A case in point is the behavior of the scale-eater fish of Lake Tanganika, studied by Hori (1993). These cichlid fish eat the scales of other fish and to do so they exhibit asymmetry of the mouth, favoring opening either to the left or to the right side. Interestingly, the mouth asymmetry is under genetic control and the more common side for the mouth opening varies with about a 5-year periodicity. This is due to the fact that the less frequent phenotype is at an advantage because it attacks prey on the "unexpected side" (see sect. 6 for further discussion of the role of frequency-dependent selection in the evolution of lateralization).

Therefore, the problem is: Do the supposed advantages associated with cerebral lateralization account for the specific disadvantages associated with directional asymmetries? The answer is plainly in the negative. All of the presumed advantages that have so far been claimed to explain cerebral lateralization *do not require* the alignment of lateralization at the population level.[2] The crucial point here is, in fact, that individual brain efficiency is not related per se to the direction of the asymmetry of other individuals. Consider, for example, the idea of the sparing of neural tissue. Such an advantage can be achieved irrespective of the direction of lateralization by simply specifying the need for an asymmetric brain but leaving to chance the specification of its direction in different individuals. The same can be argued for all other supposed explanations of brain lateralization. For instance, having one hemisphere that is dominant, and therefore in control of the course of action taken in response to different stimuli presented simultaneously to each hemifield, surely confers an advantage to the organism, but this advantage can be obtained irrespective of which hemisphere (left or right) is dominant in different individuals.

5. The riddle of directional asymmetries

Is the presence of brain asymmetry at the individual and not the population level a sufficient condition to produce advantages for survival? And, if so, why has population-level lateralization emerged? An obvious solution to the conundrum would be to argue that the alignment of the direction of lateralization in the population is simply the by-product or cascade of the expression of genes determining somatic asymmetry. For example, the genes that determine asymmetry of the gastrointestinal tract and cardiac system (Levin et al. 1995; Ramsdell & Yost 1998) may set a baseline for population-level asymmetry on which brain and behavioral lateralization could be based. There are examples of genes and growth factors associated with somatic asymmetry affecting certain aspects of brain development, as in the case of fibroblast growth factor (Ohuchi et al. 2000). However, a role of such genes in determining behavioral lateralization in humans and other vertebrates seems rather unlikely (Malaschichev & Wassersug 2004; Tanaka et al. 1999). Moreover, there is clear evidence that in higher vertebrates the genetic expression of the presence of behavioral asymmetries is independent of its direction. For example, mice can be artificially selected for the strength of their paw preference, but not for the direction of this lateralization (Collins 1985).[3] Also, the inheritance patterns of human handedness are consistent with one-locus genetic models in which one allele specifies right-handedness, whereas another specifies left- or right-handedness at random (Annett 1995; McManus 2002; McManus & Bryden 1992); that is, the latter determines the presence of lateralization but not its direction.[4]

Thus, natural selection could have led (at least in principle) to individually asymmetric organisms without aligning the direction of the asymmetries at the population level. In other words, it would be possible to benefit from the (computational; see sect. 3) advantages of individual lateralization without necessarily suffering the disadvantages conveyed by directional asymmetries (i.e., without predictability of behavior). In fact, in the absence of specific selective pressures to produce directional asymmetries, and with all the advantages that can be obtained by individual asymmetries, it would not make any sense to align the direction of the asymmetries at the population level.

Our argument obviously rests on the assumption that individual asymmetries are advantageous by themselves. This seems to be logically tenable on the basis of the alleged computational advantages of brain asymmetry (mentioned in sect. 3), but is there any empirical evidence that individual asymmetries are in fact of advantage to the fitness of organisms?

Most of the research investigating the advantages of being lateralized has, so far, been carried out on directional asymmetries. The studies by Rogers (2000) and Rogers et al. (2004) mentioned previously compared the performance of a group of strongly lateralized chicks with a group of weakly lateralized chicks and found that the first group was more efficient in detecting a model predator. Another study (Güntürkün et al. 2000) also looked at directional lat-

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eralization at the population level, but compared the performance of individuals. This study, on pigeons, showed that stronger visual asymmetry enhances success in visually guided foraging: visually guided foraging is a population-level asymmetry (right eye dominance), but the procedure used was to correlate the strength of right versus left eye asymmetry of individuals with their efficiency in discriminating grain from pebbles. Computational studies in humans have also suggested that lateralization may provide a computational advantage for learning (Kosslyn et al. 1989; Reggia et al. 1998; see also Tang 2003, for extension to rodents). To our knowledge, however, there has been only one study of the advantage of a type of lateralization occurring at the individual level and not at the population level. McGrew and Marchant (1999) reported an association between individual-level asymmetry and success in foraging for termites by wild chimpanzees. 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. There is no evidence for a population-level bias in this task in the wild chimpanzees studied at Gombe; nonetheless there is individual lateralization, with some individuals preferentially using the same hand to probe and the other to stabilize the twig (lateralized), whereas others vary which hand is used for either purpose (ambidextrous). McGrew and Marchant (1999) studied the efficiency of termite fishing by the chimpanzees and found that individually lateralized chimpanzees, irrespective of the direction of their lateralization, gathered more prey for a given amount of effort than did ambidextrous chimpanzees. Thus, individual lateralization is clearly advantageous.

6. A solution to the riddle: Do population-level asymmetries arise as a result of the need to coordinate behavior among behaviorally asymmetric individuals?

If lateralization at the individual level would suffice both logically and empirically to produce computational (and thus fitness) advantages, why then do we observe population-level asymmetries for a wide range of vertebrates and on many tasks? The answer we propose is based on a simple idea: Sometimes what is better for an (asymmetrical) individual to do depends on what the other (asymmetrical) individuals in the group do. In other words, we propose that there are "social constraints" that force individuals to align their asymmetries with those of the other individuals of the group. Note that this hypothesis includes the assumption that the proposed cognitive advantage is a fitness advantage – that is, an advantage at the individual level, not at the level of the group in itself.

Let us consider again evidence for one type of lateral bias in fish. Suppose that anatomical asymmetries in the C-start reaction make it more likely for a fish to escape to the right following detection of a predator. For a single fish to escape to the left or to the right would be very much the same thing (assuming no lateral biases to be present in the predator). Now consider a group of fish. Fish sometimes group together, as do most vertebrates, because individual advantages arise from staying in a group (the main advantage being sharing the risk of being preyed upon with the other members of the group – the "dilution" effect; see Burger & Gochfeld 2001; Foster & Treherne 1981; Pilcher 1986). If we assume, as seems reasonable, that the size of the group has been selected for its anti-predatory advantages, and that any reduction in size would reduce individual fitness, it is apparent that it would be convenient for each individual fish to align the direction of its asymmetric escape responses with the direction of the (asymmetric) escape response of the other individuals of the group. Thus, social life would encourage the alignment of lateralization at the population level.

An obvious objection is that in this very simple example one would predict "complete" lateralization (i.e., that all individuals would align as totally left- or totally right-types), and this is not what we have observed in natural animal populations. Even disregarding biological noise in measurement, a most striking characteristic of population-level lateralization is in fact that it is not 100%; usually a percentage variable from 10% to 35% of individuals do not conform to the pattern of the majority of the individuals. We know, of course, that this minority group is probably quite heterogeneous, at least on the basis of the now quite extensive literature on human left-handedness (see McManus 2002). But leaving aside this problem and, for the moment, assuming that we are looking at a form of laterality largely determined by genes, the point is that a part of this minority group certainly represents a genetically different group (McManus 2002). If lateralization at the population level is determined by social pressures, why then do some individuals resist such pressures? To understand this point our hypothesis should be formulated more formally.

Maynard Smith (1982) first introduced the idea of an "evolutionarily stable strategy (ESS)" in the context of games theory applied to behavioral biology. Stated simply (e.g., Dawkins 1976), the idea conveyed by the notion of ESS is that sometimes what is better for an individual depends on what the other individuals of the group do. An ESS is not stable because it is the best possible strategy but simply because, once it has been adopted by the majority of the individuals in the population, no other alternative strategies can develop successfully (violations of the ESS strategy would have a negative outcome in terms of fitness).

Ghirlanda and Vallortigara (2004) recently examined whether behavioral lateralization at the population level can arise as an ESS in the context of prey-predator interactions. They considered predators and group-living prey meeting in contests in which the prey have two lateralization strategies available, "left" and "right," and they assumed that, when a predator attacks, lateralization can affect a prey's probability of escaping in two ways. First, prey lateralized in the same direction have a greater chance of keeping together as a group. Second, predators are better at capturing the prey type that they meet more often. For instance, predators may learn to anticipate prey escape movements, or to approach prey from a given direction. If $p(x)$ is the survival probability of a prey when a proportion x of its groupmates employ the same lateralization strategy, a general way of writing $p(x)$ is

$$p(x) = p_0 + cg(x) - l(x) \quad (1)$$

where p_0 is a baseline escape probability, $g(x)$ represents the benefit gained, under attack, by keeping together with a proportion x of fellow prey, and $l(x)$ represents the cost of having the same directional bias as a proportion x of other

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prey, due to predators learning to handle better the more common prey type (both $g(x)$ and $l(x)$ are assumed to be positive). The parameter c allows regulation of the relative importance of $g(x)$ and $l(x)$.

The condition for a given proportion a^* to be an evolutionary equilibrium is that the escape probabilities of left- and right-type prey be equal; that is

$$p(a^*) = p(1 - a^*) \quad (2)$$

Such a state of equilibrium is stable if natural selection works to restore the proportion a^* whenever slight deviations occur. This means that a small increase in the proportion of left-type prey should increase the probability of right-type prey escaping, and vice versa.

The existence and nature of stable equilibria in the model depend, of course, on detailed assumptions on the functions $g(x)$ and $l(x)$. Ghirlanda and Vallortigara (2004) made the simplest assumption concerning the two functions (see their paper for details) and obtained a quite general result. When c is small, the only stable population consists of left- and right-type prey in equal numbers. This would correspond to situations in which lateralization-mediated effects of group living on probability of escaping are small, as in the case of solitary prey or for those kinds of lateralization that do not influence group cohesion. When c becomes larger, stable populations consist of left- and right-type prey in unequal numbers (because the model does not assume any intrinsic benefit of left or right lateralization, there are always two possible solutions: one with a majority of left-type prey and one with a majority of right-type prey). The intuitive content of such a situation is that the majority of prey gain protection by keeping together but pay a cost because predators are better at handling them. A minority of prey manages to enjoy the same probability of escaping by trading off protection from the group with an advantage in the face of predators.

One interesting aspect of formulating the hypothesis that social mechanisms are responsible for the evolution of population-level lateralization in terms of ESS is that models like that of Ghirlanda and Vallortigara (2004) include an effect that is known among evolutionary biologists as "frequency dependent selection." This refers to an advantage of the minority group which depends on the frequency of these individuals (i.e., an advantage that disappears when these individuals increase in number). Raymond et al. (1996) have provided evidence for frequency-dependent maintenance of left-handedness in humans. They proposed that left-handers have a frequency-dependent advantage in fights and for that reason a fitness advantage. Consistent with this hypothesis, they found a higher proportion of left-handed individuals in interactive sports that reflect some elements of fighting, but not in non-interactive sports.

In fish, advantages associated with the minority type of lateralization could, in addition to predator-evasion responses, be associated with survival of cannibalistic attacks by conspecifics (Vallortigara & Bisazza 2002). Moreover, the evidence for a preferred side for copulatory attempts in Poeciliid fish (see Vallortigara & Bisazza 2002) may suggest another possible frequency-dependent advantage: given that females actively keep watch for unwanted copulatory attempts, if for the majority of males copulatory attempts occur on a particular side, then males of the minority type, which attempt to copulate on the other side, might have a selective advantage.

Our hypothesis offers a new way of looking at variations in the strength of lateralization in different species and tasks. Sometimes these have been interpreted as suggesting that lateralization in the human species would be stronger than in all other nonhuman species, possibly as the result of a "second" mutation after the first one that would have produced only slight directional asymmetries in nonhuman species (Corballis 1997; 2002).[5] However, there is evidence that some forms of lateralization in nonhuman animals are as strong as eye, hand, and foot preferences in humans. For example, a study of the preferred foot for holding food in nine species of Australian parrots found that eight species displayed a significant preference for the left foot and one for the right foot, with the overall strength of the footedness for the left-foot-preferring species being 90% (Rogers 1980). A strong lateralization was also observed in wild kookaburras, in which the (left) eye preference used to scan the ground in search of prey was found to be 85% (Rogers 2002a). These examples are notable evidence against the claim that humans are more strongly lateralized than nonhuman animals, but we should note that other examples of laterality collected from species in the wild, so far, are less strongly biased: 70% for a side preference to pivot when performing the righting response in the frog, *Litoria latopalmata* (Rogers 2002a), 68% left-side bias for aggressive responses in the lizard, *Urosaurus ornatus* (Hews & Worthington 2001), and 70% of juncos oriented next to a wall so that their right eye was able to look outward, provided that the position of forms of protective cover were not conflicting with this bias (Franklin & Lima 2001).

A different way of explaining the strength of lateralization may be to argue that the percentage of the minority group is the result of frequency dependent selection: it may therefore assume a range of values, depending on the advantage of the particular form of lateralization under consideration to the minority group relative to the majority one. As a general rule, we can predict that, whenever the group advantage of lateralization is large, the relative percentage of the majority group (usually referred to as the "strength" of lateralization) should be larger. This would mean that species with more complex social structures would provide more conditions for individual behavioral lateralities to be forced and constrained into directional behavioral lateralities. If so, maybe the claim that humans tend to have a stronger lateralization over a greater number of functions is correct, but for a different reason than that advocated by Corballis (1997; 2002) – namely, we suggest, because of the very sophisticated social life of humans.

Coevolution of lateral biases in prey and predators might also be expected. A possible example comes from evidence that avoidance responses in three species of toads were elicited more strongly when a dummy predator (snake) stimulus was on the toad's left side compared to its right side (Lippolis et al. 2002). Considering that toads have been shown to possess a complementary right-side bias for predatory responses, if the predators of toads (e.g., snakes) also have a bias to attack to their right side, then the predator-prey situation would be balanced. (Recent evidence for population-level asymmetry in snakes has been reported, though for the direction of coiling and not directly associated with predation; Roth 2003; and see also Shine et al. 2000 for morphological asymmetries affecting reproductive behavior.) Note, however, that according to the model of

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Ghirlanda and Vallortigara (2004), coevolution of lateral bias in prey and predators could occur *only* after at least one-directional (i.e., population-level) bias has been established in either the prey or the predator species. In other words, predatory pressures alone cannot establish directional asymmetries in the absence of a specific pressure to coordinate behavior at the level of the group. Only after a pressure to align the direction of asymmetries has been firmly established in at least one species, either in the prey or the predator, can alignment of the asymmetries in the other species occur, as a result of mutual evolution.

How can the hypothesis that lateralization at the population level evolved as an ESS be tested empirically? As an evolutionary hypothesis (i.e., a hypothesis concerning a past event), it is difficult to test in current living organisms. In principle, the hypothesis would predict 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. Two problems arise when organisms that are currently living are considered. First, for modern vertebrates, arguing for completely solitary behavior is very difficult, at least in higher vertebrates (birds and mammals). Second, it is quite plausible that many currently living vertebrates that are today considered to be "solitary" actually derive from more social ancestors (as might be the case in orangutans; see Kaplan & Rogers 2000) and that, therefore, they have retained population-level rather than individual-level asymmetries. A similar point can be raised with respect to ontogenetic development. 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 (cf. Bisazza et al. 2002; and see Green [1997] for evidence of lateralization in urodel amphibians). It is thus plausible that directional asymmetries in the relatively solitary adults are retained from the juvenile stages. Another complication is that social behavior varies in degree between species and according to group size. Nonetheless, a test of our hypothesis can perhaps be limited to certain currently 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 the 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 (Hamilton 1971). Fishes can be easily categorized as "shoaling" or "not shoaling" species. Bisazza et al. (2000) 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. 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. Six species were found to be gregarious (i.e., to school) and all six were the ones lateralized for turning bias at the population level; ten species were found to be non-gregarious (i.e., not schooling) and six of these were not lateralized at the population level but they were lateralized at the individual level (see also Vallortigara & Bisazza 2002). Therefore, although the correlation is not perfect (and in biology it would be surprising if it were), the data fit our hypothesis quite well.

There are, however, some outstanding issues that deserve more discussion. First, is it possible that for the same organism we can observe individual-level lateralization for certain functions and population-level lateralization for other functions? In fact, this is observed in several species. Several primate species that do not show clear evidence of population-level lateralization in limb usage do show evidence of lateralization in other cognitive tasks (Hopkins & Carriba 2002; Weiss et al. 2002). Moreover, whereas lateralized motor performance may not be present at the population level, lateralized sensory processing may well be present. For example, New Caledonian crows display a clear population-level laterality to cut tools from one edge of pandanus leaves (Hunt 2000; Hunt et al. 2001), and so use one eye preferentially to guide the cuts they make with their beak, but recent observations indicate that, although individual birds have strong individual biases to hold stick tools while probing for insects, there is no population bias for this motor act (Rutledge & Hunt 2004; Weir et al. 2004). Similarly, in a group of 21 marmosets, Hook-Costigan and Rogers (1995) found that 13 marmosets preferred to use their right hand to pick up food and the rest to use their left hand, but 20 of the 21 subjects showed a clear right-eye preference to look through a small hole to view food and other stimuli. Similar variations in individual- versus population-lateralized behavior appear to be present in chimpanzees. In termite fishing, chimpanzees are individually lateralized, but current evidence suggests that they are population-level lateralized for other functions, possibly for area 44 of Brodmann (Cantalupo & Hopkins 2001) and for asymmetry of facial expressions (Fernandez-Carriba et al. 2002). So far, sample sizes of the chimpanzees tested in the wild have been quite small; in contrast, large samples of chimpanzees have been tested in captivity in different colonies and have revealed significant right-handedness (Hopkins et al. 2003).

We feel that far too much emphasis has been placed on using hand preference as the only, or best, indicator of whether or not primates are lateralized. Although there are some examples of handedness in primates (left-handedness for face manipulation in orangutans: Rogers & Kaplan 1996; right-handedness in captive chimpanzees: Hopkins et al. 2003), the topic remains controversial. Part of the controversy appears to stem from variations between species (Hook 2004) and between the tasks scored, sex, and age (MacNeilage et al. 1987; Ward et al. 1990). In fact, hand preference in primates may be a better indication of temperament or a predictor of behavior at the individual level rather than being a useful measure of lateralization. Right-handed chimpanzees have higher levels of exploration than do left-handed ones (Hopkins & Bennett 1994). Similarly, right-handed marmosets explore a novel environment and interact with more novel objects than do left-handed marmosets (Cameron & Rogers 1999). These data are best explained as the hand preference of the individual being a reflection of the active hemisphere (perhaps the dominant hemisphere), such that left-handers have a more active right hemisphere and right-handers a more active left hemisphere, coupled with the presence of population-level hemispheric specialization. Hence, left-handers express the characteristics of the right hemisphere (heightened

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fear, avoidance), whereas right-handers express the specialized characteristics of the left hemisphere (approach, object manipulation). In other words, the absence of population-level handedness in primates tells us nothing about whether or not they have hemispheric specialization. Humans share having a lateralized brain with other primates[6] even though we appear to differ from other primates, to some extent, in terms of right-handedness. However, even that difference may be limited to certain tasks such as writing, for Marchant et al. (1995) found in human tribal groups that do not have written language no evidence of strong right-handedness for any activity using the hands other than tool use. This raises the possibility that the strong right-handedness of humans might be, in some way, related not only to certain tasks but also to social interactions.

Should we predict that individual lateralization would be observed only in those tasks that do not involve any relevant interactions with other asymmetric individuals? Indeed, termite fishing seems to be a case in point, since no relevant interaction with other lateralized individuals is involved either with conspecifics (apart perhaps from teaching by the mother) or with prey. However, again it should be stressed that the issue of handedness in chimpanzees is controversial, because they seem to be population-level lateralized only when tested in captivity (Hopkins et al. 2003). Could it be that captivity favors social pressures leading to the alignment of asymmetries?

As an alternative possibility we should consider that the initial occurrence of population-level behavioral lateralization for a particular task/function, promoted by the pressure to coordinate it with the behavioral lateralization shown by other individuals, may produce changes in brain organization that might involve the alignment of lateralization of other tasks related to the first one. It could also be conceived that, once alignment for a particular task or set of functions has occurred, alignment of the other functions might occur by default in the side of the brain that has remained free to be used for those functions for which no direct selective pressure has occurred.

Relatively few studies have looked at lateralized behavior in social communication per se. However, the research on vocal communication and facial expressions in primates has revealed lateralized perceptual processing and motor functions. Rhesus macaques initiate facial and vocal expressions (both positive and negative) on the left side of their faces, and the right side follows (Hauser 1993; Hauser & Akre 2001). This means that there is a population bias for the right hemisphere to control these emotional expressions, and this is consistent with the preference of this species to turn its head to listen to conspecific vocalizations with the left ear, allowing the vocalizations to be processed primarily by the right hemisphere (Hauser 1998; Hauser & Andersson 1994). Marmosets also initiate fear/threat (negative) expressions on the left side of their faces but, interestingly, their social contact call (positive) is initiated on the right side (Hook-Costigan & Rogers 1998). In humans, negative emotions are expressed on the left side of the face (Davidson 1995) and the right side of the mouth opens first and wider during speech (Wolf & Goodale 1987). Perhaps associated with a similar lateralization of facial expressions, semi-wild orangutans have been found to preferentially expose the left side of their face to observers, as they look sideways at the observer (Kaplan & Rogers 2002). Whatever the side preference, knowledge of which is valuable in revealing neural mechanisms, the point we wish to make here is that population biases are not at all uncommon in social behavior, as has been noted with respect to humans by Kimura (1982).

7. Developmental mechanisms to align lateralization at the population level

Although genes are clearly involved in determining lateralization, it would be incorrect to assume that their role is primary for all forms of lateralization. In the case of some forms of visual lateralization in birds, light exposure of the eggs just prior to hatching has an overriding effect in aligning, and sometimes generating, lateralization in the population, as has been shown in chicks (Rogers 1982) and pigeons (Güntürkün 1993). One way to show lateralization in birds is to test the birds monocularly: When chicks use the right eye (and hence the left hemisphere, because the main input from each eye goes to its contralateral hemisphere[7]) they are able peck at grain and avoid pecking at pebbles, whereas when they use the left eye they peck randomly at these two targets (Rogers 1997). This lateralization is not present in chicks hatched from eggs incubated in the dark, for such chicks peck randomly at pebbles and grain regardless of which eye they are using (Deng & Rogers 2002b; Rogers 1997) unless they peck very slowly (Rogers et al., in preparation).

Light exposure of the late-stage embryo establishes this particular type of lateralization at this stage of development, because the embryo is turned in the egg so that it occludes its left eye and only the right eye is exposed to light entering through the egg shell and membranes (Rogers 1990). This exposure of the right eye to light leads to development of an increased number of visual projections from the left side of the thalamus (which receives inputs from the right eye) to the right Wulst region of the forebrain compared to the equivalent and opposite projection from the right side of the thalamus to the left visual Wulst (Rogers & Deng 1999). Apparently, this asymmetry in the organization of the visual projections puts the right eye and its neural connections in charge of certain visual functions.

Lateralization of attack responses shows the same dependency on light exposure of the eggs (Rogers 1982; 1990). In this case, the response is higher in chicks using the left eye than it is in chicks using the right eye, provided that the eggs have been exposed to light. In chicks hatched from eggs incubated in the dark, the levels of attack are the same whether they use the left or right eye. By testing chicks binocularly and looking at the area of the visual field used before a peck is directed toward an unfamiliar conspecific, Vallortigara et al. (2001) found that the light-exposed chicks had a preference for the left monocular visual field over the right monocular field and also over the binocular field, whereas the dark-incubated chicks preferred the right binocular field as well as the left monocular field. In other words, the dark-incubated chicks retain a form of asymmetry but it is in relative use of the binocular versus monocular field rather than an absolute difference between the left and right eyes. This shift in visual emphasis is likely to depend on the known changes in asymmetry of the thalamofugal visual pathways that develop as a consequence of the light exposure of the embryo (Koshiba et al. 2003; Rogers & Deng 1999).

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In these cases, genetic expression may determine the presence (or absence) of lateralization at the individual level, whereas the light exposure aligns the direction of lateralization so that the population is lateralized. There are other forms of population-level lateralization in chicks that do not depend on light exposure of the embryo, and these include imprinting and social recognition (Andrew et al. 2004; Deng & Rogers 2002c), response to olfactory versus visual cues (Rogers et al. 1998), and lateralized auditory responses (Andrew & Watkins 2002). Other forms of environmental stimulation may, of course, influence the development of these particular forms of lateralization but, so far, this has been little investigated (Casey & Lickliter 1998; Casey & Martino 2000; Casey & Sleigh 2001; and see Denenberg [1981] for evidence in other species).

However, considering only those lateralized visual functions that are either generated or aligned by light exposure of the embryo, we can ask whether the dark-incubated chicks are entirely lacking in asymmetry or whether half of the population is lateralized in one direction and half in the other direction (i.e., individual but not population lateralization versus no lateralization at all). The answer is not as simple as it might seem. Some results suggest that the dark-incubated chicks are a single group without any lateralization (e.g., performance on the pebble-grain pecking), whereas other results (e.g., attack responses) suggest that the scores may fit a bimodal distribution wherein half the individuals are lateralized in one direction and half in the other direction (see Deng & Rogers 2002b). It is clear, however, that the dark-incubated chicks retain some flexibility with respect to the hemisphere they put in charge of performing the pebble-grain task, and that they also experience conflict between the hemispheres, which impairs their performance when they are tested binocularly. The latter is shown by the fact that, when tested binocularly, they can perform the pebble-grain task well following glutamate treatment of either the left or right Wulst, the region of the forebrain receiving the thalamofugal visual projections, but they perform poorly if neither Wulst is so treated (i.e., if the two Wulst regions compete for control). For this particular visual function, therefore, light exposure of the embryo not only aligns the direction of lateralization but also generates the lateralization. In the case of attack responding, it seems that the light exposure aligns the lateralization in the population but does not generate it. This, therefore, may be an example of genes having a major role in determining the presence of lateralization in the individual and of light exposure of the oriented embryo determining the population lateralization. Of course, genes are likely to determine the orientation of the embryo, but the flow on effect of this would be influenced by environmental factors (e.g., whether or not the eggs are exposed to light).

We suggest that it may not be coincidental that population lateralization, which serves social functions, depends on environmental stimulation, which in turn must depend on the behavior of the hen (how long she vacates the nest) and the influence of social factors on her behavior while she is incubating the eggs (see sect. 9).

We have already discussed the experiments showing that when chicks have to perform two tasks simultaneously (forage and monitor overhead for predators), those hatched from eggs exposed to light before hatching (strongly lateralized for visual functions) are superior to chicks hatched from eggs incubated in the dark (weakly lateralized). Exposure to light before hatching also influences social behavior. Rogers and Workman (1989) scored the social hierarchy in young chicks hatched from eggs exposed to light with those hatched from eggs incubated in the dark, and they found that the hierarchy was more stable in groups of light-exposed chicks compared to groups of dark-incubated chicks. The explanation given for this was that social behavior may be more predictable in groups with population lateralization (i.e., light-exposed): for example, a chick might be able to reduce agonistic interactions with its conspecifics by avoiding their left side (discussed also by Rogers 2002b).

We also have some empirical evidence that, when chicks are searching for food, those hatched from eggs exposed to light attend to different cues than do those hatched from eggs incubated in the dark (Chiandetti et al., in press). We tested pairs of chicks on a task requiring them to learn to take food from small cones of paper. Cones with a black and white checked pattern were loaded with food grains and placed along one side of an arena, whereas grey cones without any pattern and without food grains inside were placed along the other side. After several training trials, the chicks were tested with empty cones with their positions reversed (i.e., located on the opposite sides of the arena than they were during training). The light-exposed and dark-incubated chicks appeared to attend differently to the proximal cues identifying the source of food or to the spatial cues identifying where the cones were located. These different searching strategies would be important in the natural environment and they lay a basis for examining associations between lateralization and foraging strategies in free-living animals.

Experience seems to play a role in establishing other lateralized behavior, as found for the right hemisphere's role in processing vocalizations in rhesus monkeys – the population bias is seen in adults but not in infants (Hauser & Andersson 1994). Results for head turning by harpy eagles to listen to vocalizations played behind them are interesting because both naive and experienced individuals turned to the right to listen to their species-typical calls but, when calls of one of their prey (howler monkey) were played, the naïve birds turned to the left and adults turned to the right (Palleroni & Hauser 2003). This, of course, may reflect a shift in the neural processes that the bird uses to process familiar versus unfamiliar sounds. Similar shifts in hemispheric dominance have been shown in the chick (Andrew 2002; Vallortigara et al. 1997) and in fish (Cantalupo et al. 1995). Overall, it is of interest to extend this research on changes with maturation and/or experience.

8. Hormonal mechanisms affecting the alignment of lateralization

The level of steroid hormones in the embryo during the final stages before hatching also affects the development of lateralization, as shown in the chick. Administration of testosterone (Schwarz & Rogers 1992), oestrogen (Rogers & Rajendra1993), or corticosterone (Deng & Rogers 2002a; 2005) to the egg just prior to the sensitive period when light exposure has its effect prevents the development of asymmetry in the thalamofugal visual projections (see also Rogers 1999).

This effect of steroid hormones on the development of asymmetry is of significance for the natural condition be-

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cause environmental factors, as well as internal ones, influence the level of testosterone deposited by the maternal bird in her egg. For example, the concentration of testosterone in the egg yolk either increases or decreases with laying order of the eggs in the clutch. The direction of change depends on the species: it increases with order of laying in the canary (Schwabl 1993) and red-winged blackbirds (Lipar et al. 1999) and decreases with order of laying in the cattle egret (Schwabl et al. 1997). Aggressive behavior of the hatchlings changes consistently with this. Given the lateralized control of attack responses and the effect of pre-hatching levels of testosterone on lateralization of the visual pathways, we suggest that the maternally deposited hormone level in the eggs modulates the strength of individual lateralization and the level of attack.

Whittingham and Schwabl (2002) have shown that in tree swallows, *Tachycineta bicolour*, the level of testosterone deposited by the maternal bird in the egg depends on the number of aggressive interactions she experiences before or during egg laying. This suggests a means by which social conditions experienced by the female might influence the degree of lateralization of visual pathways of her offspring and also some associated behavior patterns. These influences during development might modulate lateralization to cause individual differences in response to social and ecological demands.

The principal stress hormone in birds, corticosterone, also modulates the development of lateralization in the visual pathways, as known from work on the domestic chick (Deng & Rogers 2002a). The level of corticosterone deposited by the hen in the egg also varies with order of laying, as shown in the canary (Schwabl 1999). These data suggest that stress levels of the maternal bird might well affect the development of individual lateralization.

Hence, for certain visual lateralizations at least, light and steroid hormone levels are influencing factors that cause variation among individuals in the presence or strength of lateralization.

9. Further hypotheses: Do animals actively manipulate environmental and hormonal factors in order to align or not align asymmetries in relation to their own ecological needs?

We conclude this target article with some hypotheses that, though clearly speculative at present, represent the logical corollary of our line of reasoning and that, we believe, deserve to be pursued experimentally. Let us start again with an example. We argue in section 7 that light exposure of the embryo represents one way of aligning the direction of lateralization for visual functions in the chick. In the natural environment it is likely that eggs do receive enough light stimulation to cause this effect, because only two hours of low light intensity is sufficient and it has been observed that in the last period before hatching the broody hen leaves the nest quite frequently (Rogers 1982; 1990; 1995). There are at least two ways in which the amount of light to which the eggs are exposed could change, thereby affecting the alignment of lateralization in the chicks. An indirect way is related to predation or any other event that disturbs the broody hen. For instance, assuming that the risk of predators approaching the nest is high and that the hen maneuvers to distract predators away from the nest, the time during which the eggs would be stimulated asymmetrically would increase. Accordingly, on the basis of the results obtained by Rogers we can expect that the chicks exposed to this increased duration of light exposure will be more efficient in the dual tasks of attending to food and attending to predators (as discussed in sect. 7; Rogers 2000; Rogers et al. 2004). Alternatively, hens in habitats where predation is higher might be forced to make their nests in deeper cover and, as a result, the eggs may be exposed to lower levels of light. In either of these cases the effect on lateralization would be quite indirect, resulting from whatever event distracted the broody hen from her imperative of attending the eggs or drove her to make her nest in different conditions. Another example might be for broods to be hatched in different periods of the year, as a function of the relative importance of, for example, risk of predation and availability of food. In different seasons the differing light levels, temperature, and foraging demands may influence the amount of light exposure of the eggs. A more direct and intriguing possibility is that the hen might *actively* manipulate the degree and direction of lateralization of her progeny by changing the duration of the periods in which she leaves the nest during brooding.

There is one field of research in which evidence for this latter hypothesis could be easily collected, namely that of unihemispheric sleep. Birds exhibit a unique behavioral and electrophysiological state called monocular or unihemispheric sleep (Bobbo et al. 2002; Mascetti et al. 1999; Rogers & Chaffey 1994). During normal sleep, they have short periods of time in which one eye is open and the contralateral hemisphere shows an EEG pattern typical of wakefulness (fast and low voltage waves), whereas the other eye remains closed and an EEG pattern of slow wave sleep (slow and high voltage waves) can be recorded in the contralateral hemisphere (Bobbo et al. 2002). Although there could be several different functions associated with monocular sleep, there is convincing evidence that an antipredatory function could be prominent: that is, birds can use monocular sleep to monitor their environment for predators while still obtaining some of the benefits of sleep. When compared to mallard ducks sleeping safely in the center of a group, ducks at the edges, in a position open to the risk of predation, show a strong increase in the amount of monocular sleep and a preference for directing the open eye away from the center of the group and towards the edge (Rattenborg et al. 1999).

Mascetti and Vallortigara (2001) have shown that exposure to light in embryos affects the direction of monocular sleep in newly hatched chicks (see also Bobbo et al. 2002). Whereas in dark-incubated chicks there is a slight bias to sleep with the left eye open throughout the first five days of life, light-incubated chicks show in the first two days after hatching a strong bias to sleep with the right eye open (Mascetti & Vallortigara 2001). In chicks the right eye/left hemisphere system is specialized to respond to important changes in the environment in order to categorize and respond rapidly to changes in social and nonsocial stimuli (Vallortigara & Andrew 1991; 1994a; 1994b). Also, initial storage of memories of the imprinting object occurs in the left hemisphere (Horn 1998), and asymmetric opening of one eye during sleep may reflect the relative importance of visually monitoring the mother hen (right eye) or of scanning the environment against predation (left eye). Thus,

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brooding hens have an excellent way by which they may modulate their progeny's propensity for vigilance against predators or their attention to social stimuli, generating more or less asymmetrical brains (even with different directions) depending on environmental conditions.

We can also speculate about the possible advantages of having variability in the progeny with respect to the degree and direction of lateralization. It is likely that phenotypic variation in behavior is adaptive, otherwise it would not be sustained in natural populations. If the environment provides severe challenges to the progeny, cognitive variability associated with lateralization (e.g., in the form of "cognitive styles") would maximize the fitness of at least some of the progeny. Note that it would be quite simple for parental behavior to evolve so as to change environmental factors such as light exposure of eggs (or, on the physiological side, to evolve so as to change the steroid contents of eggs). It appears more difficult to see how offspring might evolve so as to manipulate such factors. This means that in any conflict between the interests of parents and offspring the control would be on the side of the parents. However, both parents and offspring may have an interest in changing the rules of play from one generation to another. As discussed above, in prey-predator interactions mutual evolution of lateral biases can be expected. If progeny have the same pattern of lateralization as their parents, those progeny will meet predators that are already pre-adapted to this sort of distribution of strength and direction of asymmetries. Any change in the asymmetry pattern (e.g., in the number of individuals of the minority group, or in the strength of lateralization in individuals) may act as a counter strategy to any pre-existing predator strategy. We can thus expect an arms race in prey-predator interaction based on systematic manipulation by parents of the degree of asymmetry and on degree of alignment of asymmetry at the level of the group. Such a condition is probably not common in recently evolved higher vertebrates, in which stable polymorphism has evolved as an ESS (e.g., data for hand use in humans from historic times point to a rather constant proportion of about 85% right-handers, as shown in Steele & Mays, 1995, although this could be task-dependent). However, it could be quite common in other species, such as fish, in which stable polymorphism is obtained in the prey-predator dynamic by cyclic, periodic changes in the direction of lateralization of left- and right-types of individuals (Hori 1993) or, as we suggest, by rapidly adapting ontogenetic processes.

10. Epilogue

Evidence from ethologically oriented research has shown that population-level lateral biases in behavior are widespread among nonhuman animals observed in their natural environments. Population-level lateralization provides animals with two sorts of disadvantages. At the individual level, no a priori assignments can exist between the biological significance of a stimulus and its being to the left or to the right of an animal's midline; therefore, any bias favoring left or right would leave the animal less able to attend or respond to stimuli appearing on the non-preferred side. At the group level, the fact that more than 50% of the individuals in a population show a similar direction of bias would make their behavior predictable to others. The fact that population lateralization may even be disadvantageous, as it makes individual behavior more predictable to other organisms, also suggests that it cannot be a mere by-product of genetic expression: there are likely to have been specific selection pressures and specific advantages to align left-right asymmetries in most individuals of a population. The traditional view that lateralization confers a biological advantage to the processing capacity of the brain can explain the first disadvantage (the individual one), but it cannot account for the second disadvantage: brains can be built to be asymmetric, and therefore have all of their alleged individual computational advantages, without any need to align the direction of the asymmetries in different individuals. In our view, the reason why the direction of lateralization is aligned in different individuals is not related to the processing capacity of the brain, but rather, to the evolutionary pressures to coordinate behaviors among asymmetrically organized individuals.

In this target article we do not specifically discuss whether there would be any specific advantage in having the majority of individuals lateralized in the same direction for most "cognitive" asymmetries, usually investigated by neuropsychologists in humans[8] (see, e.g., Hugdahl & Davidson 2003). This is because this issue has not been investigated empirically as yet. However, as mentioned in section 9, there are lateral biases affecting social interaction and communication that deserve to be examined in light of these hypotheses. One example is related to brain asymmetries in face processing. There is evidence that portraits are typically produced with the left side of the face over-represented, 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 et al. 1999). It has been suggested that the motivation to portray emotion or to 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 present their left or right side depending on tasks and social context (e.g., showing the right side when lying, and, as mentioned previously, the left side of the face during sideways viewing in orangutans; Kaplan & Rogers 2002). Of course, this strategy would work only assuming a population structure for the lateral bias (and indeed the situation can be studied using theory of games, as Ghirlanda and Vallortigara, 2004, did with prey-predator interactions).[9] This is an entirely new field that deserves to be explored further (see also Güntürkün [2003] for head-turning biases requiring mutual coordination during social interaction in humans).

Obviously, we do not think that our ESS/"frequency-dependent selection" hypothesis can explain every form of cognitive lateralization.[10] It cannot in itself explain left hemispheric dominance at the population level in songbirds or right hemispheric dominance in spatial processing in birds and mammals. However, to reiterate, our hypothesis is not that all forms of directional asymmetries are directional because they were originally selected as ESS strategies. Some lateralities can be directional by default, as a result of the fact that other lateralities have been selected for directionality. For instance, it could be that response to predators is aligned to a particular hemisphere (say, the

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right) because of the advantages of reacting to predators in a similar way at the group level. At this point, behavioral responses also associated with anti-predatory behavior, such as spatial analysis, which were in principle free of any social constraints, would result in being forced to be aligned in the same (right) hemisphere. Something similar can be suggested for vocal production in songbirds: motor displays associated with courtship behavior are likely to be constrained by social interactions and thus aligned at the population level. Hence, vocal production associated with courtship and sexual selection might also be constrained to be located in the same hemisphere for the above-mentioned reasons (sparing of neural tissue, avoiding interference, extra time for interhemispheric coupling, and so on; see sect. 3).

Whether or not our hypotheses prove to be correct, we believe that our attempt to explain directional lateralization in populations may have a merit, namely, to place a hitherto separate area of research into an evolutionary and ecological perspective. Until now, ethologists and evolutionary biologists have considered brain lateralization (when familiar with it) a rather specialized topic, somewhat of an artifact of extreme laboratory conditions or of neuropathological syndromes. Conversely, psychologists and neuropsychologists have not considered the existence of lateral biases in behavior as a Darwinian puzzle – that is, as a problem requiring an explanation within the framework of evolutionary biology. Now is the time to integrate the study of cerebral lateralization in the realm of biology and renew our search for the adaptive value of brain and behavioral asymmetries.

NOTES

1. Fluctuating asymmetries, consisting of random deviations from bilateral symmetry in individuals, have been described for a number of different species; they are associated with environmental stress or with reduced heterozygosity and are believed to be due to the incapacity of individuals to undergo identical development on both sides of the body (e.g., Leary & Allendorf 1989). As such, they are usually very small in magnitude and thus different from lateralization at the individual level, which is typically pronounced though equidistributed in the population. Some genetic models have incorporated the idea of fluctuating asymmetry in the notion of "developmental instability" (e.g., Yeo & Gangestad 1993); however, the hypothesis that behavioral asymmetries at the individual level could be accounted for in terms of fluctuating asymmetries has recently been tested and not confirmed in fish (Bisazza et al. 1996; 1997; but see Hopkins et al. 2001).

2. It is opportune at this point to consider again the issue of the ecological disadvantages of lateral bias in behavior. One could argue that lateral biases in behavior may produce weaker or fewer disadvantages when the laterality is less complete. In a similar vein, one could argue about possible compensation mechanisms (such as visual scanning, as occurs in birds). However, this does not affect the basic issue we are discussing here, because the main disadvantage we are speaking of is not the fact of being lateralized (at, say, 50% or 100% degree as to the strength of lateralization), but the fact that the direction of the bias (however small) is the same for most individuals in the population. We agree that, at the individual level, the disadvantages of the bias can be minimized, making the individual laterality at the minimum possible level, but even at this minimum level it would, apparently, be better to maintain a 50:50 distribution of the bias in the population. To put it in another way: whereas at the individual level there seem to be advantages in terms of better functioning of the brain that force individuals to maintain a certain degree of bias (possibly at a minimum), there seems to be no obvious reason for making the direction of the bias similar in most individuals (given that this does not appear to be dictated either by genetics or by any advantage for the brain itself; see sect. 5).

3. In technically more correct terms, Collins (1985) demonstrated that differences in direction were not due to residual heterozygote alleles in B6 inbred strain.

4. If genes for lateralization do not exist (and admittedly they have not been identified as of yet), our logical arguments here are flawed on empirical grounds. However, the prevalent view among researchers of lateralization is that these genes do indeed exist (see McManus [2003] for a general review and Geschwind et al. [2002] for recent evidence in twins of heritability of cerebral lateralization in humans). It should also be noted that, although strength and direction of lateralization can be selected independently in the case of pawedness in mice (Collins 1985), this does not mean that inheritance of the direction of lateralization is absent in vertebrates. There is no evidence for heritability of direction in the strain of mice studied by Collins, but perhaps for good reason because the behavior for which Collins selected – paw preference – showed no population lateralization in this strain but only individual lateralization. Heritability of direction of hand preferences, however, has been reported in chimpanzees (Hopkins et al. 1994; 2001), and concordance in the direction of lateral bias between parents and offspring has been reported in capuchin monkeys (Westergaard & Suomi 1997) and in fish (Bisazza et al., 2000; 2001). Moreover, it should be emphasized that even for mice there are differences in different strains: a systematic survey in 12 inbred strains (Biddle & Eales 1996; Biddle et al. 1993) revealed that the direction of lateralization may not be genetically neutral, as previously assumed, because some strains showed a significant bias of paw usage to the left or to the right. Degree and direction of lateralization according to Biddle et al. (1993) may be separate genetic traits because some strains (e.g., NOD/Lt and SWV, which are both weakly lateralized) show significant deviations in opposite directions towards left and right paw usage.

5. A few researchers still deny the existence of any lateralization at all in nonhuman animals: for example, Crow (2002) has proposed that in humans a single mutation led to the first appearance of lateralization and to language. Considering the enormous amount of evidence for lateralization in nonhuman species, from the level of behavior to that of asymmetrical allocation of NMDA receptor subunits in the hippocampus (Kawakami et al. 2003), which we have reviewed here only in brief (for more extensive reviews, see, e.g., Andrew 2002; Güntürkün 1997; 2003; Malaschichev & Wassersug 2004; Rogers 1989; 2002b; Vallortigara & Bisazza 2002; Vallortigara et al. 1999), we are of the opinion that such a hypothesis does not deserve any discussion other than to say that it is plainly contradicted by facts.

6. Evidence for lateralization other than handedness abounds in nonhuman primates: spanning from greater left-sided frontal activation in response to diazepam (Davidson et al. 1993), right-hemispheric dominance for face analysis in split-brain monkeys (Hamilton & Vermeire 1988; Vermeire & Hamilton 1998; Vermeire et al. 1998), left-hemispheric dominance for vocal perception (Heffner & Heffner 1984; Petersen et al. 1984; Poremba et al. 2004), timing asymmetries of facial and vocal expressions (Hauser 1993; Hauser & Akre 2001; Hook-Costigan & Rogers 1988), to hemispheric processing of local and global stimuli (Hopkins 1997) and other cognitive tasks (Hopkins & Fowler 1998; Hopkins et al. 1993). These behavioral data are also substantiated by a variety of old (e.g., deLacoste et al. 1988 and references therein; Groves & Humphrey 1973) and new (Cantalupo & Hopkins 2001; Gannon et al. 1998) evidence for neuroanatomical asymmetries in the nonhuman primate brain.

7. Although the main input from each eye goes to its contralateral hemisphere, some afferent projections from both the optic tectum and thalamus (GLd) recross the midline into the ipsilateral hemisphere. Therefore, it is probably an oversimplification to say that monocular tests simply show the function of the contralateral hemisphere; it depends very much on the task at

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hand and on the presence of independent scanning of the two eyes. For the pebble-floor task described here, however, the results clearly show that the function is indeed controlled by the visual Wulst region in the contralateral hemisphere (Deng & Rogers 1997; 2002a).

8. Lateralization of more "cognitive" functions also has been proved to have important antecedents in nonhuman species. An example is relative to the control of species-specific vocalization. A dominance of functions located to the left side of the nervous system has been demonstrated in several different species of passerine birds (reviews in Nottebohm 1980; Williams 1990) and in monkeys (Heffner & Heffner 1986; Petersen et al. 1978; Poremba et al. 2004), mice (Ehret 1987), frogs (Bauer 1993), and catfish (Fine et al. 1996). This suggests a left-hemisphere specialization for the processing of species-specific vocalizations, which could represent an evolutionary precursor to lateralized speech perception and language processing in humans (although there are exceptions in which the right hemisphere is used for processing vocalizations). Another example is the selective involvement of the right side of the encephalon in spatial tasks involving the use of geometric information; this has been largely documented in birds (Clayton & Krebs 1994; Kahn & Bingman 2004; Rashid & Andrew 1989; Tommasi et al. 2003; Vallortigara 2004a; 2004b; Vallortigara & Regolin 2002; Vallortigara et al. 2004; see also Matsushima et al. 2003, for a review) and in mammals (Bianki 1988; Cowell et al. 1997; Crowne et al. 1992; and see Maguire et al. 1997, for similar evidence in humans). Finally, specialization of the right hemisphere for face recognition in humans (Sergent & Signoret 1992) might be an elaboration of similar processes found in social recognition in nonhuman species. Split-brain monkeys show similar specializations of the right hemisphere to discriminate faces and facial expressions (Hamilton & Vermeire 1988; Vermeire et al. 1998). In sheep, the evidence that the right hemisphere is selectively involved in face recognition has been collected using both behavioral (Peirce et al. 2000) and neurobiological (*c-fos* expression: Broad et al. 2000) methods. In birds, the left eye (mainly supplying the right hemisphere) seems to be involved in recognition of individual conspecifics (Vallortigara 1992; Vallortigara & Andrew 1994a; 1994b). Intriguingly, evidence for a left-eye bias during scrutiny of conspecifics in several species of fish and amphibian tadpoles has been reported (Bisazza et al. 2002; Sovrano et al. 1999; 2001).

9. All of these issues need to be examined in great detail, both empirically and using computer simulations, because they are too complicated to be mastered simply by verbal description. Consider expressivity of the face (but the same holds for lateralization of emotional behavior in general). 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 (Krebs & Dawkins 1984). 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 behaving cooperatively (aligned) and a minority (frequency-dependent) not aligned.

10. It should be stressed that what we propose here is an evolutionary hypothesis for the emergence of directional asymmetries. It is likely that such a scenario evolved well before humans evolved; thus, they might have simply inherited directional lateralization, which appeared originally in those early vertebrates that first showed some form of "social" life.

Open Peer Commentary

Partial reversal and the functions of lateralisation

Richard John Andrew

Department of Biology and Environmental Sciences, School of Life Sciences, University of Sussex, Brighton, BN1 9QG, United Kingdom.
bafe8@central.sussex.ac.uk

Abstract: The use of lateralised cues by predators and fellows may not strongly affect lateralisation. Conservatism of development is a possible source of consistency across vertebrates. Individuals with partial reversal, affecting only one ability, or with varying degree of control of response by one hemisphere do exist. Their incidence may depend on varying selection of behavioural phenotypes such as risk taking.

Vallortigara & Rogers (V&R) convincingly assemble evidence that a similar pattern of lateralisation of abilities occurs widely in vertebrates and is present in a majority of, but not necessarily all, individuals. They argue that such consistency implies sustaining selection pressures. The conservative nature of developmental processes in evolution is underestimated. Recent reviews (e.g., Cooke 2004; Levin 2004) argue for a very early establishment in development of the left/right axis, followed by complex processes that are basically similar across vertebrates and were probably present in early chordates. Changes in the pattern appear to occur relatively late in development and perhaps usually involve one and the same specific ability (as discussed below). Genes involved in the development of bodily asymmetries do affect brain asymmetries as well (habenular asymmetry and *situs*: fish, Concha et al. 2000; amphibia, Wehrmaker 1969). The left/right differences responsible for specialisation of processing in the central nervous system (CNS) are complex and varied (e.g., at the neuronal level in hippocampus: Kawakami et al. 2003). Evolutionary change would be difficult.

Interactions with predators and fellows are suggested to provide the selection pressures that sustain consistency of lateralisation. A fertile field for investigation is opened up. Do predators commonly use, for example, eye use as an index of likely prey behaviour? Perhaps the position of the nearest escape route and refuge is much more important. Both fish (Eaton & Emberley 1991) and anuran amphibia (Ingle 1981) sustain a bias toward mechanisms mediating startle-induced escape, so that movement is in the direction of safety. Another issue is the evidence that escape may be more likely if a frightening stimulus is seen on the left. This is probably best regarded as part of the problem of adjusting the balance between risk taking, for example to feed, and avoiding risk, which is unavoidable in real life. A lateralised animal can choose to use the superior detection of novelty and potential danger given by left-eye scanning at any point during feeding, and will presumably do so when appropriate. Scanning takes up feeding time; nevertheless, the availability of a superior ability helps rather than hinders overall.

If predators do indeed use eye use effectively enough to predict the behaviour of their prey, there remains the question of the opposing selection forces that in some species at lease give interindividual consistency in eye use despite enhanced danger of being caught. Consistency is argued to arise from interaction with fellows. Certainly eye use could be important in communication by revealing intentions. Given inter-individual consistency, this use would tend to be honest, in that use of the less-appropriate eye system would incur costs in assessment or control of response. A role for the coordination of social groups is less clear. Following the movement of fellows would seem to be very effective in hold-

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ing shoals or flocks together. The study by Bisazza et al. (2000) is ground breaking, but not unambiguous: Social species tested singly are likely to be affected differently than solitary species tested singly, so that motivational rather than lateralisation differences may have been crucial.

A new factor to be considered is that reversal of some but not all abilities ("partial reversal") generates new behavioural phenotypes in some vertebrates. A new line of zebrafish (*frequent situs inversus* [*fsi*] strain, A. Barth, University College London) produces a high proportion of offspring with habenular reversal and associated reversal of the visual control of response (Barth et al. 2005). Reversed fish show increased persistence in emergence despite the presence of a potentially frightening object: that is, they are risk takers. Left-handed individuals are risk averse in some primates (chimpanzee, Hopkins & Bennett 1994; marmoset, Cameron & Rogers 1999; rhesus, Westergaard et al. 2003). At least in humans, such reversal would be partial, in that lefthanders do not reverse their advantage in assessing position in coordinate space from right to left hemisphere (Jager & Postma 2003). A reasonable explanation for the new phenotypes is enhanced competition in the right-eye system/left hemisphere between control of response and abilities like assessment of novelty and spatial analysis, which have not reversed.

Comparable pairs of phenotypes may exist in other vertebrates: Goldfish show almost equal incidence of a brain asymmetry (whether the right or left optic nerve is dorsal in the chiasma), and one phenotype is subject to enhanced risk when predation is common (Roth 1979).

Reversal is not the only way in which adaptive variation in behaviour can be produced. The effects of degree of exposure to light on the outward-looking eye in chick embryos is perhaps the best studied example, thanks to the work of L. J. Rogers. A key feature, which has been somewhat neglected, is that in normal development it is always the right eye that looks outwards. Reversal is impossible (without experimental intervention). Instead, it is the degree, not the direction, of brain asymmetry that is affected. Further, most behavioural asymmetries may be present in either light-exposed (Li) or dark-exposed (Da) chicks, or both, according to test conditions (Andrew et al. 2004; Rogers et al. 1998). There is no clear evidence of any reversal of abilities. Instead, Li chicks appear to show an exaggeration of the ability of the right-eye system to control behaviour, expressed in enhanced inhibition of response to stimuli, other than the target of ongoing response, and (probably) in a reduced ability of the left-eye system to inhibit responses like attack and copulation. The former is well exemplified by the head positions assumed before attack pecks (Vallortigara et al. 2001). Here both Li and Da chicks show the same (expected) use of left lateral fixation, whilst establishing that the other chick is a stranger. Da chicks shift to right frontal before pecking. The right eye is used when the target of pecking is visible (Tommasi & Andrew 2002). Li chicks continue left fixation, as the frontal position is assumed. This masking of right-eye control of pecking in Li chicks presumably reflects the ability of the right-eye system to control response even when the left eye has more complete sight of the target.

The visual control of response is thus the ability affected both in partial reversal in fish and in the very late effect in development of light exposure in the chick. It suggests that the generation of different behavioural phenotypes by this method is widespread.

The main thrust of the target article is clearly correct and important. A standard pattern of lateralisation is present in most groups of vertebrates. The degree of incidence of individuals that depart from the pattern must depend ultimately on balances between powerful advantages and disadvantages.

Do asymmetrical differences in primate brains correspond to cerebral lateralization?

Douglas C. Broadfield

Department of Anthropology and Department of Biomedical Science, Florida Atlantic University, Boca Raton, FL 33431. **broadfie@fau.edu**

Abstract: An evolutionarily stable strategy (ESS) may apply to characters expressed across species for predation and feeding, because these characters are conservative. However, the evolution of complex, polymorphic behaviors is more difficult to define as an ESS. Lateralization may be selective for certain simple traits, but lateralization of complex traits is likely the result of coadaptation of otherwise non-lateralized features.

In determining the evolution of lateralization in the brain, one must consider first what the supposed lateralization means. In their target article, Vallortigara & Rogers (V&R) demonstrate probable evolutionary causes for lateralization in species such as fish and birds. For species such as fish and chicks where responses to a task or avoidance are, in general, unilateral, it is possible to apply Maynard Smith's (1982) concept of an evolutionarily stable strategy (ESS). For example, one would expect a population to evolve a particular trait that enabled its members to avoid predators or find food more efficiently. That is, for an ESS to exist in a population, an alternative phenotype cannot enter the population. However, a population would be unlikely to evolve an ESS if there were more than two pure strategies (i.e., if there was more than one continuous variable acting on a character). In the examples outlined by Rogers (2002b) regarding responses to predators, it is possible to assume that the evolutionary mechanism would favor a preferable reactive response. These simple (e.g., avoidance) responses may lead to preference for one side or visual field over the other. However, is such an explanation sufficient in explaining the evolution of lateralization with regard to social behaviors? The answer to this question involves resolving potential conflicts.

First, does asymmetry immediately confer lateralization of function? Studies on asymmetry in the primate brain offer little on the lateralization of function (Gannon et al. 1998; Sherwood et al. 2003). For example, Gannon et al. (1998) found a leftward asymmetry in the planum temporale of chimpanzees (see also Gannon et al. 2001; Hopkins et al. 1998). We noted that the degree of the asymmetry was like that found in humans, but we never assigned similar function to it. Indeed, our take has always been that with few exceptions the brains of nonhuman primates are very symmetrical compared to the brains of humans. In a later study, we noted asymmetry in area 44 of great apes (Sherwood et al. 2003). Although this area was determined by Brodmann (1912) and von Bonin (1949; 1950) to be analogous to area 44 of humans, there is no current understanding of the function of this and other areas. The results of these studies suggest that individuals or populations possessing a particular asymmetry may exhibit little or no change in the functioning of the involved brain regions. Cerebral asymmetries may relate to lateralization of function for certain tasks such as language (Damasio & Geschwind 1984; Geschwind & Levitsky 1968; Wada et al. 1975), but there is little evidence outside of conservative features such as vision that asymmetry in a particular brain region correlates to lateralization of function. However, even asymmetry in visual areas does not always lead to greater lateralization. For example, in a study of the visual striate cortex in a sample of chimpanzees, Holloway et al. (2003) noted that an individual demonstrating a high degree of asymmetry in this region displayed no difference in the general function of his visual system over that seen in other animals.

Examination of the brains of humans, nonhuman primates, and those of our fossil ancestors reveals a striking difference: Only human brains express an outward asymmetry (Holloway et al. 2004). Chimpanzees demonstrate a number of humanlike asymmetrical homologies, but these asymmetries are in very localized regions of the brain. It has been suggested that the features most unique to the human brain, which at the same time are those that tend to be

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most due to lateralization, did not arise until about 30,000 years ago (Klein & Edgar 2002). This would suggest that the asymmetrical features present on the brains of our ancestors were possibly used for some other "lateralized" task and were later co-opted for the function they have today (Broadfield et al. 2001). An alternative hypothesis suggests that these early asymmetries conferred similar human function, yet the development of the neuroarchitecture or function of the region was limited. Only later evolutionary forces or opportunities would have encouraged the further lateralization of function in the direction seen in modern humans.

Once a feature is expressed in a population it has the opportunity to be acted on. In the case of an asymmetry produced in the brain either through genetic or environmental control, or both, selective pressure may only act on the trait if it results in a new or altered behavior. In almost any population it can be assumed that the greatest selective pressures would be those created by predation, feeding, and mating. Indeed, many traits that have been shown to be related to asymmetries in responses, handedness, or lateralization are related to avoidance or feeding behaviors (Vallortigara et al. 1999). A feature may spread through a population for various reasons. It may offer some selective advantage as in the case of avoidance behavior or feeding. Alternatively, a feature may pass through the members of a population due to its relationship to a selected locus. In the case of language homologies in the primate brain, there is little evidence, despite similarities between area 44 of apes and humans in the cytoarchitecture, that apes display at best rudimentary homologous function in the area for language. This may suggest that certain asymmetrical areas of the brain did not become lateralized in function until later in human evolution, possibly only after area 44 and other regions were co-opted.

Asymmetries present in the brain or behavior of certain species appear to be related to lateralization of function (cf. the target article and Vallortigara et al. 1999). However, even though the evolutionary explanation for these features, and thus for the selection for cortical lateralization, is favored across species due to the conservative nature of the selective traits, an ESS does not appear applicable to more complex behaviors involving different strategies or even in certain cases when the strategies are equal, including the development of language. Instead one must consider whether lateralized complex traits are the result of coadaptation, in which case the social pressures selecting for them are the product of the trait.

Cerebral lateralisation, "social constraints," and coordinated anti-predator responses

Culum Brown

Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, EH9 1PE, United Kingdom, and School of Biological Sciences, University of Canterbury, New Zealand. **CulumBrown@yahoo.com**
http://www.geocities.com/culumbrown

Abstract: Lateralisation is traditionally viewed by neuroscientists and comparative psychologists from the perspective of the individual; however, for many animals lateralisation evolved in the context of group living. Here I discuss the implications of individual lateralisation within the context of the group from an evolutionary ecology perspective, with particular reference to coordinated anti-predator behaviour.

For the past decade scientists have recognised that virtually all vertebrates show some form of cerebral lateralisation that is manifested in their behaviour. But why should the brain be split in two and how did lateralisation evolve? Is there some kind of fitness advantage associated with having a lateralised brain? As Giorgio Vallortigara and Lesley Rogers point out in the target article, the study of lateralisation has long been the realm of neuroscientists and psychologists, but the fact that lateralisation exists in many individuals has compelling implications from behavioural ecology and evolutionary perspectives, and may be particularly important for group-living species.

In general the lateralisation pattern is similar for all vertebrates, though the degree of lateralisation as well as its direction varies within and between species, as well as from individual to individual. Fishes, for example, generally view with the right eye those stimuli that are likely to evoke emotive responses, whereas other objects are viewed with the left eye. However, this pattern is by no means fixed. Even within the family *Poeciliidae* intriguing variation exists (Bisazza et al. 1997). Some species have a tendency to view predators with the left eye or show no bias at all. Indeed, the variation is even greater when fish belonging to different families are compared (Bisazza et al. 2000). If we can begin to understand the source of this variation we may be able to shed some light on the evolutionary forces shaping the development of lateralisation in vertebrates.

Heuts (1999) suggested that differential exposure to predators owing to the occupation of varying habitats might explain interspecific variation in lateralized escape responses in fish. Likewise, intraspecific variation in eye use has also been explained by shoaling versus non-shoaling habits (Bisazza et al. 2000), which may vary with predation pressure and other environmental variables (Brown & Warburton 1997). Brown et al. (2004) tested this prediction directly by examining the lateralised responses of a single poeciliid species collected from regions of high and low predation pressure. Fish from high predation pressure showed a significant preference for viewing predators with their right eye and novel objects with their left eye, whereas fish from low predation areas showed no significant preferences. In accordance with the work of Rogers et al. (2004), this result strongly suggests that predation pressure may have played a key role in the evolution of lateralisation.

Within a species the preference for eye use is never absolute; rather, a frequency bell curve exists that may be shifted by varying degrees to the right or left resulting in an average species hemifield bias (Facchin et al. 1999). The fact that there are differences between individuals in the degree and direction of lateralisation is particularly intriguing. Trait diversity within a population provides the variability upon which selection can operate in the face of environmental heterogeneity. In the case of predator avoidance it makes little sense to repeatedly observe or avoid predators in a predictable manner since the predators will learn to approach from the least-preferred side. This is the mechanism behind fluctuating asymmetries in one well-documented piscean predator-prey system (Takahashi & Mori 1994). The fitness of both the predators and prey in this system is under frequency dependent selection based on the pattern or degree of lateralised traits. It should come as no surprise, therefore, that different species or populations show different patterns of lateralisation. The relationship between the frequency of the predators' preferred attacking side and the corresponding prey avoidance response should vary independently between populations. There is no reason to suggest that asymmetry would be biased in any given direction unless there were some form of phylogenetic constraint.

Few authors have considered the implications of individual differences in cerebral lateralisation at the group level. In group-living species that rely on coordinated anti-predator responses to increase their chances of survival during a predator attack (e.g., schools of fish, flocks of birds, herds of buffalo, etc.), individual differences in lateralised behaviour may have serious implications both for the survival of the individual and for the safety of the group as a whole. For many animals this is the context in which lateralisation evolved. At first glance cerebral lateralisation provides a great advantage since each animal can monitor its fellows and predators simultaneously. Upon closer examination, it becomes apparent that conflicts are likely to emerge within the group. For example, if all individuals prefer to monitor conspecifics with the left eye and predators with the right, then there ought to be competition for locations within the group that best

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satisfy those requirements (i.e., preference for a position on the right-hand side of the group). Now consider the situation when some of the individuals within the group show the opposite preference. Under this scenario, not only are most individuals more likely to be located in their preferred position within the group but the response of the group as a whole will also be greatly improved. At the group level, therefore, opportunities exist for the coexistence of many phenotypes and may help to explain why 10–35% of individuals show opposing hemifield biases to the rest of the population. Thus, with the correct ratio of left- and right-handed individuals within the group, predator detection could be optimised (just as it is important to have left- and right-footed individuals in a football team).

Predator detection is one thing, but what of the coordinated response that must inevitably follow? If individuals within the group show variable turn preference, it is difficult to imagine how the group could respond as a cohesive unit. Perhaps non-lateralised individuals play a role in maintaining communication between left-biased and right-biased individuals and in facilitating rapid transfer of information between group members, thereby maintaining a high degree of coordination within the group. Nevertheless, there are examples of anti-predator responses where having two distinct subunits within the group is advantageous (e.g., fountain effect: Pitcher 1986).

There is some evidence that non-lateralised animals have reduced fitness as measured by foraging and anti-predators behaviours (chickens: Rogers et al. 2004; chimpanzees: McGrew & Marchant 1999; and fishes: Bisazza & Dadda 2005). If cerebral lateralisation manifests itself by improved performance in multiple important behaviours such as foraging and anti-predator responses, one would expect that there would be selection against non-lateralised individuals in the wild, but few researchers have studied the frequency of phenotypes in wild populations. It could be that the two extreme phenotypes are more fit than are the non-lateralised phenotypes at an individual level; however, non-lateralised individuals may have enhanced fitness within the context of the group and may play some pivotal role in maintaining group cohesion.

Developmental systems, evolutionarily stable strategies, and population laterality

Michael B. Casey

Department of Psychology, The College of Wooster, Wooster, OH 44691.
mcasey@wooster.edu

Abstract: Multiple endogenous and exogenous prenatal influences interact to form a system that induces the development of individual lateralization across a range of perceptual and motor abilities in precocial birds. As these influences are nearly invariant for all species members, they produce a phylogenetic influence that creates high levels of population laterality and social cohesion in the postnatal state.

Vallortigara & Rogers (V&R) provide many excellent arguments to support their hypothesis for the emergence of population laterality in some highly social mammalian and bird species, based on Maynard Smith's (1982) evolutionarily stable strategy (ESS) argument. Not surprisingly, the key to any such strategy is the developmental system that supports its formation and stability. For every ESS that occurs, a developmental system of transacting organismic and environmental influences must induce, facilitate, and maintain its social structure (Gottlieb 1992; Lickliter & Honeycutt 2003; Oyama 2000). V&R have extensively documented the influence of prenatal visual experience on the development of individual and population laterality in the domestic chick. However, we should not view an exogenous influence such as prenatal light stimulation as an isolated factor. It is part of a much larger developmental process that ultimately leads to the chick's transition from the prenatal to the postnatal environment. Several studies suggest that endogenous factors (such as the hatching process in precocial birds) also serve as both developmental system and ESS in the formation of population-level motor lateralities that influence postnatal social behavior.

Two such behaviors have been investigated under laboratory conditions in domestic chicks and bobwhite quail: turning bias and stepping preference. More than 75% of domestic chicks and bobwhite quail demonstrate a right-foot stepping preference (footedness) and a left-side turning bias that appear to be influenced by both prenatal visual experience and asymmetrical hatching behaviors. Although it has been shown that prenatal visual experience can facilitate the development of both footedness (Rogers & Workman 1993) and turning bias (Casey & Karpinski 1999) in domestic chicks and the development of turning bias in bobwhite quail (Casey & Lickliter 1998), asymmetrical hatching behaviors have been found to be a critical factor as well (Casey, in press; Casey & Sleigh 2001).

Hatching behaviors in most precocial bird species (domestic chicks, quail, turkeys, pheasants, etc.) involve a series of seven stages in which the embryo twists its body and bends its limbs to a final orientation in which the right side of the body is positioned upwards toward the air space, the head is tucked under the right wing, and the right shoulder and beak are aligned toward the air space (Hamburger & Oppenheim 1967; Kuo 1932; Oppenheim 1973). The embryo's body obscures the left eye. This process begins on day 16 of a 21-day incubation period for domestic chicks and covers 29% of the chick's prenatal development. This hatching sequence is nearly invariant across precocial bird species (Oppenheim 1972). As hatching nears, the beak pierces the inner membrane and enters the air space at the top of the egg. These coordinated behaviors and the body orientation they produce prepare the chick for pipping the shell and emerging from the egg (Kuo 1967). The final hatching stage is defined by rapid respiration, repeated leg extensions into the egg's narrow end, and multiple head thrusts upward, causing the beak and egg tooth to move against the top of the eggshell (Bakhuis 1974). The coordinated movements of the head, neck, and legs rotate the chick's body within the tight confines of the shell (Bekoff 1988). These full body rotations are always counterclockwise from the original pip mark and result in an incision of the shell driven by the right side of the chick's body.

When late-stage hatching behaviors are disrupted, population level motor laterality is eliminated and individual degree of laterality is significantly weakened (Casey & Martino 2000). Furthermore, it is not merely the asymmetrical position of the embryo's head within the egg that exerts a canalizing influence; the hatching behaviors themselves are key. The hatching behaviors are among the chick's first coordinated movements that are clearly tied to complex neural activity (Bekoff 1986) and they are a powerful influence on the development of postnatal motor laterality. As these stereotyped behaviors occur in all chicks that hatch successfully, they serve to induce the development of individual and population-level turning bias and footedness.

The embryo's orientation achieved 4 to 6 days prior to hatch prepares the chick for exiting the egg, but also allows the right eye to receive differential amounts of light exposure. In fact, it is the only orientation that will allow visual stimulation to the right-eye system alone and successful hatching (Asmundson 1938; Bekoff 1995). This is a powerful evolutionary selection factor in that only those chicks that achieve the optimal body orientation prenatally have any chance of surviving into a mature form, and those that do will have had nearly identical early experiences in the form of prenatal visual stimulation and asymmetrical hatching. Both of these early developmental influences occur at an essential period of sensory and motor neuronal plasticity (Bekoff & Sabichi 1987; Corner & Bakhuis 1969) and underlie the development of hemispheric lateralization and behavioral asymmetries. As such, they serve to synchronize the population in a particular direction and result in robust levels of individual and population laterality.

The interaction of asymmetrical hatching behaviors and prena-

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tal visual experience, both part of the complex multi-day hatching process, is a clear example of a developmental system and an ESS wherein multiple influences (both exogenous and endogenous) provide a supportive and facilitative, even inductive, environment for development. Such developmental mechanisms constrain the range of evolutionary potential and outcomes (Greenough 1991), and may ensure postnatal social cohesion in the form of population laterality as V&R argue. In this context, the structure of the environment (the presence of visual stimulation at a critical point in development) and the structure of the organism's own development (the species-typical orientation in the egg during late-stage development prior to hatching) interact to produce early experiences that shape the chick brain's structural laterality and functional behavioral asymmetries. As long as these factors remain relatively invariant (e.g., occurring in essentially the same manner for all members of the species), a high degree of individual and population laterality for a variety of perceptual and motor abilities (Rogers 1982; 1990; Rogers & Workman 1989; Rogers et al. 1998; Tommasi & Vallortigara 1999) is reliably produced across generations, and the evolutionarily stable strategy is preserved.

Genes as primary determinants of population level lateralisation

Miguel L. Concha

Programa de Anatomìa y Biologìa del Desarrollo, Instituto de Ciencias Biomèdicas, Facultad de Medicina, Universidad de Chile, Clasificador 7 Correo 7, Santiago, Chile. **mconcha@med.uchile.cl**

Abstract: Vallortigara & Rogers (V&R) propose a fundamental role of the environment in determining population-level lateralisation and suggest that genes play no primary function in this phenomenon. Here I argue that genes involved in the coordination of visceral organ laterality and in coupling of different forms of lateralisation do play a role in the control of lateralisation within the population.

Vallortigara & Rogers (V&R) suggest that genes play a vital role in determining lateralisation in individuals but have no primary function in the control of lateralisation at a population level. They propose that social life (e.g., prey-predator interactions) drives changes in environmental stimuli (e.g., light exposure of eggs) able to direct lateralisation within the population (e.g., lateralised eye use in birds). They also draw attention to the unlikelihood that population-level lateralisation is a mere by-product of genetic pathways determining somatic asymmetry. Although I am in agreement with a role for epigenetic factors in driving lateralisation within the population, I argue that genes do play a primary function in at least some forms of population-level lateralisation.

Recent evidence demonstrates that morphological asymmetries in limbic system-related nuclei such as the habenulae are established early in development by means of inhibitory interactions that take place across the dorsal midline of the zebrafish forebrain (Concha 2004). In these interactions, one side of the brain competes with the contra/lateral for the ability to acquire specific morphological traits. As the outcome of competition is in principle unpredictable (left and right sides have equal competitive abilities), signals that others than those involved in the competition itself must operate to confer advantages to one side of the brain, thus causing laterality decisions to become consistently biased within the population (Concha et al. 2003). Such laterality signals are expressed at early stages of development in discrete regions of the left forebrain and involve molecular components of a genetic pathway commanded by the TGFb Nodal secreted protein (Concha et al. 2000). Interestingly, Nodal signalling also plays a key role in shaping laterality of visceral organ asymmetry (Schier 2003) and is expressed asymmetrically in the left lateral plate mesoderm from where it is transferred to the left forebrain (Long et al. 2003). In mutant embryos with disrupted Nodal signalling, the laterality of asymmetry becomes randomised in the heart, pancreas, and brain, and is uncoupled between the different organs (Concha et al. 2000; Yan et al. 1999). This observation underscores the intimate relationship established during development between the mechanisms of brain and visceral organ asymmetry, and suggests that population-level lateralisation of the habenulae is the end result of genetic pathways primarily involved in coupling visceral organ laterality. In support of this view, zebrafish larvae with *situs inversus* show inverted visceral organ and forebrain asymmetries, and a reversal in lateralised behaviours such as eye use (Barth et al., in press). It is possible that Nodal signalling directs lateralisation of limbic system-related nuclei in all vertebrate species; however, this remains to be confirmed as laterality of habenular asymmetry is not well conserved among the different vertebrate groups (Concha & Wilson 2001).

It is important to note that other types of population-level lateralisation such as language cerebral dominance, dichotic listening, and handedness are not reversed in humans with *situs inversus* and thus are unlinked to visceral organ laterality (Kennedy et al. 1999; Tanaka et al. 1999). Handedness, in particular, is another case in which genetic expression of behavioural asymmetry is controlled independently from its direction. Indeed, V&R take this example to support their view on the role of social factors as determinants of population-level lateralisation. However, an elegant paper on the nature versus nurture basis of human handedness (Klar 2003) argues against this interpretation by demonstrating that hand preference is genetically determined as it can be linked to directionality of scalp hair-whorl rotation, a biologically specified trait that unlike handedness is not influenced by social factors. This report also proposes that a single gene, independently from the genetic pathways controlling visceral organ asymmetry, controls both handedness and whorl orientation. In this "random-recessive" genetic model, the single dominant gene causes right-handedness and clockwise whorl rotation in the dominant homozygous and heterozygous situations, and the recessive and nonfunctional allele confers a statistical random chance in recessive homozygosis (Klar 1996; 2003). It is interesting to notice the close resemblance between the mechanisms that control laterality in the zebrafish forebrain (as mentioned above) and those that determine directionality of human handedness (Klar 2003). In both cases, genetic determinants of lateralisation per se generate asymmetries with a random laterality outcome, which is then directed within the population by "laterality genetic signals" (e.g., the Nodal signalling pathway in zebrafish and the RGHT gene in humans). Moreover, in both cases the genetic mechanisms controlling population-level lateralisation are intimately linked to mechanisms that determine coordination of laterality between different asymmetric structures of the body (e.g., coordination of visceral organ laterality in zebrafish and coupling between the dominant hemisphere and right-handed preference in humans).

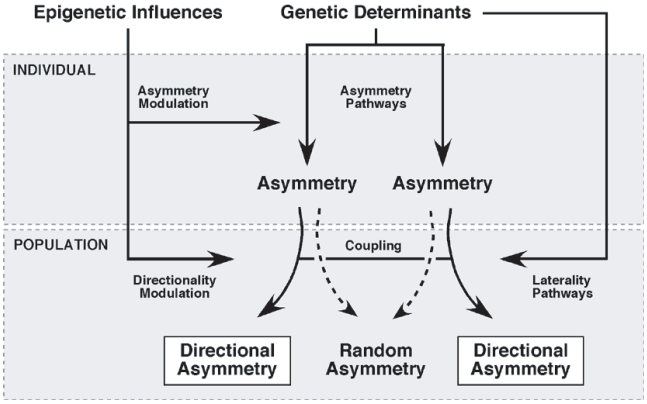


Figure 1 (Concha). Genetic and epigenetic determinants of population-level lateralisation.

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It is therefore possible that genetic and developmental pathways responsible for directing asymmetry within the population were acquired early in vertebrate evolution as a means (or a consequence) of coupling/coordinating different types of asymmetry within the body. In this context, uncovering a possible common origin of vertebrate lateralisation becomes fundamental to better comprehend how genetic and epigenetic factors determine population-level lateralisation.

In summary, I propose that both genetic and epigenetic factors play primary roles in specific forms of population level lateralisation (Fig. 1). V&R describe in detail the epigenetic determinants of population-level lateralisation whereas I argue for a role of genetic determinants primarily involved in either coordination of visceral organ laterality or in the coupling of different forms of brain lateralisation.

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The trade-off between symmetry and asymmetry

Michael C. Corballis

Department of Psychology, University of Auckland, Private Bag 92019, Auckland 1001, New Zealand. **m.corballis@auckland.ac.nz**
http://www.psych.auckland.ac.nz

Abstract: Population-level asymmetry may be maintained, not by an "evolutionarily stable strategy" pitting a dominant bias against its nondominant opposite, but rather by a genetically based system pitting a directional bias against the absence of any such bias. Stability is then achieved through a heterozygotic advantage, maintaining balanced polymorphism. This model may better capture the fundamental trade-off between lateralization and bilateral symmetry.

One of the myths of our time, propagated by myself, among others, is that cerebral asymmetry somehow defines the human condition – we are, it has been claimed, the lopsided ape (Corballis 1991). We have been fooled into this myth by a number of factors. First is the desire to see humans as superior to other animals, and the human left hemisphere as somehow uniquely endowed with properties that transcend mechanical laws – the pineal gland knocked sideways (e.g., Popper & Eccles 1977). Second, bipedalism in hominids freed the hands for activities other than locomotion, thereby exposing cerebral asymmetry in the manual activities that we humans have so adroitly developed. Other manifestations of cerebral asymmetry are less obvious than human handedness, but no less present. Third, cerebral asymmetry is a conspicuous characteristic of language, which is itself almost certainly uniquely human, at least with respect to its generative property. Some of our lateralized activities may well be distinctive to our own species, but cerebral lateralization itself is not. Vallortigara & Rogers (V&R) are to be commended for exposing the myth, in a forum that should get the message across to neuropsychologists as well as to behavioural ecologists.

As V&R observe in the target article, not all individuals in a population follow the predominant pattern – the minority who "go the other way" seem to vary from about 35% to about 10%. V&R seek the origin of this uneven division in frequency-based selection, which they illustrate in terms of escape strategies. If a predator threatens, it is a good idea to run off to the left with the crowd, where there is safety in numbers, and the probability of any individual being caught is low. But the predator is likely to chase the crowd, maximizing the chances of capturing at least one victim. This means that the maverick who joins the minority who run off to the right may also have a good chance of escape, but only so long as this group remains a minority. Frequency-based selection, though, may be unstable, as in the example of cychlids, where the dominant asymmetry of the mouth periodically changes direction (Hori 1993).

Another possibility is that the fundamental distinction is not between left- and right-dominance, but rather between asymmetry and symmetry. As V&R recognize, bilateral symmetry is itself an adaptation to the equivalence of left and right in the natural world (Corballis & Beale 1976) and goes back at least to the origins of the Bilateria some 600 million years ago, and perhaps even earlier (e.g., Finnerty et al. 2004). But bilateral symmetry is also a constraint on function, and is abandoned, or at least relaxed, when lateral specialization is more adaptive. This suggests a trade-off between pressures to symmetry and pressures to lateralization.

This trade-off is captured in contemporary genetic theories of handedness. Instead of proposing a right-hand allele and a left-hand allele, these theories assume that one allele predisposes to right-handedness and the other does not (Annett 2002; Klar 1996; McManus 1999). This assumption provides for a better fit to data on the inheritance of handedness, and can also account for other characteristics of laterality, such as the finding that left-handers are more variable with respect to other asymmetries, including cerebral dominance for speech (Annett 2002; McManus 1999). It also explains why the distribution is uneven, since there is a systematic bias toward right-handedness but no such bias toward left-handedness. Both Annett and McManus make it clear that their models incorporate cerebral asymmetry as well as handedness, and the same principle may well apply fairly generally to the genetics of asymmetry (Morgan & Corballis 1978).

The two alleles are assumed to be held in balance by a heterozygotic advantage in fitness (Annett 1995; Corballis 1997), ensuring that the proportion of left-handers cannot exceed 50%. Nevertheless, variation is possible, governed by the relative fitness of the two homozygotic genotypes. Following McManus (1999), we may call the two alleles D for dextral and C for chance. If we set the fitness of CD heterozygotes at 1, the ratio of p(D): p(C) is given by (1–fCC):(1–fDD), where fDD and fCC are the respective fitness of DD and CC genotypes relative to that of the CD genotype. Thus, if DD and CC are equally disadvantaged relative to DC, the two alleles will be present in the population in equal proportions. So long as there is a heterozygotic advantage, so that fDD and fCC are both < 1, both alleles will remain in the population, but their relative frequency may vary. A heterozygotic advantage can ensure maintenance of both alleles in the population even when one of the homozygotes is lethal, with zero fitness, as in the example of sickle-cell anaemia. This is due to a rare form of haemoglobin, which is lethal in those homozygotic for the allele, but heterozygotes have an advantage in malarial zones (Lewontin 1974).

With respect to symmetry vs. asymmetry, it remains largely a matter of speculation why the two homozygotes should have lower fitness than the heterozygote. V&R give examples from birds where laterality leads to more efficient performance, especially in dual-tasking, but it is not clear why heterozygosity might prove more adaptive than homozygosity. Perhaps homozygosity simply acts to hold lateralization in check, so the bird is not overly exposed to threat from the weaker flank. In the case of human cerebral asymmetry, Annett (2002) has summarised evidence that DD homozygotes may be deficient in spatial processing, whereas CC individuals may be at risk for verbal impediments. CD individuals, like Baby Bear's porridge in the Goldilocks story, are just right – neither too hot nor too cold. Another perspective is provided by suggestions that bilaterality (CC) may be associated with more general deficits in academic ability (Crow et al. 1998), and also with a tendency to magical ideation (Barnett & Corballis 2002). Perhaps, then, the two alleles may express, not only the tension between symmetry and lateralization, but also the age-old conflict

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between reason and superstition. Or even, dare I suggest, between science and religion.

The cerebral torque and directional asymmetry for hand use are correlates of the capacity for language in *Homo sapiens*

Timothy J. Crow

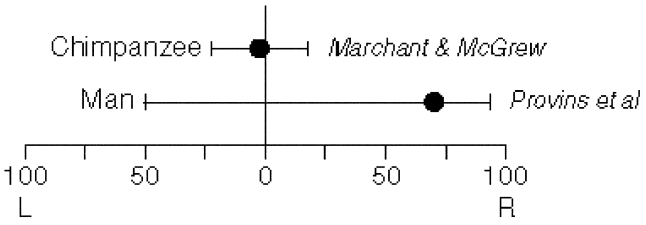
SANE Prince of Wales International Centre, Warneford Hospital, Oxford OX3 7JX, United Kingdom. **tim.crow@psych.ox.ac.uk**
http://www.psychiatry.ox.ac.uk

Abstract: The claim of consistent hemispheric specialisations across classes of chordates is undermined by the absence of population-based directional asymmetry of paw/hand use in rodents and primates. No homologue of the cerebral torque from right frontal to left occipital has been established in a nonhuman species. The null hypothesis that the torque is the sapiens-specific neural basis of language has not been disproved.

Table 1 of the target article makes the claim that 11 different functions have been reliably associated with the left hemisphere and 14 with the right hemisphere across four classes of chordates (fish, amphibia, birds, and mammals) and across four different orders of mammals (rodents, carnivores, artiodactyls, and primates) to buttress the conclusion that "In the past few years . . . something really new has appeared: namely, evidence for lateral biases affecting everyday behavior in the natural environment of a variety of species" (sect. 1 of the target article). But Table 1 lacks a single reference to the literature. Any diligent reader who follows up the reviews (e.g., Rogers & Andrew 2002) that Vallortigara & Rogers (V&R) give in search of the primary sources will find a literature rich in anecdotal claims but exceedingly meagre in well-documented evidence for consistent directional asymmetries within a species, and particularly in evidence that any such trend is maintained across a species boundary. The null hypothesis (the Broca-Annett axiom: Crow 2004) is that population-based directional cerebral asymmetry with its anatomical basis – the cerebral torque from right frontal to left occipital – is present as the substrate of the capacity for language in *Homo sapiens* but in no other vertebrate species.

Where there have been systematic studies, the evidence does not support V&R's thesis. Collins (1977; 1985) analysed inheritance of strength and direction of pawedness in mice, and V&R (in note 4 of the target article) acknowledge the main finding, "There is no evidence for heritability of direction in the strain of mice studied by Collins" but explain it away on the basis that Collins picked the wrong strain! In fact Collins studied eight inbred strains and partially inbred stocks of wild strains. Elsewhere, Rogers (2004) states that "some strains of rats show handedness (a population bias to use the same paw), some do not" but does not specify which strains. If some strains of mice and some of rats are truly directionally lateralised and some are not one might think that some interesting cross-breeding or even transgenic studies are in prospect. But a simpler explanation is that directionality of pawedness in rodents is randomly determined, as Collins's studies suggest, and that reports to the contrary are attributable to observer bias or small sample size in less systematic studies. Either way, the implicit claim for cross order and class consistencies in lateralisation in Table 1 is undermined.

Handedness in primates and the great apes is more relevant and the evidence more damaging to V&R's thesis. Finch (1941) found that in contrast to the human population chimpanzees show no directional lateralization on a population basis. Similar observations were made by Annett and Annett (1991) on gorillas. Annett and Annett's conclusion that population-based directional asymmetry is specific to *Homo sapiens* is substantially reinforced by the studies of Marchant and McGrew (1996) of chimpanzees in the Gombe National Park (see Fig. 1).



	Number of individuals	activities
Chimpanzee	38	46
Man	1960	75

Figure 1 (Crow). Hand preference for everyday activities in chimpanzees and *Homo sapiens* compared. Data for chimpanzees refer to a community of 38 animals (*Pan troglodytes schweinfurthii*) observed in Gombe National Park by Marchant and McGrew (1996). Data for *Homo sapiens* were collected by questionnaire from populations of undergraduates by Provins et al. (1982). Medians and boundary values for 95% have been extracted from graphs in the original publications.

Holder (1999) made careful cross-species comparisons in a series of primates in Africa and concluded that "No species level left- or right-handedness was found for any of the five species (common chimpanzee, red colobus, redtail money, grey-checked mangabey, and mountain gorilla) studied." In their seminal review of the primate literature, McGrew and Marchant (1997) concluded that "non-human primate hand function has not been shown to be lateralized at the species level – it is not the norm for any species, task or setting, and so offers no easy model for the evolution of human handedness."

V&R disagree: "Heritability of direction of hand preferences . . . has been reported in chimpanzees (Hopkins et al. 1994; 2001)". But in a review of the data of Hopkins (1994), Palmer (2002) found that re-examination

> revealed several puzzling patterns: 1) funnel plots showed higher percent right hand use among individuals for which fewer observations were recorded, 2) when individuals with fewer than 25 observations were excluded statistical support for population-level right-handedness either became marginal . . . or disappeared . . . and 3) the proportion of statistically ambilateral chimpanzees actually increased with increasing number of observations per individual, rather than decreased as would be expected for true population-level right-handedness.

But if directional asymmetry on a population basis is absent in the chimpanzee, our closest primate relative, as the reports of Finch (1941), and Marchant and McGrew (1996) strongly suggest, how can observations on birds and fish far distant on the vertebrate tree be relevant to what we observe in *Homo sapiens?* Whatever the reliability of the directional asymmetries reported in these disparate species, the case presented in Table 1 by V&R that there are cross-order and class consistencies that include cerebral lateralisation in man collapses.

Note 6 states that "Evidence for lateralization other than handedness abounds in nonhuman primates. . . . These behavioral data are . . . substantiated by . . . new (Cantalulpo & Hopkins 2001; Gannon et al. 1998) evidence for neuroanatomical asymmetries in the nonhuman primate brain." In my earlier review (Crow 2003a) of Rogers & Andrews' (2002) volume, I commented on this "new anatomical evidence" as follows:

1. Cantalupo and Hopkins (2001) present measures of an area of the inferior frontal gyrus on magnetic resonance images of 20 chimpanzees (*P. Troglodytes*), 5 bonobos (*P. paniscus*), and 2 gorillas (*G. gorilla*), and suggest that this area shows a "human-like asymmetry" that justifies its identification with Broca's area for

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speech production in man. The salient problem with this claim is that there is no clear asymmetry to the left of the inferior frontal gyrus *in man*. In a review of postmortem studies including 183 brains, Witelson and Kigar (1988) wrote: "the main result . . . is that there is no evidence of a statistically larger left than right 'Broca region'." Recent MR analyses of the asymmetries of the normal adult brain (Good et al. 2001; Watkins et al. 2001, with sample sizes of 465 and 142, respectively) have failed to identify areas with a leftward asymmetry that could be equated with Broca's area. Watkins et al. write that "no significant asymmetry was detected in anterior language regions." So much for the "uncanny" similarity detected by Cantalupo and Hopkins and reported in *Nature!*

2. Gannon et al. (1998) reported leftward lateralization of the planum temporale in 17 out of 18 chimpanzees by a method (inserting plastic triangles into the lateral sulcus) that clearly was not blind and is a crude approach to the asymmetry (65% L > R) rediscovered by careful anatomical dissection of the human brain by Geschwind and Levitsky (1968). Yet chimpanzees were found to be more lateralized than Man! Buxhoeveden et al. (2001) quantitatively assessed the minicolumn structure of the planum temporale down the microscope and found that in the widths and separations, for example, asymmetries were present in the human cortex that were absent in the chimpanzee and rhesus monkey. Zilles et al. (1996) devised a method for quantifying the torque on MRI scans and found that the right frontal to left occipital bias that can be demonstrated in the human brain is absent from that of the chimpanzee.

Given this background, I submit that the older studies in nonhuman primates in which V&R assert that "evidence for lateralization other than handedness abounds" deserve careful reexamination.

The authors' failure to acknowledge the deficiencies of some of the studies they cite (as described in Crow 2003a; 2004) and the conclusions of systematic reviews (e.g., McGrew & Marchant 1997) suggests that the authors can maintain the interpretation of their Table 1 only by ignoring contrary evidence, and by non-specific reference to "the enormous amount of evidence for lateralization in nonhuman species" (note 5). The literature is enormous but the hard evidence that there are population-based directional asymmetries that cross species boundaries, let alone those between orders and classes of chordates, is lacking.

Causal relations between asymmetries at the individual level?

Rebecca G. Deason,[a] David R. Andresen,[b] and Chad J. Marsolek[a]

[a]*Department of Psychology, University of Minnesota, Minneapolis, MN 55455;* [b]*Department of Psychology, Stanford University, Stanford, CA 94305.*
deas0007@umn.edu andr0196@psych.stanford.edu
chad.j.marsolek-1@umn.edu http://levels.psych.umn.edu

Abstract: Studies with humans have failed to produce evidence that any direct causal relation exists between the asymmetry of one function in an individual and the asymmetry of a different function in that individual. Without such evidence, factors external to an individual's nervous system, such as social interactions, may play crucial roles in explaining the directions of all asymmetries at all levels.

An increase in brain capacity and efficiency may be obtained through lateralization of function. However, Vallortigara & Rogers (V&R) point out that this benefit may be obtained at the level of an individual, and it need not imply an alignment of the direction of lateralization in the majority of individuals of the population. Given this consideration, the authors ask why behavioral asymmetries at the population level frequently are aligned in a common direction, and they suggest that social-interaction pressures may be responsible. In other words, a causal relation may exist between the asymmetry of a function in one individual and the asymmetry of that function in other individuals in a society, and the causality may involve social interactions. This is an interesting hypothesis. But, returning to the level of an individual, is there evidence that a causal relation exists between the asymmetry of one function in an individual and the asymmetry of a different function in that individual? If not, then the directions of all asymmetries at both the population and individual levels may rely on social interactions or similar factors.

Consider the situation in which an initial lateralization for a particular function exists within an individual. This could affect subsequent asymmetries. In the human neuropsychology literature, theories have been put forward positing that an initial asymmetry may play a causal role in the development within an individual of another asymmetry.

According to one theory (Hellige 1993; Kosslyn 1987), initial lateralizations act as "seeds" for subsequent lateralizations. Interactions are more effective within a hemisphere than across hemispheres, which affects the tuning of functions during development. This causes the directions of subsequent asymmetries to be aligned with those of the related seed asymmetries (i.e., asymmetries "snowball" from initial to subsequent asymmetries). According to another theory (Cook 1984), homotopic areas of the hemispheres mutually inhibit each other, and adjacent areas within one hemisphere also mutually inhibit each other. Following the inhibition of an area in one hemisphere, the surrounding area is activated, which inhibits its homotopic area in the other hemisphere. A cycle ensues, with the result that complementary functions are performed in contiguous neural areas in one hemisphere, and these functions exhibit opposite-direction asymmetries. By these theories, a strong empirical prediction is that the directional measures of two asymmetries should exhibit a *negative* correlation within individuals when the asymmetries have been caused by opposite-direction seeds or when they reside in contiguous areas, or a *positive* correlation within individuals when the asymmetries have been caused by the same seed or common-direction seeds (Marsolek & Andresen 2003).

A similar theory (Ivry & Robertson 1998; Jacobs & Kosslyn 1994; Sergent 1983) focuses on how asymmetries in lower-level perceptual processing may cause asymmetries in higher-level processes. Typically, the left hemisphere is more efficient at processing or attending to information from cells with small receptive fields or information from high spatial-frequency modules, whereas the right hemisphere is more efficient at processing or attending to information from cells with large receptive fields or information from low spatial-frequency modules. This should cause higher-level functions that are advantaged by different kinds of visual input to be lateralized in the directions of the relevant lower-level asymmetries. By this theory, a strong empirical prediction is that the directional measures of two asymmetries should exhibit a *negative* correlation within individuals when the asymmetries have been caused by preferences for the different kinds of visual input, or a *positive* correlation within individuals when the asymmetries have been caused by preferences for the same kind of visual input (Marsolek & Andresen 2003).

We tested these predictions by measuring asymmetries in four visual functions previously shown to be asymmetric at the population level (Marsolek & Andresen 2003). Previous research has indicated that specific-exemplar shape recognition and specific spatial-relations encoding exhibit right-hemisphere advantages, whereas abstract-category shape recognition and abstract spatial-relations encoding exhibit left-hemisphere advantages (Chabris & Kosslyn 1998; Kosslyn 1987; Marsolek 1999; Marsolek & Burgund 1997). We replicated these results in a single group of subjects using a common set of stimuli, and found the previously observed asymmetries when data were averaged across subjects. We then calculated an asymmetry score for each of the four tasks for each subject. These scores were highly reliable according to split-half reliability tests. The important finding was that an asymmetry in

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any one task did not correlate (positively or negatively) with asymmetries in any of the other three tasks. These results provide evidence against any causal relations between different functional lateralizations within an individual. Hemispheric asymmetries for different functions within an individual appear to be independent. These results are consistent with previous research in which asymmetry scores were measured for several tasks and principal-components analyses indicated that the asymmetries did not load onto the same factor (Boles 1998). Positive relationships between two or more asymmetry scores were found, but these likely were cases in which a common neural function subserved the tasks.

The conclusions from research on relations between asymmetries in individual humans may provide an interesting extension to the theory proposed by V&R. Admittedly, the conclusions in those studies are limited to the functions measured. But, if no causal relation exists between an asymmetry in one individual and another asymmetry in that individual, it is possible that the directions of all asymmetries at all levels rely on social interactions or similar factors.

Behavioral symmetry and reverse asymmetry in the chick and rat

Victor H. Denenberg

Biobehavioral Graduate Degree Program and Department of Psychology, University of Connecticut, Storrs, CT; and Biochemistry, University of Washington, Seattle, WA. **Denenberg@mac.com**

Abstract: Chicks reared in the absence of light and rat pups reared without extra stimulation fail to exhibit behavioral laterality, implying that a threshold amount of environmental stimulation is necessary for the brain to follow an asymmetry pathway. Reverse asymmetry has been reported in the chick, but not the rat, though a sex difference resembling reverse asymmetry has been found in the rat.

Vallortigara & Rogers (V&R) present a compelling case for their evolutionary hypothesis that social constraints are the key factor leading to population asymmetry of ethological behaviors. They support their argument with wide-ranging data from fish, amphibians, reptiles, birds, and mammals. The predominant laterality pattern involves left hemisphere dominance for visual discrimination, communication, approach, and inhibition of negative behaviors; the right hemisphere is characterized by spatial processing, fear and escape, attack, and copulation. V&R wisely point out that their gene-based evolutionary hypothesis is not deterministic because (1) some species have behavior patterns opposite to the "standard" one described above, and (2) environmental events occurring near the time of birth or hatching can markedly influence the asymmetry pattern of the brain. This last point is illustrated by Rogers' (1982; 1990) elegant experiments with the domestic chick. Normally, the chick's right eye is exposed to light in the egg but the left eye is occluded. These control animals show right-brain dominance for copulation and attack, whereas the left brain is dominant for visual discrimination learning. If the eggs receive no visual stimulation prior to hatching, none of these behaviors is lateralized (Rogers 1982). However, if visual stimulation is reversed so that the left eye is exposed, the behaviors are again lateralized but in the opposite direction (Rogers 1990).

I want to follow up on the last two chick findings – lack of asymmetry and reverse asymmetry – by discussing what appear to be similar phenomena in rats. In 1981 I published in this journal a review of laterality research, a model system of hemispheric asymmetry, and a summary of our own laterality studies with rats (Denenberg 1981). Control rat pups were reared without any experimenter-imposed stimulation between birth and weaning, whereas experimental pups were removed from the maternity cage for 3 minutes daily between birth and weaning (a procedure called "handling"). In adulthood, 4 males from each litter were subjected to a left-brain lesion, a right-brain lesion, or sham surgery, or were left undisturbed. Our results showed that the handling procedure brought about left-brain dominance for open-field activity and right-brain dominance for taste aversion, muricide, and clockwise-turning in an open field. In marked contrast, the control rats showed brain laterality for only one behavior: increased taste aversion to a control injection of saline, but not to the lithium chloride. In a later study, using unilateral eye patches during adult testing, we found handled males to have right hemisphere control for spatial learning in the Morris maze, while nonhandled males showed no evidence of laterality for this behavior (Cowell et al. 1997).

At the time those studies were published, the scientific dogma was that animals do not have lateralized brains. Hence, the focus was upon the handling intervention that produced lateralized behaviors against the control background of no behavioral laterality. Twenty-five years later, the focus has shifted and the lack of behavioral asymmetry is now a topic of interest. Our nonhandled rat and Rogers' (1982) chick not exposed to light are similar in that both have brains with minimal behavioral laterality. This leads to the hypothesis that the level of environmental stimulation needed to direct the brain to select an asymmetrical developmental pathway must exceed some threshold. If stimulation is below this level, the brain will not be lateralized or will be lateralized to a much lesser degree. In this context, the role of the environmental stimulation is to tell the developing organism something about the nature of the world it will be living in. Thus, the light-deprived chick is told that it will be living in a world devoid of visual information, and the nonhandled rat pup is told that its world will have little variability (e.g., no exposure to novel events, no major temperature change, no increase in environmental complexity, no unusual attention by the mother). In such "simple" worlds the demands upon the brain are fewer and therefore brain redundancy (symmetry) gives the animal a back-up fail-safe system.

Following this line of reasoning, if the developing organism is exposed to sufficient stimulation (variously called environmental complexity, variation, or novelty), brain redundancy (symmetry) is given up for brain specialization (asymmetry) since the latter increases neural capacity (Levy 1977), and for the other reasons that V&R discuss.

In the chick, asymmetrical visual input resulted in behavioral laterality in one direction or the other, while lack of visual stimulation produced animals with behavioral symmetry. The handling stimulation given rat pups, in contrast, does not have an asymmetry dimension, yet that stimulation produced animals with asymmetrical brains. On that ground, asymmetrical input is not a necessary condition to produce behavioral asymmetry of the brain.

In order to determine whether reverse asymmetry can be obtained in the rat, it will be necessary to devise procedures to present the developing animal with asymmetrical sensory input, as Rogers (1990) has done. However, there is a set of findings in the literature that hints at an opposite pattern of hemispheric asymmetry. All of our studies were done with male rats, with one exception. Handled male rats have a clockwise turning bias in the open field, and nonhandled males are unbiased (Sherman et al. 1980). When this study was repeated using handled and nonhandled female rats, the exact opposite pattern was found (Sherman et al. 1983). The male findings have been independently confirmed in two laboratories (Camp et al. 1984; Tang et al. 2003); and Camp et al. have also confirmed our female findings. These data suggest that behavioral lateralization of the female rat brain may show a profile different from that found for the male rat.

At this time it is not known whether the sex difference represents an asymmetry reversal or whether females are using different cues (e.g., local versus spatial), hence different hemispheres, than males in navigating through the field.

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Interactions between genetic and environmental factors determine direction of population lateralization

Chao Deng

Department of Biomedical Science, University of Wollongong, Wollongong, NSW 2522, Australia. **chao@uow.edu.au**

Abstract: Direction of the embryo's head rotation is determined by asymmetrical expression of several genes (such as *shh*, *Nodal*, *lefty*, and *FGF8*) in Hensen's node. This genetically determined head-turning bias provides a base for light-aligned population lateralization in chicks, in which the *direction* of the lateralization is determined by genetic factors and the *degree* of the lateralization is determined by environmental factors.

Using the concept of an "evolutionarily stable strategy (ESS)/frequency-dependent selection" hypothesis, and "social selective theory," Vallortigara & Rogers (V&R) explain well the evolution of lateralization of avoidance-aggressive behavior or the lateral biases in prey-predator interactions at the population-level. However, other forms of lateralization might not fit this theory. One reason is that not all behavioral lateralization (e.g., lateralization of song control in birds and other cognitive functions) at the population level is predictable for other organisms; therefore, the population lateralization of these behaviors could not be simply said to be more disadvantageous as V&R suggest in their example about the lateralization involved in prey-predator interactions.

The authors have summarized the developmental mechanisms by which lateralization is aligned at the population level. Taking the development of visual lateralization in the chick and pigeon as examples, lateralized light stimulation of right eye during the later stages of incubation induces the motor, visual, and cognitive lateralization at the population level (Casey & Martino 2000; Rogers 1982; Rogers & Andrew 2002). This results because, during this period, the embryo of these birds turns its head against the left side, so that the left eye is occluded by the body and the right eye is positioned next to the air sac. Recent studies have shown that a left-right asymmetry in position of the visceral organ and direction of the embryo's head rotation are determined by asymmetrical expression of sonic hedgehog (*Shh*), *Nodal*, *lefty*, and *FGF8* genes in and around the chicken organizer (Hensen's node) during and after the gastrulation stage of embryonic development (Boettger et al. 1999; Levin et al. 1995; Meyers & Martin 1999; Schier 2003). Therefore, population lateralization aligned by asymmetrically light stimulation during the embryonic development is based on genetically determined head turning.

Chicks hatched from dark-incubated eggs showed asymmetry in using the left or right monocular field (Deng & Rogers 2002a; Vallortigara et al. 2001), but they did not present a population lateralization on tested behaviors (attack and copulation responses and grain-pebble categorization). V&R state that genetic expression determines the lateralization at the individual level, and light exposure aligns the direction of lateralization at the population level. However, I argue that if the head turning direction has been determined by the genetic expression, only the right eye could be stimulated visually while the incubated eggs were exposed to the light. It is certain that light exposure prior to hatch aligns the various forms of visual lateralization at a population level, but the direction of the lateralization has already been determined by genetically determined head position. In the laboratory, we have observed that nearly all embryos turn their heads to the left side; only in very rare cases is the embryo's head turned to the other side. Therefore, in the natural condition, there are only two possibilities for the light-induced lateralization in chicks or pigeons: no lateralization (dark incubation) or lateralization aligned with right-eye stimulation. This suggests that the visual lateralization in the chick (as mentioned above) is caused by interaction between genetic and environmental factors.

In the laboratory condition, we have found that visual lateralization aligned with left eye (exposure to light) could be achieved at a population level by manipulating the embryo's head position (Deng & Rogers 2002b). By withdrawing the embryo's head from the egg on day E19 of incubation and applying a black patch to the right eye, we can expose only the left eye to light. Under this experimental condition, the visual lateralization is observed to be in a reversed direction from the normal right-eye lateralization. This result suggests that in the chick (perhaps also in pigeons) visual lateralization aligned with light exposure of the left eye is physiologically possible. However, this option does not exist in the natural condition since the genetic factors have determined the embryo's head turning only to the left. In addition, all studies done by manipulating various steroid hormones (testosterone, estrogen, and corticosterone) have shown that the hormone treatment can only reduce the degree of visual lateralization but cannot change the direction of lateralization (Rogers & Deng 2005; Rogers & Rajendra 1993; Schwarz & Rogers 1992). All of these manipulating experiments support the crucial role of genetic and environmental interaction: genetic factors determining the direction of lateralization, and environmental factors determining the degree of lateralization. Therefore, in the natural condition, no matter how large the changes or whether the animal is actively manipulated as proposed by V&R, if the changes are only in hormone level or light stimulation but not in head-turning direction (determined by genetic factors), the effect will be only on the degree of lateralization and not on the direction of lateralization.

It is very interesting that several genes (including *Nodal* and *Lefty2*), which play key roles in controlling the direction of embryo head turning, are evolutionarily conserved in vertebrate (Przemeck et al. 2003). For example, *Nodal* is expressed asymmetrically in all vertebrates (Stern 2002). Therefore the head-turning bias should have evolved very early and been conserved. In fact, turn bias of the embryonic head has also been observed in the human embryo and newborns (Ververs et al. 1994), which has suggested that this head-turning bias induces right-sided lateralization of perception and action at the population level in humans (Güntürkün 2003a). This raises a question, for those forms of population lateralization (e.g., lateralization of song control or other cognitive function) that could not be easily explained by the ESS/"frequency-dependent selection" hypothesis, of whether their direction of lateralization at the population level is determined by genetic and environmental interactions.

Rethinking brain asymmetries in humans

Bianca Dräger, Caterina Breitenstein, and Stefan Knecht

Department of Neurology, University of Münster, 48149 Münster, Germany.
dragerb@uni-muenster.de **caterina.breitenstein@uni-muenster.de**
knecht@uni-muenster.de
http://neurologie.uni-muenster.de/ger/mitarbeiter/breitenstein/
http://neurolog.uni-muenster.de/cms/front_content.php?idcat=34

Abstract: Similar to directional asymmetries in animals, language lateralization in humans follows a bimodal distribution. A majority of individuals are lateralized to the left and a minority of individuals are lateralized to the right side of the brain. However, a biological advantage for either lateralization is lacking. The scenario outlined by Vallortigara & Rogers (V&R) suggests that language lateralization in humans is not specific to language or human speciation but simply follows an evolutionarily conserved organizational principle of the brain.

Vallortigara & Rogers (V&R) show that brain asymmetries are a species independent, ubiquitous phenomenon. They focus on discussing the causes for population asymmetries in various nonhuman species and give evidence that directional brain asymmetries are in some cases behaviorally adaptive and in other cases without any perceptible advantage. Even though they intentionally leave out human asymmetries, V&R's contribution reframes the discussion of brain lateralization in humans. The discussion initiated in the target article provides new vantage points for an old debate.

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The principle clue we have about the neural substrate of human language is that some critical components are lateralized to one (usually the left) side of the brain. Exceptionally, however, they are also found in the right side, and in some individuals in both hemispheres (Knecht et al. 2000; Pujol et al. 1999; Rasmussen & Milner 1977; Risse et al. 1997).

Until now, there have been no convincing answers as to (1) why language functions are lateralized to one side of the brain, (2) why the degree of lateralization is variable among subjects, and (3) why language in the majority of subjects is lateralized to the left side of the brain. Finally, we have little knowledge of the mechanisms underlying hemispheric lateralization in humans.

Human brain functions are generally organized bisymmetrically. It is believed that this bisymmetrical organization of the brain and other parts of the body (in apes and all other bisymmetric organisms) evolved through a selective advantage because bisymmetric organisms can move faster in fight and flight than can radial-symmetric organisms (Kinsbourne 1978). It appears that for a neural function unrelated to locomotion, there is no apparent need for a bilateral implementation in the neuronal structure of the brain.

For a long time, it was assumed that lateralization of language functions aids the processing demands required for a full exhaustion of linguistic capacities (Geschwind & Galaburda 1985; Hiscock 1998; Luria 1973). It was postulated that transfer of language information within only one hemisphere is more efficient than across hemispheres. Repeated transcallosal transitions of neural impulses between hemispheres during complex linguistic operations were believed to decrease processing speed and efficacy (Miller 1997). Although seductive, this argument is in conflict with the empirical evidence. A non-lateralized, bilateral representation of language seems to exist without any obvious behavioral disadvantage because linguistic proficiency is influenced neither by the side, nor by the degree of language lateralization (Knecht et al. 2001).

Given the lack of any convincing answers to the question of *why* language is lateralized to one side of the brain, it seems that the development of the asymmetry principle may date back to a time prior to the comparatively recent emergence of the human species. For the motor system, transcallosal inhibition presents an important mechanism to optimize performance. It serves to solve incompatibilities between sensorimotor functions of homologous hemispheric regions during limb movements or speech processing (Boroojerdi et al. 1996; Karbe et al. 1998; Meyer et al. 1998). Overall, the language-dominant hemisphere seems to exert more inhibition of the non-language-dominant hemisphere than vice versa (Netz et al. 1995). Transcallosal inhibition is not fully developed before the age of five (Heinen et al. 1998). This correlates with the time window for transhemispheric shift of language functions after brain lesions in children and may determine the freedom of the brain to instantiate language functions during childhood (Vargha Khadem et al. 1985). Therefore, it is thinkable that the development of a lateralized language network is dependent on the development of transcallosal inhibition. The later in life the transcallosal inhibition becomes effective, the weaker the lateralization for language may be. Subjects in whom the neuronal language representation is fixed prior to transcallosal inhibition may have bilateral language representation.

However, though the concept of transcallosal inhibition may explain individual lateralization with respect to degree, it does not in itself explain the alignment in the direction of lateralization at the population level.

Left-hemispheric language dominance may be a characteristic of the biological pre-adaptations for language rather than of the neural language system in modern man. It has often been proposed that the language dominance of the left hemisphere evolved from its control over the right hand, and may be a relatively recent evolutionary adaptation of the neural system of skilled movement and gesture (e.g., Corballis 2003; Hewes 1973; Kimura 1987). The language and the hand motor system are still tightly linked in modern man (Floel et al. 2003; Pulvermuller et al. 2001; Rogalewski et al. 2003). As V&R inform us, in some animals an asymmetry of motor functions may be behaviorally adaptive. Today the degrees of hand and language lateralization in humans are correlated, although right-handedness is not a precondition for left-hemispheric language lateralization (Knecht et al. 2000; Pujol et al. 1999; Szaflarski et al. 2002). Through the course of evolution the relation between handedness and language may have become weakened but the basic organizational principle was likely conserved.

In summary, it is feasible that the implementation of language during the development of the human brain may have simply followed an older conserved, organization principle of the brain, which we share with other evolutionarily older species. In the absence of direct advantages or disadvantages of any typical or atypical brain organization of language, the principle itself may be the reason for its preservation during the development of the human brain. The interindividual variability of cerebral language lateralization indicates the degree of freedom with which the brain can instantiate language. This degeneracy poses a chance for the restitution of language function after brain damage.

Darwin's legacy and the evolution of cerebral asymmetries

Onur Güntürkün

Department of Biopsychology, Institute of Cognitive Neuroscience, Faculty of Psychology, Ruhr-Universität Bochum, 44780 Bochum, Germany.
onur.guentuerkuen@ruhr-uni-bochum.de
www.bio.psy.ruhr-uni-bochum.de

Abstract: Vallortigara & Rogers (V&R) assume that the alignment of escape responses in gregarious species is the central evolutionary organizer of a wide range of cerebral asymmetries. Although it is indeed likely that the benefits of a population asymmetry in social species outweigh its costs, it is hard to see (a) why the population should not oscillate between two subgroups with mirror-image asymmetries, (b) why solitary animals should keep their inherited population asymmetry despite a resulting fitness reduction, and (c) and why so many vertebrate species have comparable cerebral asymmetries.

Applause! The proposal put forward by Vallortigara & Rogers (V&R) represents the first serious attempt to integrate comparative cerebral asymmetry research into evolutionary thinking. Whereas previous approaches simply neglected most of the inherent problems, outlined explanations for a single trait, or referred to some mysterious scenarios during human evolution (thereby neglecting asymmetries of nonhuman animals), the present proposal takes a comprehensive scope and thus presents a deep riddle of the evolution of the vertebrate brain, together with a possible solution. Indeed, population-level asymmetries are widespread; and, indeed, they might be disadvantageous. The solution offered by V&R assumes that in socially living animals the advantages of aligning one's own behavior with that of the group outweigh the disadvantages. Although this is a very elegant approach, I still have several reservations, possibly resulting from my different understanding of the mechanisms of Darwinian evolution.

As outlined by the authors, alignment of escape responses within a group can save the life of an individual. Since, however, predators anticipate escape strategies, some of the advantages of population-level asymmetry are lost. On the other hand, a minority of individuals that have a reversed escape bias enjoy two benefits: they still stay in groups plus they bluff the predator. According to strict Darwinian thinking we would expect the minority group to have a higher fitness and to increase in size, at least when they are not too few to be singled out. Consequently, the evolutionarily stable strategy would not result in two mirror-imaged groups of different size, but of equal size. Although Ghirlanda and

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Vallortigara (2004) have put forward an interesting solution to this problem in their games theoretical proposal, their approach suffers from the classic modelling problem in that it rests on a large number of assumptions that are hard to estimate. Additionally, the approach does not really specify the mechanism that should hinder the minority to become larger. However, even if we were to accept that somehow the population is "stuck" into a majority and a minority, we would, as argued below, face further problems with the theory of V&R.

If population-level asymmetry produced a majority of gregarious individuals living with both benefits and disadvantages, we should expect solitary species not to show any population asymmetry since they would only suffer from the negative consequences without having any advantage. V&R argue that solitary species might have derived from social animals or gregarious juveniles and still go on with their inherited habit. This counterargument is again not really Darwinian since it implicitly assumes that new species arise from older ones (thereby undergoing many changes) but still somehow cannot get rid of their population asymmetry, although they pay for it without gaining anything. As a Darwinist, I have a hard time swallowing that.

A closely related problem shows up if we look at the distribution of asymmetries across vertebrate classes. As beautifully compiled in the book by Rogers and Andrew (2002), cerebral asymmetries not only are found in all branches of the vertebrate tree of life, but they resemble each other in a significant way. To have a pattern like that, V&R would have to assume that their proposed mechanism suffices to keep population asymmetries the same across more than 300 million years and across countless changes of lifestyles and organismal shapes. The authors do suggest at one point that some asymmetries might be related to others, such that asymmetry A may stay in one hemisphere because asymmetry B is also there. In this case, the population asymmetry of A does not have to make sense in itself, but is a consequence of a major architecture where the population asymmetry of some components (like B) do indeed increase fitness. To some extent, this argument immunizes the theory against all criticism since many observed lateralized traits at the population level do not have to contribute to fitness any more. However, if population asymmetry is simply a consequence of aligning individuals to a group, we would expect over hundreds of million of years and millions of developed and vanished species, all sorts of population asymmetries and not this rather coherent picture.

In my view, the (relative) coherency of cerebral asymmetries within and between the different classes of vertebrates makes it likely that we inherit a basic dichotomy of computation that shows up in diverse species and functions in a similar way. A motor position bias that makes an escape response more likely in one direction than in another is probably not sufficient to have intracerebral aligning effects on asymmetries of vocalization, spatial orientation, face recognition, and so forth. Since so many asymmetries are lateralized in a similar way and are inherently not related to escape responses, the alignment of response asymmetries within a species is more likely a consequence and not the cause of a basic dichotomy of the mind. Individuals that enjoy a population response when faced with a predator would then indeed benefit, as proposed by V&R. But this advantage would not be the deeper reason for the alignment of a plethora of cerebral asymmetries across vertebrates.

The left-side bias for holding human infants: An everyday directional asymmetry in the natural environment

Lauren Julius Harris[a] and Jason B. Almerigi[b]

[a]*Department of Psychology, Michigan State University, East Lansing, MI 48824;* [b]*University Outreach and Engagement, Michigan State University, East Lansing, MI 48824.* **HarrisL@msu.edu** **Almerigi@msu.edu**
www.psychology.msu.edu/people/faculty/harris.htm

Abstract: To Vallortigara & Rogers's (V&R's) evidence of everyday directional asymmetries in the natural environment of a variety of species, we offer one more example for human beings. It is the bias for holding an infant on the left side, and it illustrates several themes in the target article.

Vallortigara & Rogers (V&R) have mustered impressive evidence of everyday directional asymmetries in the natural environment of species ranging from man and ape to frog and fish, evidence they predict will help link neuropsychology and evolutionary and developmental biology and make us "rethink" certain "basic issues on the evolution of cerebral lateralization" (sect. 1 of the target article). We agree and offer another example for human beings: the bias for holding an infant on the left side, so that its head is to the left of the holder's midline. This example also illustrates several themes in the target article: the ubiquity of everyday directional asymmetries, how "a dynamic relationship might be established between lateralized behavior in interacting asymmetric organisms" (sect. 2), and the benefits of such relationships.

The left bias has long been noted. For example, in late nineteenth-century France, a writer reported observing "how people carry their children" and becoming "convinced that those who carry them on the right arm are the exception" (H.M. 1889, p. 764). Later, a left bias was reported in 73% of mothers observed on London streets (Burt 1937) and, in a hospital study in the United States, in 83% of mothers of newborns (Salk 1960). Notably, this last figure was for mothers who had normal pregnancies and deliveries and could hold their infants immediately after birth. Among mothers initially separated from their infants because of prematurity or illness, the figure declined to 52%.

More recent studies have confirmed these reports, with 65–85% left-side biases found for mothers and other women (e.g., de Château 1983; Harris et al. 2000). Declines or even reversals in the bias also have been found in depressed and "emotionally uninvolved" mothers (de Château 1991; Weatherill et al. 2004), possibly suggesting that similar emotional states figured in cases of separation, prematurity, and illness. Newer studies have also revealed other details. To begin, the bias looks selective – robust for holding infants, but weaker, inconsistent, or reversed for books, packages, and other inanimate objects (e.g., Alley & Kolker 1988; Almerigi et al. 2002). It also changes with age of the child, peaking for newborns and young infants (e.g., Dagenbach et al. 1988), then declining and even reversing for children 2 or 3 years old (e.g., Lockard et al. 1979); and it generally is stronger and more reliable in women than men (e.g., Brüser 1981; de Château 1983; Manning 1991). In tests using infant dolls, it also has been found in children as young as 4 years of age, but sooner and stronger in girls (e.g., Almerigi 2004; de Château 1983). Finally, some investigators have found the bias in nonhuman primates, though only females were tested (e.g., Manning & Chamberlain 1990; but see Dienske et al. [1995] for opposing results). Altogether, the evidence suggests that for the bias to occur, the thing-to-be-held must have certain physical and psychological qualities to which people, perhaps females especially, respond socially and emotionally – qualities not necessarily unique to but best represented in the very young.

Several explanations of the bias have been proposed and a variety of benefits foreseen. The heartbeat explanation posits that the heartbeat, being more detectible on the left side of the chest, makes left-side holding more soothing for the infant as well as the holder by its reflection back from the infant. The bias therefore

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peaks in early infancy when infants most need soothing and help with arousal control. The handedness explanation posits that most people, being right-handed, hold on the left to keep their right hand free, whereas left-handers hold on the right. This lets the dominant hand perform other acts requiring object-manipulation skill benefiting the infant, including feeding and general care. For right-handers, the eventual shift to the right therefore might reflect the gradual reliance on that side for its greater strength as infants grow bigger, heavier, more active, and less in need of the dominant hand's assistance. The infant-posture explanation credits the bias to the disposition by most infants in early infancy to turn to the right while lying supine. Held on the left, they therefore turn toward the holder, facilitating nursing and en face communication. The emotional monitoring explanation posits that in responding to infants, most adults – women especially – are in a state of "action-approach" with higher left-anterior, right-posterior hemispheric activation. The result is leftward-directed attention, predisposing a left-side hold and facilitating communication by enhancing the holder's monitoring of the infant's needs as revealed through its vocalizations and facial expression. Conversely, in cases of separation, emotional uninvolvement, or the other special circumstances noted earlier, the holder is in a state of "inaction-withdrawal," with higher right-frontal, left-posterior activation resulting in reduced left-side attention and emotional monitoring.

These explanations have limitations as well as strengths. For handedness, the fundamental limitation is that proportionately almost as many left-handers as right-handers hold on the left side, meaning that the dominant hand of the left-handers is constrained rather than free. Handedness also cannot obviously explain the bias selectivity or sex difference, and, if the bias in nonhuman primates is confirmed, it assumes what is still in dispute – that these species show handedness at the population level (McGrew & Marchant 1997). As for the heartbeat explanation, an infant held over the shoulder is out of range, but the left-bias persists (see also Todd & Butterworth 1998), as it does through periods of waxing and waning of the infant head-right posture (Dagenbach et al. 1988. The emotional monitoring explanation, although supported by behavioral studies (e.g., Almerigi et al. 2001; Bourne & Todd 2004; Harris et al. 2001; Vauclair & Donnet 2005), is untested in the special circumstances noted earlier. Most likely, to account for every detail of the bias, all of these and still other explanations will have to be incorporated into a comprehensive model. Further implications of individual explanations also need testing. For example, if, for right-handers, the bias's decline over time reflects increasing reliance on the right side for its greater strength, then the bias for left-handers should increase, not decrease. Predicted benefits also need testing. Does the left-side hold enhance emotional monitoring, and is it more soothing, whether from the heartbeat or other factors such as the lowered pitch of the holder's voice in infant-directed speech (Reissland 2000)? Ultimately, we believe that the scientific study of this everyday bias will deepen our understanding of the relation between laterality and the ontogeny of adult-infant, especially parent-infant, interactions important for survival. It also exemplifies the importance of a multidisciplinary approach to the study of laterality, one embracing historical, ethological, comparative, developmental, and neuropsychological perspectives.

Behavioral left-right asymmetry extends to arthropods

Boudewijn Adriaan Heuts and Tibor Brunt

Swammerdam Institute for Lifesciences, University of Amsterdam, Kruislaan 320, 1098SM Amsterdam, The Netherlands. **heuts@science.uva.nl**
tibor.brunt@gmail.com

Abstract: We present behavioral lateralizations of spiders and ants and their probable survival value. They clearly conform to the vertebrate lateralizations reviewed by Vallortigara & Rogers (V&R) and to earlier arthropod studies. We suggest two complementary reviews: (1) differences in lesion susceptibility and muscle strength between left and right body side, and (2) perceptual biases and predator inspection in invertebrates.

Ants (*Formicidae*) and spiders (*Araneae*) possess behavioral left-right asymmetries similar to the extensive vertebrate examples in the target article. We found a significant majority of spiders in the field with mainly left-leg lesions (Table 1). Also, their weak leg lesions caused by capture were significantly biased to the left. The influence of the catching procedure was ascertained by selecting weak-leg lesions, such as legs held in an abnormal orientation (due to lesions of the joints) or legs with body fluid drops. However, interspecifically produced leg lesions among spiders in the laboratory were not lateralized. But in ants, appendage severance was significantly more frequent on the left than right side (for details on the cause of the lesions, see Heuts et al. 2003).

The 305 left-leg versus 254 right-leg lesions (obtained from 18 spider families) are a robust indication of the greater vulnerability of left legs than right legs in spiders in general. Separate spider families and species were also significantly left-biased and never significantly right-biased (cf. Heuts & Lambrechts 1999). The left-side vulnerability may be due to anatomical factors (joint strength and leg length; see, e.g., Bauer 1972) and/or a complex of various behavioral factors such as a propensity to move the legs of one side when alarmed, or left/right attack biases in spider predators (a possibility clearly discussed by V&R). We could not demonstrate a significant difference between the length of left and right legs (by measuring dead specimens and pictures in Roberts 1984; 1995). So, we discarded our original hypothesis that leg length might play a role. We rather believe that the significant catching-produced left-leg lesion preponderance points either to a greater weakness of left legs, or to a tendency in spiders to hold or move their left and right legs in a different way when alarmed or attacked, or both. Clearly, this deserves further research.

Interestingly, there are a few direct observations of spider leg use when interacting with spider prey. Ades and Ramires (2002) showed in a small sample of spiders that a predator spider species used its left first leg significantly more often than its right leg for touching (inspecting) a spider prey before killing it. These authors also mention that the predator inflicted significantly more left-side than right-side body lesions. We could not demonstrate such a left bias in our sample of 42 spider species. A preliminary check of our notes yielded left first-leg use for touching potential spider prey in three *Tegenaria atrica* spiders. This suggests a similar preferential left leg use in spiders and vertebrates (mentioned by V&R) in situations that do not require strong muscle tension.

Twelve ant species kept mainly to the right on their foraging "streets" whereas there was only one species which kept to the left (Table 1). On streets in trees, 49 *Lasius niger* colonies kept to the right versus 26 to the left. In this ant species a significant majority of couples in the laboratory had the left side of their bodies exposed to their partners when resting. This identical left body side exposure when resting and foraging in streets also correctly predicted that lone foraging *L. niger* would significantly more often turn to the right than to the left (the ratio is 14 to 2). The existence of a specific behavioral lateralization (sharp left turns) in *L. niger* and four other ant species when running on unknown ground in an "alarm" situation (24 left vs. 4 right turns) makes sense because these sharp left turns increase the chance of remaining on the spot

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Table 1 (Heuts & Brunt). *Statistically significant lateralizations in large taxons of spiders and ants*

	Left	Right
Catching-produced lesions (spider families)	12	3
All lesions of undisturbed and caught spiders in the field (specimens of 18 families)	305	254
Lesions of spiders injured mainly by other spider species in the laboratory (specimens of 14 families and 42 species)	62	59ns
Keeping to the left or right on natural and laboratory foraging trails (temperate and tropical ant species covering the two main ant subfamilies)	1	12
Keeping to the left or right on tree trails (colonies of the ant *Lasius niger*)	26	49
Exposing left or right body side to closest nest-mate when resting in laboratory colonies (couples of *Lasius niger* nest-mates)	33	13
Turning mainly to the left or right when running slowly around the natural nest at more than 10 cm from the closest nest-mate (number of *L. niger* colonies)	2	14
Turning mainly to the left or right when disturbed (alarmed) around natural nest (number of *L. niger* colonies)	8	0
Showing a left-versus right-turn increase when put (alarmed) onto an unfamiliar surface in the laboratory (number of specimens from five species of the two main ant subfamilies)	24	4
Left-versus right-appendage severance in mainly interspecific fights in the laboratory (number of specimens from 42 ant species)	239	197

ns = not significant.
Data of a separate ant species (*Lasius niger*) are also given.
Statistical tests in Siegel (1956; critical $p = 0.05$ in two-tailed tests).

when a potential danger must be countered, whereas the blunt turns to the right during foraging are beneficial to a fast and efficient transport of food, especially so in dense "traffic."

In their review of invertebrates, Bradshaw and Rogers (1993) noted right-claw anatomical and behavioral dominance in a crab species, suggesting stronger right than left appendage muscles like that in our ants (an assumption based on their sharp and fast left turns). Insect behavioral lateralizations have been briefly reviewed by Heuts and Lambrechts (1999), who mention several studies on lateralized flower attacks in bees.

With regard to vertebrates, Bradshaw and Rogers (1993) mention a significant bias to left-side lesions in whitefish attacked by lampreys, as in spiders and ants. However, it falls outside the scope of this commentary on the vertebrate work of V&R to discuss the lateralizations of invertebrates. Nor do we address the hypothesis of stronger right-side than left-side muscles in animals (two hypotheses that do not come up in the target article). We just want to point to striking similarities between general trends in vertebrates and the lateralizations of spiders and ants. Fish approach a predator more closely for inspection if it is on their left side; the spiders of Ades and Ramires (2002) and one of our spider species similarly inspected a spider opponent by touching it with a left leg. Various fish species and toads probably expose their left side to conspecifics because they inspect conspecifics with their left eye; our ants exposed their left side to nest-mates when resting and when keeping to the right on their foraging trails. Like various birds and fish that forage for food, our lone foraging *Lasius niger* ants also showed a significant right-turning bias (that might facilitate their keeping to the right when not alone on foraging trails). Within the vertebrates, our earlier work on fish supports the experiments of V&R because we also found that schooling Cyprinids were significantly right-biased in their swimming turns, whereas various non-schooling bottom-dwelling Cichlids were not lateralized (Heuts 1999). This, again, supports the hypothesis that aligning oneself to the lateralization of conspecifics is beneficial in schooling species because it guarantees the maintenance of the school and its "dilution effect" in the face of predators, whereas ground-dwelling species do not profit from schooling and show no lateralized swimming (when special situations such as pair formation in Cichlid fish are disregarded).

We conclude that the arthropod lateralizations and their probable survival value clearly conform to those of vertebrates, both in our studies and in those reviewed by V&R.

The riddle of nature and nurture – Lateralization has an epigenetic trait

Martina Manns

Department of Biopsychology, Institute of Cognitive Neuroscience, Faculty of Psychology, Ruhr-University Bochum, 44780 Bochum, Germany.
Martina.Manns@ruhr-uni-bochum.de
http://www.bio.psy.ruhr-uni-bochum.de

Abstract: Vallortigara & Rogers's (V&R's) proposal that directional asymmetries evolved under social pressures raises questions about the ontogenetic mechanisms subserving the alignment of asymmetries in a population. Neuro-ontogenetic principles suggest that epigenetic factors are decisively involved in the determination of individual lateralization and that genetic factors align their direction. Clearly, directional asymmetry has an epigenetic trait.

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In order to explain the presence of lateralization at the population level, Vallortigara & Rogers (V&R) present the challenging hypothesis that social constraints force individuals to align their asymmetries with those of other individuals of the group. This proposal wants to unravel the riddle that a population bias persists in a natural population despite obvious disadvantages for the individuals. This is a valuable approach because it tackles lateralization as a feature that can be explained by evolutionary mechanisms. Since behavioral lateralization must be implemented in the neuronal substrate, the question arises of how directional asymmetries are established during ontogeny. An answer has to take into account that a population-level lateralization suggests a genetic foundation despite the obvious plasticity of functional asymmetries. V&R argue different scenarios but intermingle phylogenetic and ontogenetic explanation levels. This results in the discussion of genetic and epigenetic factors as opposing alternatives to be responsible for aligned asymmetry formation. But considering general neuro-ontogenetic principles, the actions of genes and environment are not contradictory.

V&R reject that population-level lateralization is the byproduct of those genes which determine visceral left-right differences because there is no direct correlation between visceral and neuronal asymmetries. This lacking correlation is not surprising given that neuronal development is not strictly genetically determined but develops through a complex interplay of genetic and epigenetic factors. Epigenetic influences can be much more critical than genetic factors or even essential to develop a lateralized functional architecture. The best known example is visual lateralization in chicks and pigeons which develops in response to asymmetric photic stimulation during embryonic development (Rogers 1996). However, the relative importance of genes and environment depends on the developmental characteristics of neuronal systems. These characteristics can differ in the sensitivity to epigenetic factors like hormones or growth factors, in the developmental speed and hence the length of sensitive phases, and in the general degree of ontogenetic plasticity. For example, developmental variations are likely to be responsible for differences in structural asymmetries underlying visual lateralization in chicks and pigeons. Whereas asymmetric photic stimulation induces morphological left-right differences in the thalamofugal pathway in the precocious chick (Rogers & Deng 1999), it is the tectofugal system that is lateralized in the altricial pigeon (Güntürkün 2003b). Moreover, light effects are modulated by steroid hormones in the thalamofugal but not in the tectofugal system (Güntürkün & Kischkel 1992). Accordingly, in principle, the direction of asymmetries in distinct neuronal systems do not need to be aligned but can be intimately related. Lateralization of escape responses in amphibian tadpoles might be implemented in Mauthner-cells asymmetries (Malashichev & Wasserzug 2004). Although the stereotyped morphology of this highly specialized cell suggests a genetic foundation, its dendritic differentiation (and hence cell body shape) is directed by synaptic contacts with sensory afferents (Kimmel et al. 1981). Therefore, Mauthner cell asymmetries might represent a secondary consequence of biased sensory input.

Sensory systems develop in close interaction with the environment. Visual pathways especially have been established as model systems to examine how light input controls the activity-dependent development of visual circuits to adapt differentiation to environment. Since the developing visual neurons react very quickly to changes of the afferent input (Wong & Ghosh 2002), subtle disturbances are sufficient to perturb the balance of left- and right-hemispheric differentiation. Thus, visual lateralization in birds is influenced by the amount of incoming light and visual asymmetries develop according to mechanisms well known for ontogenetic plasticity (Manns & Güntürkün 2003; Prior et al. 2004). As the result of an asymmetric turning of the embryo's head, it is always the right eye which receives more light than the left one. As a consequence, the majority of birds develop a dominance of the right eye/left hemisphere for visual object analysis. This points to a crucial aspect of asymmetry formation and not only to a minor facet, as mentioned by V&R: Whereas individual asymmetry formation is determined by epigenetic factors, genes give an overall framework directing the influence of these epigenetic factors in the same direction and hence align the lateralization pattern in a population. Genes seem to determine population asymmetries by different mechanisms: (1) Genetically controlled morphogenetic events lead to positional asymmetries that direct the action of an environmental factor always in the same direction. (2) Genes determine differences in developmental speed of the left and right hemispheres, causing left-right differences in the susceptibility to epigenetic factors. (3) The asymmetric expression of specific genes leads to left-right differences in the amount of neuronal substrate. For example, the asymmetric activation of the Nodal pathway in the neuronal tube determines asymmetries in the dorsal diencephalons of vertebrates. However, such endogenous left-right differences can be modified or even overridden by environmental factors. Telencephalic imprinting areas in chicks display endogenous asymmetries which can be modified by biased light input (Johnston & Rogers 1999). While cerebral lobar volumes in humans have a genetic component (Geschwind et al. 2002), pre- and postnatal events can affect planum temporale asymmetry development and disrupt twin concordance in brain structure (Eckert et al. 2002). The tight interactions between gene-dependent pre-specifications and epigenetic control are beautifully exemplified in the development of expertise for face recognition in the right hemisphere of human brains. Visual input is necessary for the establishment of face recognition competence. However, light affects only the right hemisphere, suggesting that this brain side is predetermined to adopt face recognition competence (LeGrand et al. 2003).

In conclusion, the individual development of neuronal lateralization is decisively controlled by environmental factors and differs among unique neuronal systems depending on their specific developmental characteristics. The alignment of the direction of asymmetries can primarily emerge as an ontogenetic byproduct of genetically controlled embryonic events. If an asymmetry pattern gives rise to an adaptive advantage, mechanisms might have been evolved which stabilize these asymmetries during ontogeny. Accordingly, it is the strength but not the direction of lateralization which is inherited in higher vertebrates (Collins 1985). This developmental mode guarantees a high degree of flexibility in the lateralization pattern of distinct functional systems and allows modulation of the lateralization pattern in the offspring generation as suggested by V&R.

Constraints from handedness on the evolution of brain lateralization

Maryanne Martin[a] and Gregory V. Jones[b]

[a]*Department of Experimental Psychology, University of Oxford, Oxford OX1 3UD, United Kingdom;* [b]*Department of Psychology, University of Warwick, Coventry CV4 7AL, United Kingdom.* **rose.martin@psy.ox.ac.uk**
http://www.psych.ox.ac.uk/general/info/memstaff.htm
G.V.Jones@warwick.ac.uk
http://www2.warwick.ac.uk/fac/sci/psych/people/academic/gjones/

Abstract: Can we understand brain lateralization in humans by analysis in terms of an evolutionarily stable strategy? The attempt to demonstrate a link between lateralization in humans and that in, for example, fish appears to hinge critically on whether the isomorphism is viewed as a matter of homology or homoplasy. Consideration of human handedness presents a number of challenges to the proposed framework.

Vallortigara & Rogers (V&R) argue that our understanding of human asymmetry, and in particular handedness, can be usefully advanced by consideration of asymmetry in other species, such as fish. However, it is unclear whether the relatively abstract considerations which they adduce can be translated into concrete expla-

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nations of human performance. Ghirlanda and Vallortigara (2004) have provided an elegant game-theory example of how the alignment of asymmetric behaviour among prey individuals may, disadvantageously, assist learning in predators but also, advantageously, increase the dilution of risk among groups of prey. Consistent with this, turning preferences in response to a simulated predator have been shown to be more likely to exhibit population-level lateralization in shoaling species of fish than in solitary species of fish (Vallortigara & Bisazza 2002). How might such a finding with fish be relevant to human lateralization?

V&R appear to provide some contradictory responses to this question, and it would be useful if these too could be brought into alignment with each other. They initially argue for an early common origin of brain lateralization in vertebrates, which suggests implicitly that human lateralization stems from an evolutionarily stable strategy that took effect prior to the appearance of humans themselves. Later, however, they indicate that the same game-theory analysis may be applied to asymmetries in specifically human (and perhaps primate) activities such as face presentation (e.g., Nicholls et al. 1999), and so the explanation appears to turn from homology to homoplasy. Certainly the evidence that population-level handedness, so prominent among humans, is almost entirely absent in nonhuman primates (e.g., McGrew & Marchant 1997) casts doubt on a general assumption of continuity in lateralization across a much broader range of species. At the end of their section 1, V&R assert that "our arguments to follow are totally indifferent as to whether lateralization in, say, fish and primates, is the result of homology or evolutionary convergence." However, it would surely be more accurate to admit that although population-level lateralization could *in principle* have arisen in accordance with the proposed type of game-theoretical analysis either on a single occasion or else on multiple occasions, to address the question of whether lateralization *in practice* evolved in this way it is necessary to examine different subordinate hypotheses in the two cases. These would focus, in the single case, on whether there is evidence of subsequent continuity and, in the multiple case, on whether a family of game-theoretical models is supported.

Consideration of the issue of chronology raises a further question as to whether the proposed game-theoretical analysis is in fact restricted in application to the evolution of population-level lateralization, or alternatively whether kindred forms of analysis can be applied to acquired behaviour. V&R appear to endorse the latter possibility, for example in suggesting that social pressures may be responsible for the predominant occurrence of right-handedness among chimpanzees tested in captivity (Hopkins et al. 2003) rather than in the wild. If so, then in order for the analysis of such evidence to have a direct bearing upon evolution, it needs to have a temporal dimension. Human handedness is a case of population-level lateralization which has been relatively well explored temporally, but even here the genetic interpretation is not straightforward (e.g., Jones & Martin 2003).

One of the surprises with regard to human handedness is that though, as pointed out by V&R, there is evidence of majority right-handedness stretching back through human history, detailed patterns of parental association appear to have changed considerably over a much shorter period. In a substantial review of previous studies reported by McManus and Bryden (1992), for example, the incidence of left-handedness among the offspring of two left-handed parents was greater in every period than its incidence among the offspring of one or, a fortiori, two right-handed parents, but declined in absolute terms from 41% in the period 1880–1939, to 26% in the period 1940–1954, and 22% in the period 1955–1979. As noted by Jones and Martin (2000), this diminution presumably reflected a secular decrease in the social – in particular, familial – pressures on preferred hand use, of the kind that have been identified by Harris (1990). The approach of V&R appears to suggest that such changes in social pressure may in principle lead to evolutionary shifts in lateralization, and it would be interesting to see this modelled formally. One important constraint here is the relatively low concordance rate for handedness in dizygotic and even monozygotic human twins, which appears to exclude many potential genetic models, though not all (see Jones & Martin 2000).

Another salient aspect of human handedness is that it does appear to be linked to perceptual asymmetries of the kind considered extensively by V&R. For example, if a chimeric face is constructed either from the left side of a photographed face and its mirror image, or from the right side and its mirror image, then right-handed people, but not left-handed people, are likely to consistently select the left-side chimera rather than the right-side chimera as closer to the original photograph (e.g., Gilbert & Bakan 1973; Luh et al. 1994). Similarly, Viggiano and Vannucci (2002) have examined the visual identification of fragmented pictorial stimuli and found that, whereas right-handed people are quicker to identify left-facing animals and vehicles, left-handed people are quicker to identify right-facing ones. The same pattern of contralaterality has been found also in memory performance (e.g., Martin & Jones 1999; McKelvie & Aikins 1993). Although there have been attempts to interpret such findings in terms of cerebral specialisations of the kind considered by V&R (e.g., Luh et al. 1994; McKelvie & Aikins 1993), there is a general difficulty in explaining contralaterality in terms of the specialisation of a single hemisphere. Instead, it has been noted (e.g., Jones & Martin 2004; Viggiano & Vannucci 2002) that what these results seem to point to is the existence of more localised, content-specific connections between particular aspects of motor and cognitive processing – motor imagery – as demonstrated also by direct brain monitoring (e.g., Jeannerod 1997). This raises the possibility of a broader range of mechanisms underlying behavioural asymmetry than that considered by V&R.

Selection pressure on the decision-making process in conflict

Toshiya Matsushima

Graduate School of Bioagricultural Sciences, Nagoya University, Furo-cho Nagoya, Japan 464-8601. **matusima@agr.nagoya-u.ac.jp**
http://www.agr.nagoya-u.ac.jp/~hikaku/Lab_of_matsusima/matusima-eng.html

Abstract: It is argued in the target article that hemispheric lateralization is advantageous when faced with conflicting choices. As decision-making processes must have been subject to a strong selection pressure, the sensitivity of response latencies could suggest a modular and hierarchical organization of behavioral execution, as was formulated by Tinbergen (1951).

The authors successfully present the full range of facts and arguments on the delicate (and complicated) issue of the lateralized brain, synthesizing the whole story under a few principles of neurobiology and behavioral ecology. I encourage the enterprise by scrutinizing the suggested advantage of lateralization – namely, the benefit that lateralized brains could have in processing incompatible functions. When several different events or targets appear coincidently (e.g., prey and predator), the brain must process the relevant signals in parallel, make a choice, and organize a unified behavioral execution (e.g., to attack or to flee, but not to execute a chimeric response). Such behavioral conflicts give rise to incompatible responses more often in owners of a symmetric brain, causing them to respond late so that they more frequently lose food or suffer predation. In contrast, lateralized brains do better by "specializing" each hemisphere for distinct functions, thereby reducing the probability of delayed response due to conflict. Here I discuss how conflicting events are synthesized in the brain, whether the conflict actually delays the response, and what selection pressures configure the decision-making process in the brain.

Animals face a variety of conflicts in everyday life. Conflict can

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occur, for example, in sexual behaviors when a sexually mature male is approaching its mate while defending against intruder males (cf. Satou et al. 1984 on salmon sexual behavior). Except on the few occasions where displacement activities are elicited, most animals solve conflictive situations through hierarchical controls. In his monumental achievement of classical ethology, Tinbergen (1951) assumed that at higher levels the brain is equipped with mutually competitive (or exclusive) modular processes, while at lower levels the controls are more synergistic, so that attacking prey and fleeing from predators could be executed as distinct responses by utilizing the same set of effecter musculatures. At the spinal/medullary level of motor controls, conflicting actions of descending signals often yield a synergistic motor execution by way of the dynamic interactions among segmental networks via excitatory local interneurons (Grillner 2003). In a case where the spinal locomotor network was driven to swim backward and forward simultaneously, the resultant inequalities of excitability among segmental circuitries yielded well-coordinated phase lags uniformly along the whole cord (Grillner & Matsushima 1991; Matsushima & Grillner 1992; Matsushima et al. 1989). In the motor mapping in superior colliculus (optic tectum), similarly, two contingent foci of excitation due to two moving objects in the visual field will interact, until the "winner-take-all" process by a set of common inhibitory interneurons referees the competition (Amari & Arbib 1977).

Conflicts might occur even for a single behavior when, for example, a foraging animal is confronted with a choice of two food targets with different features/values, such as large food versus proximate food, or small food versus costly food. In the case of domestic chicks, binary choice depends on the anticipated profitability of prey items, or the ratio of net energetic gain (e) to accompanying handling time (h). In operant conditioning tasks, chicks make choices so that the choice ratio fairly closely parallels the ratio of anticipated profitability (e/h); the more profitable the food, the more frequently the food is chosen (Izawa et al. 2003). When one of two options had much higher profitability (6 pellets of millet vs. 1 pellet, both delivered immediately), chicks chose the 6-pellets option in most trials. When the two options had nearly the same values of profitability (6 pellets delivered after a 2-sec delay vs. 1 pellet after a 0.16-sec delay), chicks made even choices in good accordance with the matching law by Herrnstein (1997). On such occasions, however, we failed to detect a significant difference in response latencies in association with the degree of conflict (or difference in the choice ratio), except for a slight and inconsistent correlation to the anticipated profitability.

We can reasonably infer that the response latency is under strong selection pressure, particularly in animals like chicks that forage in groups. Group foraging could have made chicks search for food competitively, so that a slightly longer latency would yield a significant loss. Another factor is the physical properties of foods; foragers of tiny-but-abundant food particles (such as grains or small insects) should optimize their behavior by minimizing the handling time proportionately to the gain per particle, as in the star-nosed mole (Catania & Kaas 1996, Catania & Remple 2005). Accordingly, with a short handling time, the time required for decision-making should inevitably be short (0.3–0.6 sec for decision-making, whereas 0.25–0.5 sec for single action of pecking in chicks), if not negligible, as is assumed by the optimal foraging theory in its simplest formulation (Stephens & Krebs 1986). In light of these hypotheses, results of the latency experiment (Rogers 2000) should be highly appreciated. In the study by Rogers (2000), in contrast to the choice condition described above, two opposing behavioral executions (foraging and fleeing) were in conflict. We may reasonably revive Tinbergen's hierarchical model by assuming a distinct module for each behavior. At the higher competitive level of control, conflict might be solved much more elaborately, thus causing a longer latency.

Natural selection of asymmetric traits operates at multiple levels

Michael K. McBeath[a] and Thomas G. Sugar[b]

[a]*Department of Psychology, Arizona State University, Tempe, AZ 85287-1105;* [b]*Department of Mechanical and Aerospace Engineering, Arizona State University, Tempe, AZ 85287-6106.* **m.m@asu.edu**
Thomas.Sugar@asu.edu **http://www.public.asu.edu/~mmcbeath**
Sugar: http://www.fulton.asu.edu/~tsugar

Abstract: Natural selection of asymmetric traits operates at multiple levels. Some asymmetric traits (like having a dominant eye) are tied to more universal aspects of the environment and are coded genetically, while others (like pedestrian turning biases) are tied to more ephemeral patterns and are largely learned. Species-wide trends of asymmetry can be better modeled when different levels of natural selection are specified.

In their target article on asymmetric functioning, Vallortigara & Rogers (V&R) present examples of lateralization in a wide array of forms for a wide variety of species. They propose that species-wide lateralizations of functioning occur because they represent evolutionarily stable strategies (ESSs) that are naturally selected. V&R argue for an interdisciplinary approach that integrates neuropsychology with evolutionary biology, but they emphasize that lateralization need not be entirely genetically determined. In this commentary, we extend this line of reasoning and further articulate that natural selection of traits occurs at several levels of robustness. We characterize three distinct levels: (1) macroevolution, or natural selection of new genetic characteristics introduced through mutation, (2) microevolution, or natural selection of population distributions in the gene pool, without adding any new genetic characteristics, and (3) social evolution, or natural selection of culturally learned patterns, without changing the genetic distributions in the population. We suggest that an evolution-based model of species-wide asymmetry should not treat asymmetric functioning as a unified concept, but instead should specify the level of natural selection associated with specific asymmetric traits (Gilbert et al. 1996; Raff 1996).

V&R note that there have always been selective advantages to symmetric functioning. This is consistent with findings that virtually all life forms are largely symmetric, with stationary organisms tending to be approximately circularly symmetric and locomoting organisms bilaterally symmetric (e.g., see Haekel 1974). Presumably, throughout evolution the universality of gravity has made asymmetric bodies less stable (McBeath et al. 1997). This tendency is further inbred by evolutionary mechanisms like sexual selection that make symmetric individuals appear more sexually attractive in a variety of species (Møller 1992; Pennisi 1995). Gravity and physical laws of balance are universal principles, so it is consistent that biological symmetry is favored at the most robust genetic level, across species.

Some symmetric functions, like the occurrence of two eyes and stereoscopic vision, appear to have evolved along diverse, independent evolutionary pathways ranging from insects to mammals. Clearly, the presence of two eyes is a symmetric adaptation that allows organisms to utilize the abundant terrestrial light energy to discern important three-dimensional spatial information about the environment. Stereoscopic organisms have the advantage of multiple "dual-eye" perspective for discerning shapes and distances, but at the expense of needing to integrate the two images. Therefore, stereovision leads to virtually universal geometric constraints.

When a stereoscopic organism views a surface (such as **a-b-c** in Fig. 1), an object at a different depth (such as the *) will produce disparate images in the two eyes. The extent of the shift in the location of the * can be used to determine its stereo depth, but it will also produce a double image, with the * appearing to be aligned with **c** in the left eye and with **a** in the right eye. Visual systems resolve this conflict by having a dominant eye. A dominant eye appears to be a geometric requirement to eliminate alignment double vision in stereoscopic organisms, and thus it makes sense

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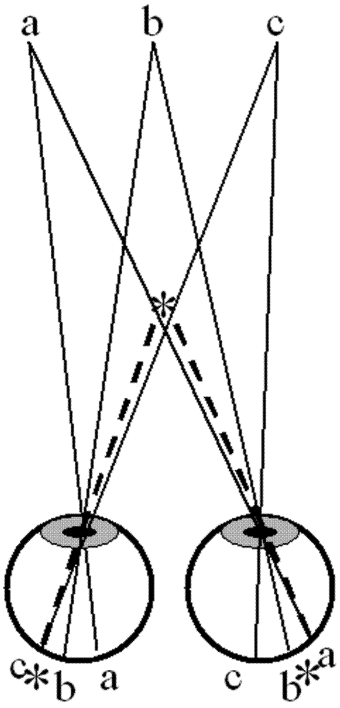


Figure 1 (McBeath & Sugar). The need for a dominant eye. When distant and close stimuli are simultaneously imaged (e.g., *abc* vs. *), the geometry of stereo optics produces image disparity between the two eyes (i.e., the * is lined up with *c* in the left eye and with *a* in the right eye). A dominant eye is needed to reduce the perception of a double image.

for it to be a genetically coded trait (Handa et al. 2004). In short, physical universals lead to genetic hard wiring, in this case a genetically encoded trait of eye-dominance. If ESSs are used to account for population imbalances of eye dominance, that is consistent with evolutionary natural selection at the genotype level, or an example of macroevolution.

Eye dominance in humans is generally clustered along with same-side dominance of other functions such as brain activity and handedness, but this need not be true in all cases (Erdogan et al. 2002). Cross-eye dominance or eye dominance that opposes handedness occurs at significantly higher rates in some subpopulations like baseball players (Portal & Romano 1988).

This type of natural selection is assumed to occur because batters typically stand with their dominant hand facing away from and their opposing eye facing toward the pitcher. Batting prospects with cross-eye dominance would therefore have a slight performance advantage. This would result in a population-culling process that biases the genetic population distribution of this sample, yet clearly occurs at a much too rapid time scale to be credited as a genetic change. This is an example of microevolution, or a selection process in which certain genetic features are favored and cluster together, without introduction of any genetic change.

Finally, there are some types of asymmetric functioning that have a clear learning component, and species-wide patterns appear to be due to arbitrary social trends. Examples of these include the attentional side biases (Eviatar 1995; Nachson 1985) and motion perception direction biases that have been found to be associated with reading direction exposure (Morikawa & McBeath 1992). People from areas that read from left to right have a bias to attend initially to the left, and to experience quick flashes of motion, like lightning, as traveling to the left. Those from areas that read from right to left experience the reverse. Similarly, walking-side and turning biases are correlated with handedness (lefties go left and righties go right), but are also strongly determined by driving side exposure. Pedestrians from right-side driving countries like the United States favor heading to the right, and those from left-side countries like Great Britain favor heading to the left (Scharine & McBeath 2002). Clearly, such asymmetric functioning due to learned habits like reading direction or driving-side exposure are behaviors that have been selected at a social and not a genetic level.

In summary, we outlined how asymmetric functioning may be due to different levels of natural selection. We agree that V&R's question regarding the etiology of species-wide asymmetric functioning patterns is very intriguing, and the findings we cited remain consistent with their proposed *evolutionarily stable strategies* explanation. Our main point is that many asymmetric functioning patterns may be occurring differentially at a socially learned level rather than at a genetic level.

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Unity in the wild variety of nature, or just variety?

I. C. McManus

Department of Psychology, University College London, London, WC1E 6BT, United Kingdom. **i.mcmanus@ucl.ac.uk**
http://www.chime.ucl,.ac.uk/~rmhiicm

Abstract: Although there are some common underlying mechanisms for many nonhuman behavioural asymmetries, the evidence at present is not compelling for commonalities in cerebral organisation across vertebrates. Phylogenetic analysis of detour behaviour in fish suggests that more closely related species are not particularly similar in the direction of turning; contingency and demands of ecological niches may better explain such asymmetries.

Recent years have seen a rapidly growing interest in behavioural asymmetries in animals, from predation in trilobites (Babcock 1993) to digging by walruses (Levermann et al. 2003), and brains are known to be asymmetric in species as diverse as *Drosophila* (Pascual et al. 2004) and *Caenorhabditis* (Hobert et al. 2002). The theoretical challenge is integrating this vast mass of disparate material with.its multiple species, multiple tasks, and multiple methodologies. Vallortigara & Rogers (V&R) are to be congratulated for asking deep questions and searching for coherence within diversity, for, as Jacob Bronowski said, "Science is nothing else than the search to discover unity in the wild variety of nature" (Bronowski 1964).

Of course, unity may not exist. Darwin described how biologists divide into "hair-splitters and lumpers," emphasising a multiplicity of independent causal mechanisms underlying the simplest of phenomena or pursuing grand "theories of everything." Unified theories may simplify or merely be simplistic.

V&R describe theories at different levels of explanation which together provide an integrated view of the advantages and disadvantages of asymmetry. Some theories are undoubtedly effective, the most innovative and compelling analysing the inter-relations between individual and group laterality and the conditions for an evolutionarily stable strategy (ESS) (Ghirlanda & Vallortigara 2004). However, that theory requires only that individuals are lateralised, for whatever reason, and that individual laterality interacts with group laterality, whether of predator or prey. The theory does not need inherited lateralities or any common cross-species cerebral mechanism.

V&R's Table 1 suggests common cerebral mechanisms across species, with predator escape being right-hemisphere driven in marsupials, amphibia, and birds, as are cognate processes in mammals and primates. The implication is that there is a primitive underlying tendency for brains to be lateralised *in a particular di-*

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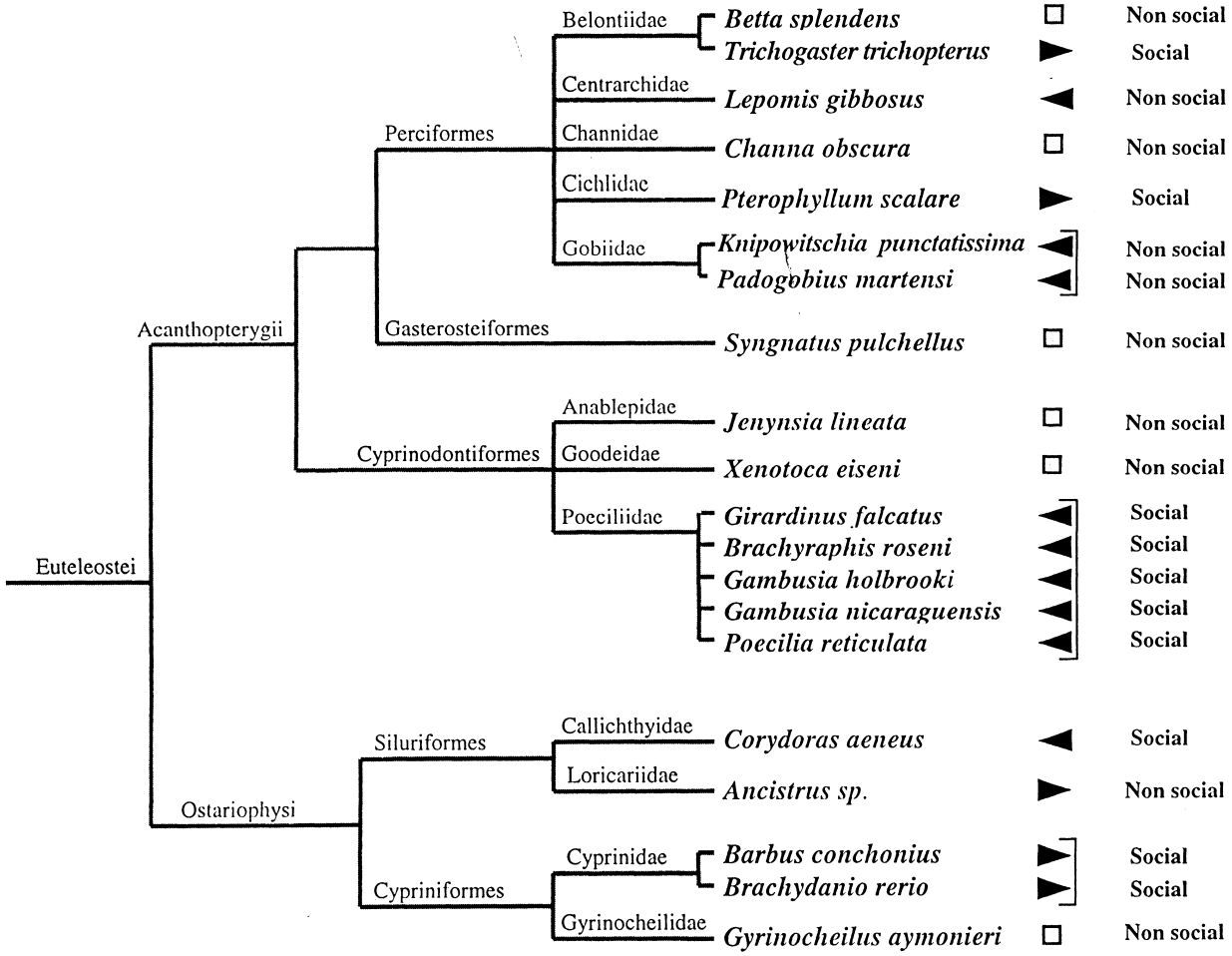


Figure 1 (McManus). Turning tendencies in 20 species of fish. Arrows indicate the direction of bias; squares indicate no bias. Reproduced with permission from Vallortigara et al. (1999).

rection. Consistency of direction of lateralisation is a hard and important question, and is difficult to explain even within a single species. One attraction of a common evolutionary mechanism across species is that it might distinguish two opposing theories of human cerebral lateralisation (and hence also of language evolution; McManus 2004). On one side are the "Universalists" who argue for human lateralisation being an example of a phenomenon found everywhere in the animal world. Opposing them are the "Speciationists," who see human cerebral lateralisation as the unique, key event in the speciation of *Homo sapiens* (Crow 2003b) and fundamental to the evolution of recursive syntax (Hauser et al. 2004).

Before accepting the hypothesis of a generality of lateralised cerebral processes across vertebrates (and perhaps even chordates and other phyla), at least two other explanations must be comprehensively rejected:

1. *Brains are lateralised because they are embedded in lateralised bodies*. V&R clearly describe how laterality in chicks is secondary to the asymmetric head position of the chick in the egg, exposing the right but not the left eye to light. The behaviour results ultimately from the asymmetric development of the heart tube and the development of anatomical *situs*. Birds therefore show similar laterality but it does not originate in a common underlying cerebral asymmetry. Likewise, vertebrate brains develop within asymmetric bodies, and behavioural asymmetries may be directly secondary to *situs*, as in the chick, or indirectly and independently due to mutation of genes originally determining *situs* but now producing neural asymmetries. Disentangling such processes requires knowledge of the genes determining *situs* and of behaviour in organisms with *situs inversus*, a condition now regularly produced in laboratory animals.

2. *The apparent generality of lateralised cerebral mechanisms is artefactual*. The literature on biological asymmetries is potentially very biased. The "file-drawer problem" makes it likely that only statistically significant asymmetries are published, absence of asymmetry being deemed uninteresting and/or unpublishable. Additionally, modern biology concentrates on a few model species that breed easily in laboratories (*Caenorhabditis*, *Drosophila*, *Xenopus*, frogs, zebra-fish, chicks, rats, and mice). These species are phylogenetically distant and form a tiny proportion of the animal kingdom so that evolutionary theories are near impossible to test. Among the many fine papers published by V&R, a particularly interesting study examines detour behaviour in 20 different fish species (Vallortigara et al. 1999). The same behaviour with presumably the same cerebral basis was tested in the same laboratory by the same experimenters. Particularly important is Figure 1 from that article, reproduced here, which shows the turning bias plotted on a phylogenetic tree.

The social species show more directional biases (although four nonsocial species are biased: three left and one right). Six social species are biased to the left and four to the right. Phylogenetically, there are associations at the ends of the branches (as in the two species of Cyprinidae, the two species of Gobiidae, and the five species of Poeciliidae), but more distant species show little similarity. The Gobiidae go to the left, as do the Centrarchidae, whereas the fairly closely related Belontiidae and Cichlidae go

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right. That may in part be due to social/nonsocial differences, except that sociality itself is only consistent at the branch ends, and itself shows variable evolution, perhaps influenced by the local ecological niche. More problematic is that the Callichthyidae go to left and the Cyprinidae go right, and both are social species. If there is a big evolutionary picture here it is not compelling, and the temptation therefore is to follow Stephen Jay Gould and argue not for adaptation but for contingency – things happen because of chance, and no big integrative story is necessary, however attractive such a theory may be (and a similar account applies to anatomical asymmetries; Palmer 1996a, 2004). Distinguishing contingency from adaptation requires more and better data, of the sort described by V&R in fishes, with more species and better mathematical modelling of the cladistics. Only then will it be clear whether there is unity due to cerebral asymmetries running down the trunk of the tree, or merely variety occurring randomly at the tips of the branches, albeit due to selection, but contingent on chance and local conditions.

Putting things right: "*Why*" before "*how*"

Á. Miklósi

Department of Ethology, Eötvös University, Budapest, H-1117, Hungary. **miklosa@ludens.elte.hu**

Abstract: In this commentary I argue for the need of an evolutionary account of lateralized behavior. Although one could raise some problems with the explanatory power of the present hypothesis, this is the approach one should pursue. It would be very important to show that the proposed idea of social coordination does indeed lead to selective advantages also when considered within a species.

The authors of the target article should be applauded for their brave attempt to put the phenomenon of behavioral lateralization into an evolutionary-ecological context. Although this is not the first time that Vallortigara & Rogers (V&R) are dealing with this enterprise (they have pursued similar arguments in Vallortigara & Bisazza 2002; Rogers 2002a), the traditional thinking (and perhaps scholarly background or ignorance) of many workers in this field has diverted attention from issues of function and evolution. Ethologists have long argued that the first step to understanding behavior is to investigate its consequences in relation to fitness. However, often such questions have been preceded by inquiries about mechanisms of behavior. Although most of such research is very important and revealing in its own right, as this example on behavioral lateralization has shown, a collection of mechanistic investigations cannot provide an adequate hypothesis for the phenomenon itself.

The authors argue that behavioral lateralization might have evolved as a result of social interaction between individuals; that is, if environment favors sociality in a species, individuals with concordant lateralization are at an advantage because they form more effective groups. This hypothesis has at least two important features. First, it attempts to incorporate new evidence showing that behavioral laterality is a general feature for all major taxonomic groups of vertebrates (although it seems to be present also in invertebrates); second, it is based on a functional aspect ("sociality"), which is a general factor in behavioral evolution.

One of the key scenarios in the target article is to describe the advantage of lateralized groups of fish (shoals) confronting a nonlateralized predator. (As the authors also note, and what is clear from other parts of the article, real predators might be lateralized because of "computational" advantages as well. However, this issue can be put aside here for reasons of simplification.) It is argued that a fish shoal of uniformly lateralized individuals should be at an advantage when encountering an attacking predator, because joint escape strategies increase the chance of individuals to survive. Therefore, it is assumed that population level lateralization would be advantageous.

Though I can see the merit of this line of argument, I also see some problems. First, at the level of execution, showing topographically equivalent behavior during predator attack is only one of the many antipredator tactics used by prey. Upon being attacked, fish shoal might expand in all three spatial dimensions, or split into two groups, and so forth (see, e.g., Fig. 12.6 in Pitcher 1986). Instead of showing a single predictable behavioral action, prey try to confuse the predator with "random" movements in many directions, then rejoin the shoal as soon as possible. Second, individuals swimming in the shoal are constantly monitoring each other, maintaining a given distance to other fish as the group moves through the water. This means that individuals are used to coordinating their behavior with that of others in the shoal. Moreover, when attacked, only a small portion of fish will actually see the predator and show an avoidance response; the others react only to the change in trajectory of their companions. This means that the visual input for the attacked fish is quite different from that for the followers. Third, in the traditional context, predators select out the weakest individuals, and potentially all groups in a given population are the same. Here, however, it is assumed that one or more individuals will actually pay the cost for the inefficiency of the group, and they are not necessarily those that are "responsible." In other words, the authors use a kind of group selection argument, but it is not clear how the individuals that do not conform to the group will be selected out. Additionally, such a model also assumes that groups are isolated, and individuals do not move among groups, which is not the case in many fish species.

Instead of comparing "solitary" versus "social" species, it might be interesting to think about whether variability in coordination could give rise to selective advantages within a species. This approach would also avoid the problem of unknown evolutionary antecedents of solitary or social behavior. In their review V&R list various aspects of behavior from mating to tool use where synchronized activity of two or more individuals is advantageous. If such activity is based on lateralized behavior, then individuals with concordant bias could be at an advantage in comparison to companions with incompatible or no lateralization. Since most of such interactions between members of a group take place among relatives, kin selection might also be at work. This would suggest that parents needing to interact with their young should prefer offspring with concordant laterality, or – in reverse – families with the same bias should have increased fitness.

Asymmetrical behavior without an asymmetrical brain: Corpus callosum and neuroplasticity

Andrei C. Miu

Department of Psychology, Babeş-Bolyai University, Cluj-Napoca 400015, Romania. **AndreiMiu@psychology.ro**

Abstract: The theory put forward by Vallortigara & Rogers (V&R) to explain the versatility of directional asymmetries at the population level argues that the strength of lateralization is controlled by social learning. This shaping of behavioral asymmetries by a non-stationary pressure probably involves a marked degree of neuroplasticity. I discuss the limits of neuroplasticity along with the evolution of the corpus callosum.

The development and evolution of cerebral lateralization are linked to the interhemispheric communication mediated by the major commissures of the brain. As Vallortigara & Rogers (V&R) emphasize, it has been believed for a long time that cerebral asymmetries are specific to the human brain, being associated with the cognitive sophistication accumulated during humanoid evolution, and particularly with the appearance of language. This scenario

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has also provided a plausible explanation for the sudden evolutionary origin of the corpus callosum (CC) in eutherian mammals, which has added to the dorsal hippocampal and anterior commissures present in the methaterian brain. This type of theory has led to the fossilization of the idea that the evolution of the prosencephalic commissures and the enhancement of interhemispheric communication have contributed to the differentiation of cerebral asymmetries. In this context, V&R have elegantly argued that cerebral asymmetries inferred in their approach from behavioral asymmetries are ubiquitous in non-callosal amniotes and even anamniotes. Their theory accounts for the versatility of behavioral asymmetries at the populational level by putting social learning in control of this evolutionarily stable strategy (ESS). The idea that social learning is involved in brain evolution has been extensively supported, particularly for primates (e.g., Reader & Laland 2002). V&R have created an elegant ethology of behavioral asymmetries to extend this principle to other vertebrates. However, their theory might be limited to anamniotes and non-callosal amniotes. I argue here the CC might have evolved to implement evolutionarily relevant behavioral asymmetries in the brain of eutherian mammals. In my view, without a CC you have behavioral asymmetries evolving under social pressure, asymmetries that have not been implemented in an asymmetrical brain.

The CC is the main commissure of the prosencephalon. Most, but not all, of its projections are homotopic. The CC mediates interhemispheric communication (e.g., Quigley et al. 2003), probably through the synchronous activation of bilateral neural networks (Engel et al. 1991). The functions of the CC have been revealed once we have started to look at the brain "in motion," that is, during development and evolution. Adult animals with CC transection do not usually display any striking behavioral deficits. However, it is intriguing that callosal denervation in adult rats facilitates behavioral-induced sensorimotor recovery (e.g., Bury & Jones 2003). This facilitatory effect indicates that CC transections loosen the remodeling of intrahemispheric circuitry and it raises the possibility that the perinatal period when callosal fiber elimination occurs is a time during which intrahemispheric remodeling is facilitated. Indeed, callosal axon elimination and synaptogenesis temporally coincide, at least in primates (LaMantia & Rakic 1990). Behavioral studies have also acknowledged that CC is involved in mediating the effects of early experience (e.g., Maier & Crowne 1993). Thus, developmental studies suggest that the maturation of CC allows the stabilization of intrahemispheric changes that have occurred in the perinatal brain. In this context, it is interesting that in all callosal regions the proportions of large-diameter fibers tend to increase with age (e.g., Godlewski 1991), probably in tandem with the age-dependent reduction of intrahemispheric neuroplasticity. On the other hand, evolutionary studies have suggested that in eutherian mammals the CC appeared as a consequence of isocortical expansion, which posed timing constraints on interhemispheric communication. Apparently, this problem could not be solved otherwise than by adding a major dorsal commisure specifically serving the isocortex (Aboitiz & Montiel 2003). The geometry of the CC was dictated by the extension of topographically organized sensory maps, mainly from the mesencephalon in sauropsids to the isocortex in eutherian mammals, and by bimanual coordination. These processes were probably driven by social learning. However, after it appeared in methaterian mammals, the CC did not increase with brain weight (Olivares et al. 2001). Why? I favor here the idea that there is a critical quantitative limit to the interhemispheric wiring which allows the brain to adapt to environment and to stabilize the most useful of these changes in an equilibrated balance. The prediction of this theory is that the gamut of electrophysiological and behavioral indices of neuroplasticity in a primary cortical field like M1 follow a stable function prescribed by the number of callosal projections wiring the two homotopic M1. These and other arguments from manipulations or observations of the brain in motion support the view according to which the CC has evolved in eutherian mammals to stabilize behaviorally relevant intrahemispheric neuroplasticity. This is one way the CC could have enabled eutherian mammal condition.

In recent years, we have assisted in the involvement of ethology in the cerebral laterality field, mostly attributable to V&R. The target article reviews evidence indicating that behavioral asymmetries are present across the vertebrate world, and capitalizes on this evidence to support a theory according to which social learning is the main pressure that has aligned behavioral asymmetries at a populational level in gregarious species. The theory is elegant and flawless, yet limited. V&R define the strength of lateralization as the percentage of conspecifics that share the same directional behavioral lateralities. They conjecture further that species with more complex social structures should display stronger lateralization. It is noteworthy that V&R have mostly invoked studies on fishes, amphibians, and birds. I argue that their theory is plausible only for anamniotes and amniotes that do not present a differentiated CC because, as I have noted briefly in the preceding paragraph, the CC is probably a structure invented by evolution to balance hemispheric communication with intrahemispheric neuroplasticity. It may be that social pressures are aligning behavioral asymmetries in populations of non-callosal vertebrates. The lack of a CC has probably maximized behaviorally relevant neuroplasticity in these species, putting social learning in control of aligning behavioral asymmetries at the populational level. It seems improbable that the same is true for eutherian mammals, which have only a limited developmental time window to implement evolutionary relevant behavioral asymmetries. After this period, the CC reduces the magnitude of intrahemispheric behavioral-induced neuroplasticity. This limited period for the stabilization of behavioral asymmetries in the brain could be essential for maintaining intrahemispheric circuits associated with language. Provided this argument is plausible, the theory of V&R must be limited to non-callosal species.

Population lateralization arises in simulated evolution of non-interacting neural networks

James A. Reggia and Alexander Grushin

Department of Computer Science, University of Maryland, College Park, MD 20742. **reggia@cs.umd.edu** **agrushin@cs.umd.edu**
http://www.cs.umd.edu/~reggia/ **http://www.cs.umd.edu/~agrushin/**

Abstract: Recent computer simulations of evolving neural networks have shown that population-level behavioral asymmetries can arise without social interactions. Although these models are quite limited at present, they support the hypothesis that social pressures can be sufficient but are not necessary for population lateralization to occur, and they provide a framework for further theoretical investigation of this issue.

Vallortigara & Rogers (V&R) provide a valuable review of the widespread left-right perceptual asymmetries occurring among nonhuman vertebrates, and present the hypothesis that during evolution a population-level (directional) behavioral asymmetry arises as a result of social constraints that force individuals to align their asymmetries. Here we consider this hypothesis in the context of recent neural network models of the emergence of left-right asymmetries and behavioral specialization. These models, at least in their limited formulation to date, suggest that although social pressures may be sufficient for directional population lateralization to occur, they are not necessary.

Computer models exploring the implications of various hypotheses about hemispheric interactions and the underlying mechanisms leading to individual behavioral asymmetries/specialization are not a new idea (Cook & Beech 1990; Kosslyn et al. 1989; reviewed in Reggia & Levitan 2003). Often these models consist of neural networks representing corresponding left and right cerebral regions, connected via a simulated corpus callosum, that undergo a learning or developmental period involving alter-

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ations in synaptic strengths. Researchers have typically assumed the prior existence of an underlying asymmetry involving the simulated cortical regions (asymmetric size, excitability, plasticity, etc.), and have tried to determine which of these asymmetries result in the emergence of behavioral lateralization as the model learns to perform some task (correct recognition of images, etc.). Somewhat surprisingly, it has been found that, regardless of which neural asymmetry is initially present, its effects are progressively amplified during the learning/development process, leading to substantial behavioral lateralization (e.g., Shevtsova & Reggia 1999). This result was initially viewed with skepticism because, in effect, these models were predicting that individual behavioral lateralization should be widespread in nonhuman animals. Thus, the growing experimental evidence reviewed by V&R for behavioral asymmetries across many vertebrate species has alleviated a concern about the validity of these models. It permits increased confidence in other more recent model predictions (Howard & Reggia 2004; Reggia et al. 2001; Tang 2003).

What do these neural models indicate regarding V&R's hypothesis? To our knowledge, only two computational studies so far have simulated the evolution of lateralization in neural networks. In the first study's model, the underlying left-right symmetry/asymmetry of each neural network's size, excitability, and plasticity is genetically encoded in a linear chromosome (Shkuro & Reggia 2003). The model assumes the existence of an initial population of individuals without population lateralization. As subsequent generations appear, each individual's neural network is created according to its genome. This network undergoes a developmental period during which it learns to perform a perceptual pattern classification task, and then the individual's performance on this task is measured. A standard genetic algorithm guides the evolutionary process. An individual's fitness is based *not* on whether behavioral lateralization occurs, but instead on the individual's performance (accuracy after learning) and perhaps also on the network's "cost." The specific hypothesis examined was that neural network asymmetries and behavioral lateralization in individuals would evolve over time if fitness were based on simultaneously maximizing task performance and minimizing neurobiological costs (energy utilization, connectivity strengths, etc.), rather than just on maximizing performance. This hypothesis was motivated by cogent past arguments that energy utilization, connectivity constraints, and other factors substantially influence evolutionary processes (Cherniak 1994; Gibbons 1998).

Evolutionary simulations modeled as described above consistently led to left-right asymmetries in the genetically determined neural networks produced, and these asymmetries in turn led to individual behavioral lateralization during development (Shkuro & Reggia 2003). In contrast, simulations where an individual's fitness is based solely on task performance/accuracy consistently have not produced network asymmetries or behavioral specialization, supporting the idea that it is the competitive trade-off between maximizing performance while simultaneously minimizing neurobiological costs that leads to lateralization. A second study that used a more sophisticated multi-objective evolutionary process supports this latter point by showing that the strongest individual asymmetries and lateralization tend to arise when a compromise is reached between high accuracy and low cost (Grushin & Reggia, in press).

Most important here is the finding that the simulated evolutionary process consistently led to directional population lateralization whenever substantial individual lateralization occurred (Shkuro & Reggia 2003). An example of this is shown in Figure 1. This population lateralization occurred in the absence of any "so-

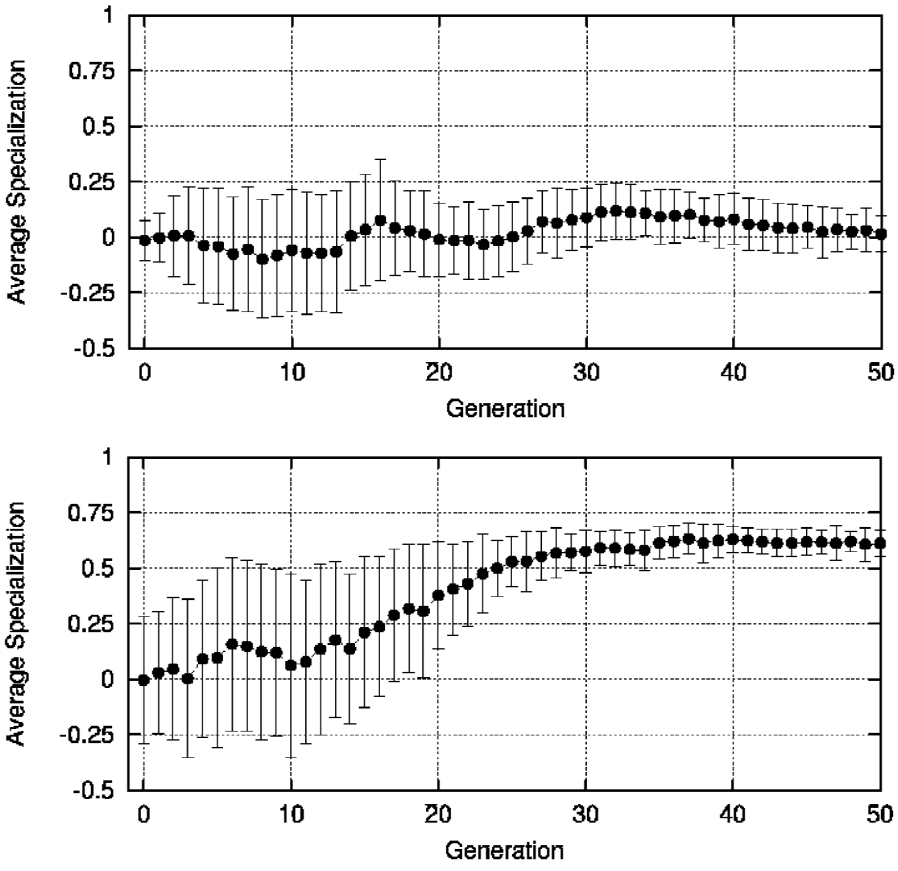


Figure 1 (Reggia & Grushin). Mean lateralization coefficient over time in populations of 100 individuals that evolve to perform a perceptual task. Top: Reproductive fitness based solely on task performance; directional lateralization does not appear. Bottom: Fitness based on both performance and cost minimization; population-level behavioral asymmetry appears. Error bars: standard deviations.

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cial interactions" between individuals during learning/development, as such interactions are completely absent in the basic genetic algorithm methods used. Directional lateralization arose because of the well-known convergence property of genetic algorithms. An early small bias in the direction of neural network asymmetries due to chance was gradually amplified by the evolutionary process, ultimately producing stable population-level behavioral asymmetries. Thus, the key conclusion from these simulations is that social interactions are not required in a simulated evolutionary process for directional population specialization to occur.

What do these modeling results imply for V&R's hypothesis that social interactions lead to biological population lateralization? The results do not contradict their hypothesis. For one thing, our model is quite simple: it is not intended to be a veridical representation of complex biological nervous systems, evolutionary processes, or genetic determinants of left-right differences (*Nodal*, *Pitx2*, etc.), the latter being poorly understood at present (cf. V&R, note 4). For another, even if one accepts the modeling results without reservation (we do not), the social interaction hypothesis remains viable as long as it is viewed as saying that such interactions are sufficient but not necessary for population lateralization to occur. If anything, this makes V&R's hypothesis more interesting, as it indicates that population lateralization may be a multifactorial process due to social interactions, convergence properties of evolutionary processes, and perhaps other yet-to-be-identified mechanisms. This multifactorial nature leads us to believe that future, more realistic models, whether formulated within a game-theoretic framework as V&R have done, as simulated neuroevolutionary processes like those described here, or as dynamical systems representing the molecular interactions relevant to asymmetric gene expression (Raya et al. 2004), will play an increasingly important role in clarifying the theoretical implications of such factors.

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Optimization through lateralization: The evolution of handedness

Robert L. Sainburg[a] and Robert B. Eckhardt[b]

[a]*Kinesiology, Bioengineering, and Neuroscience, Pennsylvania State University, University Park, PA 16802;* [b]*Kinesiology and Program in Genetics, Pennsylvania State University, University Park, PA 16802.* **rls45@psu.edu eyl@psu.edu**

Abstract: The target article proposes that behavioral asymmetries evolved in response to social pressures, accounting for the unequal distribution of handedness across the population. In contrast, we provide evidence that human handedness reflects individual adaptations that enhance movement skill, and that the distribution across the population is best explained by a genetic polymorphism, either balanced or tending toward fixation for right-handedness.

Vallortigara & Rogers (V&R) argue that population-level alignment of behavioral asymmetries is adaptive because individuals acting under social pressures must coordinate their behaviors with others. They propose that behavioral asymmetries have become "evolutionarily stable" because the genetic bases underlying different phenotypes are resistant to perturbation, a concept borrowed from game theory (Dawkins 1976; Smith 1982). To support their hypothesis, the authors report an extensive compilation of observations on lateralization in vertebrate populations, from schooling in fish to vocalizations in rhesus monkeys. Whatever the adaptive nature of each of the myriad examples of behavioral asymmetries discussed, the target article simply attempts to address the cause of the distribution of lateralization within a population. Nevertheless, the article suggests that it is social pressure that ultimately gives rise to the emergence of lateralized behavior within individuals. The major premise is that behavioral lateralization is a singular phenomenon that arose early in phylogeny from social pressures related to predator/prey interactions.

In contrast to population-level adaptations that are driven by interactions between individuals, we argue that human motor lateralization reflects individual adaptations that enhance movement skill. First, neural imaging studies show that handedness arises from neural control factors, as evidenced by asymmetries in morphology and activation profiles between corresponding motor-related structures in the two cerebral hemispheres (Amunts et al. 1996; Chen et al. 1997; Dassonville et al. 1997; Gitelman et al. 1996; Kawashima et al. 1997; Kim et al. 1993; Taniguchi et al. 1998; Tanji et al. 1988; Urbano et al. 1996; Viviani et al. 1998; Volkmann et al. 1998). Second, each hemisphere/limb system appears to be specialized for distinct but complementary functions: the dominant system for controlling limb trajectory and the non-dominant system for controlling limb posture. We recently termed this hypothesis Dynamic Dominance because dominant arm trajectory control entails more efficient coordination of muscle forces with the interaction forces that arise between the segments of the moving limb (Bagesteiro & Sainburg 2002; Sainburg 2002; Sainburg & Kalakanis 2000).

We propose that during phylogeny, pressure for more precise individual coordination resulted in redistribution of control processes between the hemispheres, thereby maximizing neural resources through hemispheric specialization. This hypothesis predicts that the "non-dominant" system should demonstrate some distinct advantages over the dominant system. Consistent with this prediction, recent findings indicate that the non-dominant system is specialized for control of limb impedance, resulting in non-dominant arm advantages in positional control and in correcting unexpected perturbations (Bagesteiro & Sainburg 2003; Sainburg & Kalakanis 2000; Sainburg & Wang 2002). Our hypothesis also implies that failure to develop strong hand preference should reflect a failure to optimize the control system, which might explain the documented high incidence of mixed-handedness in developmental coordination disorders (see Sigmundsson & Whiting 2002). Studies in patients with unilateral brain damage have provided additional evidence to corroborate our dynamic dominance hypothesis. Haaland and others (Haaland & Harrington 1994, 1996; Haaland et al. 2004; Prestopnik et al. 2003a; 2003b; Winstein & Pohl 1995; Wyke 1967a; 1967b) revealed consistent deficits in the "intact" arm of stroke patients, which appear to reflect loss of functions for which the ipsilateral hemisphere is likely specialized: Dominant hemisphere lesions produced deficits in trajectory speed, whereas non-dominant lesions produce deficits in final position accuracy. Haaland et al. (2004) concluded that such findings are most consistent with the Dynamic Dominance hypothesis. Overall, these findings provide strong evidence that the driving force for motor lateralization in humans reflects individual optimization, rather than social coordination.

The uneven distribution of handedness in the human population is consistent with the pattern expected for a genetic polymorphism, which is either transient, or balanced at the current distribution. This idea is consistent with evidence demonstrating a genetic basis for handedness. Klar (1999; 2003) presented convincing evidence for a single gene that controls handedness and hair whorl orientation. If this particular model is correct (and there are others; e.g., Corballis 2003), then the scope for largely behavioral coordination, according to Klar's model, would seem to be limited to the small fraction of the population that is genetically unspecified. Interestingly, however, these individuals tend not to develop strong hand preference (Annett 1998; 2000; Bryden et al. 2000; Oldfield 1971), which directly contradicts the idea that handedness distribution is determined by social pressures. Instead, the population asymmetry associated with handedness can simply emerge as a byproduct of individual adaptation that gives rise to the expression of a polymorphism. Evidence now available

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does not allow us to discriminate between the alternative possibilities that (1) current ratios of handedness in human populations represent a transient polymorphism in which right handedness will approach fixation, or (2) the polymorphism is balanced (Annett & Manning 1990). Until we can determine which is the case, we cannot determine whether the distribution of handedness in the population is stable or is undergoing modifications under the process of evolutionary adaptation.

Because of the strong individual advantages that handedness affords motor coordination in individuals, social pressures are likely to be irrelevant to its evolution. Instead, we suggest that handedness emerged late in human evolution, in response to the need for more flexible and exquisite levels of coordination as required for manipulating tools and throwing projectiles. This suggestion removes one of the stated disadvantages to the existence of such an asymmetry: that it would result in predictability of behavior by predators. It is highly likely that by the stage of human evolution in which our ancestors were evolving the enhanced motor coordination necessary for control of projectiles, they had assumed the role of top predators in the ecosystems that they dominated (Brace 1997; Eckhardt 2000; Stuart et al. 2004; Thieme 1997). Regardless of when handedness emerged as a consistent behavioral asymmetry, substantial evidence indicates that this asymmetry is an emergent phenomenon with strong adaptive value. In contrast to the premise of the target article, the distribution of handedness in humans is consistent with a genetic polymorphism that is either balanced, or tending toward fixation for right-handedness.

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When dominance and sex are both right

James A. Schirillo and Melissa Fox

Department of Psychology, Wake Forest University, Winston-Salem, NC, 27109. **schirija@wfu.edu** **foxma3@wfu.edu**

Abstract: We have found that the left side of faces displayed in Rembrandt's portraits capture how humans rank male dominance, helping to coordinate avoidance behaviors among asymmetric individuals. Moreover, the left side of faces may also coordinate approach responses, like attractiveness, in human females. Therefore, adding sexual selection to dominance paints a more realistic picture of what the contralateral right hemisphere is doing.

A central tenet of Vallortigara & Rogers's (V&R's) thesis is that lateralization might differentiate approach responses (e.g., to search for food) from avoidant responses (e.g., to escape from predators) "in animals as different as fish, amphibians, reptiles, birds, and mammals" (target article Abstract). V&R cite evidence for both attack and avoidance behavior being governed predominately by the right hemisphere, and more specifically (in sect. 1, para. 5) on how "impairment of the left hemisphere leads to the expression of more intense emotions (Nestor & Safer 1990), likely because the latter are controlled by the right hemisphere" (also see Davidson 1995; Devinsky et al. 1994; Graae et al. 1996). More recent fMRI evidence further supports the claim that the right hemisphere in humans is specialized for social and emotional functions (Tabert et al. 2001).

The full complexity of this issue began to be revealed by Davidson's (1984) seminal work. His hypothesis states that the left hemisphere promotes approach behavior while the right hemisphere promotes avoidance behavior. Related work in our lab also suggests emotional lateralization of brain function. This commentary conveys how this might produce a population-level bias. V&R claim that "the physical world is indifferent to left and right, and any lateralized deficit might leave an animal vulnerable to attack on one side or unable to attack prey or competitors appearing on one side" (sect 2, para. 1). However, our findings suggest that if part of the lateralized emotional motor output is represented in the contralateral side of the musculature of the face, humans' ability to extract this information may be critical to survival (Schirillo 2000). Thus, our research agrees with Maynard Smith's (1982) premise that, as V&R put it, "the alignment of the direction of lateral biases in most individuals in a population [ ] may have evolved as an 'evolutionarily stable strategy' . . . to coordinate behavior among asymmetric individuals" (target article, sect. 2).

V&R's Table 1 lists cases in which the left hemisphere specifically inhibits intense emotions, especially negative emotions, while the right hemisphere may be specialized for aggression. If this is the case, in humans the lower two-thirds of the right-side of the face (innervated by the left hemisphere) should display positive emotions, while the comparable left-side of the face (innervated by the right hemisphere) should display negative emotions. Looking for such asymmetries in individuals' responses to portraits painted by Rembrandt, we have found an important gender difference (Fox & Schirillo 2004). We had 73 subjects (23 males) rate 373 of Rembrandt's portraits on a 1 to 5 scale, with 1 designating their desire to "most likely approach" and 5 designating their desire to "most likely avoid" a portrait. Subjects preferred to approach almost any portrait depicting a female over any depicting a male (i.e., their ratings of females ranged from 2.5 to 3.1, while their ratings of males ranged from 3.2 to 3.7). But as views of females in the portraits shifted from showing the most-rightward profile (left cheek) to the most-leftward profile (right cheek), the portraits were rated increasingly as more approachable (Fig. 1, the solid trend line). This is remarkable in that portraits of males produced the exact opposite pattern of results.[1] The most-leftward facing male portraits were rated most avoidable, and became increasingly less avoidable as they shifted to the rightward facing profiles (Fig. 1, the dashed trend line). Thus, Rembrandt's extreme left-facing portraits provide the best cues of when to approach females and avoid males. This is strong supporting evidence that the right hemisphere (innervating the left side of the face) evokes more intense human emotions and, more important, that this is a sexually selective attribute.

The significance of this finding comes from the fact that in 74% of Rembrandt's female portraits the left-cheek faces the viewer, while the right-cheek faces outward in 74% of male portraits. This finding promotes the notion that "social constraints" (e.g., those exhibited during facial display) force individuals to align their asymmetries with those of the other individuals in the group (sect. 6).

Our findings also dovetail nicely with those of Nicholls et al. (1999), who demonstrated that portraits that typically expose the left-side of the face are overrepresented. Nicholls et al. argue that the leftward bias is determined by the sitters' desire to display the left cheek because it is controlled by the more emotive, right cerebral hemisphere. Moreover, the fact that portraits of scientists from the Royal Society show no leftward bias (Nicholls et al. 1999) suggests that the subjects' motivation may be to conceal negative emotions. Our data go further, implying that the motivation is to display emotional states that are closer to neutral (e.g., ~3.1–3.2). Our findings may also suggest why the Western art literature reports that in ~68% of female portraits the left cheek (the approachable side) is toward the viewer, but in only ~54% of male portraits is the left cheek (the avoidable side) exposed to the viewer. This difference in orientation preference by gender supports the notion that cerebral lateralization does not require the alignment of lateralization at the population level (sect. 4). That is, our findings suggest that most individuals' brains are emotionally lateralized and this is represented in their facial musculature. More important, these features differ along the stereotypic gender roles of approaching females for sex and avoiding aggression in males. This important gender difference provides a rationale for how cerebral hemispheric lateralization may produce approach/avoidant behavior at the population level.

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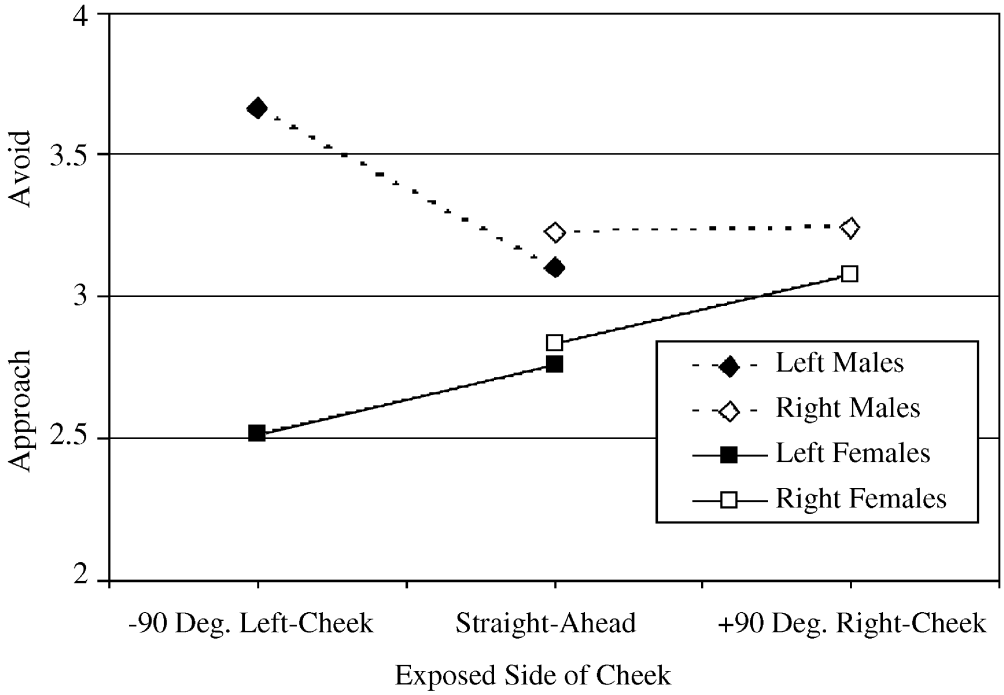


Figure 1 (Schirillo & Fox). Trend lines of 73 ratings of 373 Rembrandt portraits.

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Special thanks to Richard King for computer programming.

NOTE

1. Twenty-three portraits with zero degree lateralization were excluded from the data set, so the trend lines in Figure 1 plot separately the linear correlation of left- and right-cheek portraits.

Cerebral asymmetry: From survival strategies to social behaviour

Jechil Sieratzki[a] and Bencie Woll[b]

[a]*Human Communication Science, University College London, London WC1N 1PF, United Kingdom;* [b]*Language and Communication Science, City University London, London EC1V 0HB, United Kingdom.*

sieratzki@vff.uni-frankfurt.de **b.woll@city.ac.uk**

http://www.city.ac.uk/lcs/deafstud_resgroup_research.htm

Abstract: We describe a possible link between coordinated lateralised group behaviour serving species survival in lower vertebrates and a striking lateralisation phenomenon found in human social behaviour: the universal preference for cradling a young infant on the left side. Our exploration offers a different perspective on the role of cerebral asymmetry for the survival of both the individual and the species.

Vallortigara & Rogers (V&R) argue that the alignment of the direction of behavioural asymmetries at the population level serves species survival by enabling individually asymmetrical organisms to coordinate their behaviour with the behaviour of other asymmetrical organisms of the same (or different) species. Drawing most of their evidence from coordinated anti-predatory behaviour in lower vertebrates, they also refer to lateralisation phenomena in the social, emotional, and communicative behaviour of higher species, including primates and humans, although without placing these behaviour patterns under the evolutionary umbrella of survival mechanisms.

We suggest a link between the lateralisation phenomena at the group level, which are the target of V&R, and a lateralisation phenomenon found in human social behaviour at a one-to-one level: the universal preference of mothers and fathers (about 80%), but not of males without children, to cradle a young infant on the left side, which is seen across cultures and in most artistic representations of mother-infant pairs (de Chateau 1987; Sieratzki & Woll 1996). The split in the population between left and right cradling mirrors V&R's data for lateralisation phenomena in lower vertebrates.

Conventional wisdom connects the use of the left arm for cradling an infant to right-handedness. However, this connection is inconsistent: the majority of sinistral mothers cradle on the left, and a substantial minority of dextral mothers cradle on their right side (Salk 1973). Close contact with the soothing maternal heartbeat has been proposed as an alternative explanation (Salk 1973); although intuitively appealing, the cardiac connection cannot account for the 20% minority of mothers who cradle on their right side (Sieratzki & Woll 1996).

In previous work (Sieratzki & Woll 1996), we have looked at the left cradling bias from the perspective of the role of the right hemisphere in the mother-infant relationship. After the trauma of birth the infant needs reassurance, and the mother wants nothing more than to provide this. To create the link, the mother offers her feelings through touch, gestures, facial expressions, and sounds. The mother's voice composes a melody with no or little lexical content, which shows a remarkable similarity in tune across cultures. This protolanguage is tuned to the infant's needs and responses; it is the emotional "heartbeat" that the infant seeks. All this originates from a deep-seated maternal instinct; even deaf mothers vocalise to young deaf infants (Sieratzki & Woll 2004).

As recognised long ago by Hughlings Jackson, the right hemisphere controls intonation and affective intent of speech, that is, prosody; and this has been documented not only in 96% of right-handed people but also in more than 70% of left-handed people. A substantial body of dichotic listening experiments with subjects ranging from neonates to adults have shown significant differences in accuracy and speed of response to left- and right-ear stimuli: whereas the right ear is better for recognising structural as-

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pects of speech, the left ear is superior for recognising melodic aspects of language – in particular, affective intonation (Bryden et al. 1991).

Similarly, the right hemisphere/left visual field shows a specialisation for socio-affective signals, and this is specifically notable for a mother's recognition of expressions of distress on an infant's face (Best et al. 1994). Our own studies of blind mothers have provided evidence that the emotional impact of touch, the most basic and inherently reciprocal mode of interaction, is also more direct and immediate if an infant is held to the left side of the body (Sieratzki & Woll 2003).

Based on the well-recognised role of the right hemisphere for perception and processing of socio-affective signals, we had theorised that the left-cradling bias was related to an advantage for mother-infant communication, which is relevant for all sensory modalities: the lullaby would not sound the same or feel the same with the baby on the other side.

This hypothesis has been confirmed by Reissland (2000) who has shown statistically significant correlations between the pitch patterns of maternal vocalisations and cradling laterality. Left cradling is associated with lower-pitch, calming, and comforting sounds; right-cradling is more often associated with higher-pitch, attention-arousing, and controlling maternal vocalisations. Depressed or insecure-anxious mothers tend to speak with a higher mean pitch and to show a higher rate of right-cradling (Reissland et al. 2003).

What does this have to do with the importance of an asymmetrical brain for the survival of the species – the topic of this target article by V&R?

Studies of posttraumatic stress disorder have shown that severe trauma may profoundly disturb the neurophysiological balance between the left and right hemispheres, leading to the loss of normal adult bonding behaviour or failure of children to develop critical social skills. The neurophysiologist J. P. Henry (1997) has proposed that "the left and right hemispheres subserve different emotional sets that correspond to 'control' and 'appraisal,' i.e., very approximately to the self and species preservative behavioural complexes, respectively." The role that we propose for the right hemisphere in mother-infant interaction may be founded in a fundamental specialisation of this hemisphere for behavioural complexes that serve the survival of the infant and thereby of the species as a whole.

The study of the lateralisation of mother-infant interaction provides insight into a fundamental aspect of hemispheric asymmetry: its role for the survival of both the individual and the species (Sieratzki & Woll 2002). If parental behaviour were only right-hemisphere determined, just subserving infant- or species-preservative interest, the survival of the individual in the environment would not be secured. If, on the other hand, behaviour were only left-hemisphere determined and directed towards self-interest, the individual would have no reason for procreation: offspring do not offer immediate benefits in terms of survival.

During the course of evolution, the cerebral hemispheres developed different aptitudes for different tasks: sequential versus spatial and detailed versus global processing, and control versus. adaptation behaviour. The connection between these properties and lateralisation phenomena in the relation of individuals to their environment remains an intriguing question.

Evolutionary tango: Perceptual asymmetries as a trick of sexual selection

Luca Tommasi

Konrad Lorenz Institute for Evolution and Cognition Research, 3422, Altenberg, Austria; Department of Biomedical Sciences, University of Chieti, I-66013 Chieti, Italy. **luca.tommasi@unich.it**
http://www.kli.ac.at/institute-b.html?personal/tommasi

Abstract: I suggest that a communicative context that has the potential to establish and maintain a shared advantage of behavioral lateralization should be identified in the domain of sexual selection, specifically in the interactions that individuals exploit to assess the fitness of potential mates.

I will develop a point that is present *in nuce* in the hypothesis of Vallortigara & Rogers (V&R), focusing directly on a class of communicative circumstances – sexual interactions – that can not only explain the establishment and the conservation of a population-level asymmetry, but also suggest the idea that this is the necessary solution.

V&R briefly mention the meager literature on asymmetries in communication, somehow overlooking the possible consequences of behavioral lateralization associated with the "analog communication" involved in sexual selection. Interactions among animals are described in the ethological literature in the form of structured rituals, such as nuptial dances and many other marvelous examples in which motor and perceptual skills, highly organized in their temporal and spatial properties, have evolved in order to allow the two participants to reciprocally assess strength, endurance, or whichever trait is relevant to the aim of the interaction (Darwin 1871; Lorenz 1952).

Ethology also has taught us that a good predictor of fitness is the assessment of physical symmetry, a parameter that has been shown to convey information about the overall performance of a potential sexual mate (see Miller [1998] for a comprehensive review). A mate choice based uniquely on the assessment of physical symmetry would intuitively be accomplished best by engaging in a face-to-face interaction. In other words, for an individual to evaluate the fitness of the mate, it would be sufficient to test the mate's persistence when face-to-face. This would select against behavioral asymmetries at a communicative level because the net result would favor the less behaviorally lateralized individuals in the most "selective" behavioral circumstance: mate choice. Computational constraints imposed by brain asymmetries pinpoint a completely different evolutionary scenario. First, it must be noticed that symmetry detection increases in precision with eccentricity (Tyler 1999). Perceptual symmetry, moreover, is not a "neural copy" of physical symmetry: the two halves of an observed object are compared point by point in the two hemispheres (as if they were through an operation of mirror reflection) only at the first stages of cortical processing (van der Zwan et al. 1998). Data from humans and other mammals suggest that configurational aspects of visual shape, including symmetry, are processed more rapidly and accurately in the right hemisphere (Avant et al. 1993; Peirce et al. 2000). This left field/right hemisphere advantage for the perception of prototypical configurations and for structural balance (the gestalt factor of "good form") is no doubt relevant to the assessment of the physical symmetry and ultimately of the "good genes" of a potential mate. Recent evidence obtained in humans, moreover, shows that the right hemisphere detects the health and attractiveness of observed faces more rapidly than does the left hemisphere (Reis & Zaidel 2001). Comparative data are not very rich in this domain and it has to be remarked that, in the case of species with laterally placed eyes, lateralized inspection has to be the rule rather than the exception. However, data indicate that a right hemisphere specialization for configurational aspects of visual shape analysis is present also in nonmammalian species (see, e.g., Güntürkün & Hahmann 1994; Regolin et al. 2004; Sovrano et al. 1999; Vallortigara & Andrew 1994a).

In a somewhat paradoxical solution, for an individual it would

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be best to assess mate symmetry by asymmetrically deviating from a face-to-face interaction, in the direction of a clockwise twist that brings the left eye (and the right hemisphere) in control of the visual input located in the left hemifield. It might well be the case that a perceptual bias crucial for assessing physical appearance leads to a state of affairs in which the coordination involved in male/female interactions results in lateralized rituals *necessarily* aligned at the population level. Boiling the argument down to the essential, neural lateralization causes the perceptual bias, which in turn, through the action of sexual selection, is maintained as the optimal solution to produce fit (lateralized) progeny. All that matters is that individuals are lateralized in the correct direction on the receiver's side of the mate choice game. Species in which the cost of parental investment is not equally shared by the two sexes might have undergone a selective pressure that aligned this "receiver bias" only in the sex that chooses the mate. For instance, all females could be lateralized in the same direction, leaving to males the weighty problem of evolving physical displays that fit the female bias. If half of the males were also lateralized, the result would still be a population bias. It would be interesting to check whether the analysis proposed by Ghirlanda and Vallortigara (2004) could accommodate the derived costs and benefits of sex-dependent asymmetries, which act at an individual level rather than at the group level.

It is not unreasonable to imagine that the rigid sequences typical of courtship would be an ideal test bench for V&R's theory. Sparse evidence points exactly in this direction (see Vallortigara et al. [1999] for a comprehensive review), although the burden of proof should come from research on courtship behavior observed in the wild. In one of the few studies carried out in the field to assess for behavioral lateralization during courtship (in black-winged stilts: Ventolini et al. 2005), the focus of observation was exclusively on males, but it was suggestive of left visual hemifield use. Evidence from human ethology (Güntürkün 2003a) also seems to support the hypothesis. Indirect evidence from recent data on sex differences in chicks (Tommasi & Vallortigara 2004) show a right hemisphere advantage in both sexes for the analysis of global aspects of spatial information, whereas local aspects seem to be encoded robustly in the left hemisphere only in males, supporting the idea that right hemisphere dominance for fast, global analysis of configural shape is present in the two sexes. It follows from these considerations that the evolution of communication might have gone hand in hand with that of lateralization, as formulated in the hypothesis by V&R, although the locus of selection should be searched for in the inescapable bond that brings the sexes together.

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Authors' Response

Forming an asymmetrical brain: Genes, environment, and evolutionarily stable strategies

Giorgio Vallortigara[a] and Lesley J. Rogers[b]

[a]*Department of Psychology and B.R.A.I.N. Centre for Neuroscience, University of Trieste, 34123 Trieste, Italy;* [b]*Centre for Neuroscience and Animal Behaviour, School of Biological, Biomedical and Molecular Sciences, University of New England, Armidale, NSW 2351, Australia.*

vallorti@univ.trieste.it **lrogers@une.edu.au**

http://psico.univ.trieste.it/labs/acn-lab/

http://www.sciences.une.edu.au/zoology/lesleyrogers.asp

Abstract: The present response elaborates and defends the main theses advanced in the target article: namely, that in order to provide an evolutionary account of brain lateralization, we should consider advantages and disadvantages associated both with the individual possession of an asymmetrical brain and with the alignment of the direction of lateralization at the population level. We explain why we believe that the hypothesis that directional lateralization evolved as an evolutionarily stable strategy may provide a better account than alternative hypotheses. We also further our discussion of the influence of stimulation and experience in early life on lateralization, and thereby show that our hypothesis is not deterministic. We also consider some novel data and ideas in support of our main thesis.

R1. Introduction

The commentators provide us with several valuable suggestions and criticisms – we are very grateful to all colleagues for their work and interest – which we have classified for simplicity within four basic categories. Some commentators disagree in part or completely with our hypothesis that directional asymmetries evolved as evolutionarily stable strategies (ESSs) and provide criticisms or alternative accounts. These will be considered in section R2. Criticisms that have arisen from misunderstandings of the hypothesis will be considered separately in section R3. Then, in section R4, we will cover the points of the commentators who stressed to various degrees the interplay of genetic and environmental factors in the determination of brain and behavioral asymmetries. Finally, in section R5 we will consider the commentaries that agree with our hypothesis, providing us with further elaboration of the hypothesis or further data in support of it.

R2. Alternative views on the evolution of directional asymmetries

Some commentators appear to be partly or totally unconvinced of our explanation for the alignment of lateralization at the population level and manifest criticisms or argue for alternative views.

Corballis argues for a heterozygotic advantage, maintaining balanced polymorphism. He refers to models that have been proposed to explain human handedness (e.g., see Annett 1995; Corballis 1997; McManus & Bryden 1992) based on the presumed existence of a single gene locus, with one allele, D, specifying dextrality, and another, C, specifying chance direction of handedness at the individual

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level so that there is no lateralization at the population level. We see two problems with this idea. One is that, as Corballis recognizes, it is not clear at all why heterozygosity might be more adaptive than homozygosity in the case of brain lateralization. Second, this hypothesis leaves the initial step unexplained – that is, the evolution of a directional bias in itself. According to the standard genetic theory of human handedness, to which Corballis seems to adhere, "sometime in the past . . . the C gene mutated from the D gene" (McManus 2002, p. 227). If this is true, we are left with a problem because there should have been a time in the past when "everyone would have carried two copies of the D gene" (McManus 2002). What sort of advantage may have arisen from having such a form of directional asymmetry? We think it is more likely that the events might have occurred the other way around: the C gene was on the scene at the start because of the computational advantages associated with possession of a lateralized brain at the individual level, and then the D gene may have mutated from the C gene, setting the stage for the evolution of population-level asymmetries. The D gene at that point could have been maintained either because of a (not yet specified) heterozygote advantage or because (as we would favor) balanced polymorphism between the two alleles occurred as the result of an evolutionarily stable strategy. The two hypotheses are, of course, not necessarily in competition: both may have provided a contribution. However, it seems to us that, whereas there is empirical evidence for a role of social interaction in population-level lateralization (Bisazza et al. 2000; Vallortigara & Bisazza 2002), there is no convincing empirical evidence that DD and CC phenotypes are at a disadvantage with respect to DC phenotype. Moreover, we do not see how the theory of the heterozygote advantage (assuming it to be a general theory of directional lateralization) can explain the evidence for changes in population lateralization associated with low or high predation pressure, as Brown et al. (2004) have shown to occur in fish. We also believe this theory meets difficulty with regard to phenomena of oscillation in the relative frequency of different types of handedness over time periods, like those observed in scale-eating Cichlid fish (Hori 1993).

Similar concerns apply to the comments of **Sainburg & Eckhardt**, who argue for genetic models like that of **Corballis** (i.e., Klar 2003), but seem to have missed the main point of the target article: directional asymmetries, such as those manifested in human handedness, may be intrinsically nonadaptive in that they convey a possibility of prediction and anticipation of the behavior of all (or most) individuals in a population (see also Raymond et al. 1996). If these asymmetries emerge from individual adaptations that enhance movement skill, as Sainburg & Eckhardt claim, why did they not remain confined to the individual level rather than becoming aligned at the population level? The point is not to argue that there are genetic influences on handedness, since we agree on that, but to try to explain *why* genes influencing directionality exist.

McManus seems to argue for homoplasy (convergent evolution) rather than homology (common ancestry) as the basis for asymmetries in vertebrates. The problem of explaining the origin of the alignment of asymmetries at the population level (directional asymmetry) remains the same regardless of which of these alternatives (homology or homoplasy) proves to be correct. Nonetheless, we are inclined to believe, in contrast to McManus, that the current evidence favors the idea of a unique, common origin of lateralization in vertebrates.

McManus argues for homoplasy on the basis of three arguments: (1) the "peculiarity" of lateralization in birds, since it is dependent on asymmetric light stimulation of the embryo; (2) the possibility of overlooking negative evidence; and (3) the fact that some of the species studied are "laboratory" rather than wild animals. Although it is certainly true that asymmetric light exposure of the embryo can modulate and, for certain visual functions, even generate lateralization, that does not mean that in the absence of such an asymmetric input the birds' brains are not lateralized for other functions. For example, light input is not needed for a variety of population-level lateralizations, including imprinting, social recognition, olfactory responses, and unihemispheric sleep (Andrew et al. 2004; Bobbo et al. 2002; Johnston et al. 1995; Mascetti & Vallortigara 2001; Rogers et al. 1998; Vallortigara et al. 2001). Birds are not different from other animals in this respect; in mammals too early experience can have a similar influence on the development of lateralization (e.g., handling and the development of a number of lateralizations in rats, as discussed by **Denenberg**). Therefore, lateralization in birds is not distinctly different from lateralization in mammals.

As to the issue of the "file-drawer problem" mentioned by **McManus**, it obviously applies to studies on humans too. We agree with McManus that for some taxonomic groups (most notably mammals) most of the evidence for lateralization comes from the study of laboratory animals. But any influence on lateralization of being bred in captivity does not apply to those species of birds, amphibians, reptiles, and fish not traditionally studied in the laboratory, most of which have been captured in the wild and brought to the laboratory for testing (see the target article). Moreover, evidence has been collected in wild animals in natural conditions: in mammals (Casperd & Dunbar 1996; Hauser & Andersson 1994), birds (Franklin & Lima 2001; Rogers 2002a; Ventolini et al. 2005), and amphibians (Rogers 2002c).

Finally, consider the phylogenetic tree of the 20 teleost species studied for asymmetries in detour behavior (Bisazza et al. 2000; Vallortigara et al. 1999). **McManus** interprets these results as evidence for homoplasy because the direction of population-level lateralization varies from species to species. However, it is difficult to argue that difference in direction reflects different patterns of laterality. It is more likely to reflect different ways in which species deal with a similar task. The target behind the barrier in the detour task was a dummy predator and the strategies of response to predators differ markedly in different species and very likely engage different sides of the brain depending on a variety of factors, including the degree of fear, the tendency to explore and to carry out "inspection of the predator" (which is not shown by all fish species), and the distance at which the species reacts to the stimulus. These differences are expected on the basis of the ecological strategies of each species.

Whether or not asymmetries of the nervous systems appeared de novo and independently in fish, amphibians, reptiles, birds, and mammals is an empirical issue that, it is hoped, will be solved soon, with more comparative data becoming available from a larger number of species and with further investigation of both the genetic and developmental processes involved in asymmetries. At present we favor

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the homology hypothesis, but we are ready to accept the other alternative. Whatever hypothesis proves to be correct, it would not detract in any way from our main hypothesis on the origin of directional asymmetries.

Martin & Jones also raise the issue of homology versus homoplasy. We certainly adhere (at present) to the idea that human lateralization stems from an evolutionarily stable strategy that took effect prior to the appearance of humans themselves, but that does not mean that analyses in terms of ESS should preclude application of this approach to specifically human or primate activities such as face presentation, as Martin & Jones argue. We say this for two reasons: First, because these specifically human or primate activities may have evolutionary roots in other, more basic asymmetries largely shared within all vertebrates groups. To give an example, asymmetries in relative attention to visual space on the left and right sides of the body, an example of pseudoneglect, have been recently observed in birds (Diekamp et al. 2005; Regolin et al. 2004) and toads (Vallortigara et al. 1998). These asymmetries may be in part responsible for, or at least associated with, asymmetries in face presentation during communication with conspecifics (e.g., Kaplan & Rogers 2002). Second, as shown by **Deason**, **Andresen & Marsolek** (**Deason et al.**), hemispheric asymmetries for different functions within an individual appear to be independent, in which case different functions should be considered separately with respect to their evolution into directional asymmetries. However, we note that Martin & Jones refer to evidence of a link between handedness in humans and perceptual asymmetries and suggest that more examples of linked asymmetries may be found. The approach outlined by Deason et al. provides a good method of investigating this in animals, as well as humans.

We now consider commentaries providing criticisms on specific points rather than proposals for alternative views. **Andrew** suggests that the use of lateralized cues by predators and prey may not strongly affect lateralization. However, empirical results of Brown et al. (2004) indicate exactly the opposite: lateralized eye use differs dramatically within the same species of fish depending on whether the subjects come from regions of high or low predation pressure. Use of lateralized cues in the prey-predator interaction has been shown by Hori (1993). It should be also noted that although the Ghirlanda and Vallortigara (2004) model has been developed in the context of prey-predator interactions (because this was the easiest type of interaction to model mathematically), the hypothesis we put forward is not restricted to prey-predator interactions (and the same reply can be addressed to similar reservations by **Güntürkün**). We contend that, whenever individually asymmetric individuals are forced to interact with other asymmetric individuals in ways that make their asymmetry relevant to each other's behavior, a balanced polymorphism between right- and left-type individuals will emerge, with an uneven number of left- and right-type phenotypes.

Andrew points out that evolutionary change would be difficult. We agree, but this is exactly the point. Specific selective pressures must have been at work to produce directional asymmetries, otherwise they would be not observed at all. The main problem that we address is not *how* directional asymmetries could have been changed, but *why* they appeared in the first instance. In fact, the aim of our target article was not to explain the consistency (or lack thereof) in the direction of lateralization among vertebrates; we are quite ready to accept variation. We wanted to know why directional asymmetries arose and were maintained in spite of their potential to be disadvantageous. Consider the argument of Andrew that left eye use in detection of predators should be regarded "as part of the problem of adjusting the balance between risk taking, for example to feed, and avoiding risk, which is unavoidable in real life." That holds true for individual lateralization as well. There would be a cost for the individual in having one side better suited to detect and respond to predators, but probably this is compensated for by some advantage. The risk can thus be assumed. But *why* align the direction of asymmetry? We do not see this situation as being any reason to cause the asymmetry to be the same in all (most) individuals. Apparently, Andrew does not see any intrinsic cost (or benefit) associated with directional (rather than individual) asymmetry. But empirical evidence shows that this is not so: In the scale-eating fish studied by Hori (1993), the directional asymmetry does affect the behavior of the prey, which in turn affects frequency-dependent selection and oscillation in the population of left- and right-asymmetric predators.

We agree with **Andrew** that social species are likely to be affected differently than solitary ones by being tested singly, and therefore that motivational differences may be important. As discussed also in the response to **McManus** earlier, motivational differences may certainly change the direction of asymmetries (e.g., because one or other side of the brain takes over control of behavior) or cause the asymmetry to disappear (because of, say, a balance in the activity of the two hemispheres). However, we do not see any compelling reason why motivational effects would turn directionally asymmetric animals into individually asymmetric animals. Most solitary species in the study by Bisazza et al. (2000), as mentioned by Andrew, were not simply nonlateralized (or with a different direction of population-level lateralization), rather, they were lateralized but only at the *individual* level. Nevertheless, experience in early life may introduce a "randomizing" effect along lines similar to those suggested by Andrew, but not as a genetically determined effect, as Andrew suggests; this has been explained by **Denenberg** and we discuss it further in section R4.

Güntürkün agrees that the benefits of population asymmetry in species in which asymmetrical individuals interact with each other outweigh the costs, but is puzzled by some issues, which we believe can easily be answered. First, according to Güntürkün, if a minority is comprised of individuals with a reversed bias allowing them two benefits (staying in a group plus bluffing the predator), one would expect that the minority group would have a higher fitness and so increase in size. Therefore, as Güntürkün sees it, the evolutionarily stable strategy would not result in two mirror-imaged groups of different sizes, but in two groups of equal size. The answer is that the advantage of the minority group is a frequency-dependent advantage; the more the minority group increases in size, the more the advantage is reduced. The minority group has an advantage *only* when it is, in fact, a minority. This is the reason why a stable polymorphism with an uneven number of right and left individuals may evolve as an evolutionarily stable strategy (see also Ghirlanda & Vallortigara 2004). Note, however, that Güntürkün is correct on one point; viz., a stable polymorphism in a population with an uneven number of individuals is not the only possibility. Another possible equilibrium condition is oscillation in the relative frequency of left- and

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right-type individuals in the population varying systematically over time periods. This would not be an argument against the hypothesis; on the contrary, it would support it, and indeed these forms of oscillatory directional asymmetries have been described (Hori 1993). Whether a temporally stable or a periodically oscillatory form of polymorphism evolves would be mostly a matter of ecological conditions, and even apparently stable manifestations of lateralization may be periodic oscillations with very long cycles.

The second issue raised by **Güntürkün** concerns solitary species, which, according to the theory, would not show any population asymmetry. This is indeed what we predict. We wondered, however, whether for current living organisms the presence of population-level lateralization in solitary species may be explained in other ways, without necessarily falsifying the hypothesis. Hence, we put forward the suggestion that solitary species might have derived from social animals or gregarious juveniles and still go on with their inherited habit. This is not our main hypothesis, but a subsidiary one for current living species (from an evolutionary point of view, we expect that solitary species were lateralized *only* at the individual level and that directional asymmetries first appeared, in evolutionary time, when individually asymmetric organisms interacted with each other in ways for which their asymmetries would matter). It may be that we do not need any subsidiary hypothesis, because we actually do not know of any solitary species in which directional lateralization has been consistently observed in a range of tasks. Nonetheless, we might find no difficulty in explaining the presence of directional lateralization in a solitary species if we know its evolutionary past. Evolution is in fact extremely conservative, and a change from individual-level to population-level asymmetry and then to the other way round (i.e., from population- to individual-level lateralization) is not likely to be "symmetrical," for the latter resembles the classical problem of putting the toothpaste back into its container. For instance, if there is little predatory pressure, and if the constraints of conservatism in development and the costs of change are very high, then directional asymmetries are likely to be maintained even in solitary species. It should be emphasized, however, that at present the evidence for those currently living species in which a crucial aspect of interaction between social behavior and lateralization can be checked experimentally fits very well with our hypothesis (i.e., in shoaling vs non-shoaling fish).

The third issue raised by **Güntürkün** is in some ways baffling to us, because we really do not see the problem. Güntürkün asks why so many vertebrate species have comparable cerebral asymmetries. As stated above in reply to **McManus**, the hypothesis that directional asymmetries arose as ESSs is "neutral" with respect to the issue of whether the pattern of lateralization in vertebrates reflects basic homology or convergent evolution. A pattern that is basically similar would favor the homology argument. In any case, it seems to us that the issue of the alignment of asymmetries across vertebrates should be kept distinct from the problem of the alignment of asymmetries in species. It is clear that mutual evolution is possible between species; hence, the fact that a species is population-level lateralized in a certain direction may constrain a similar (or complementary) direction of lateralization in another species if these species interact with each other in any significant way. But it should be emphasized that this is possible only when the first step has already been taken, that is, when at least one of the species is population-level lateralized. And, whatever basic dichotomy of computation is needed to ensure brain efficiency in individual animals, it does not require, in itself, that the left-right allocation of the dichotomized computations should be the same in more than 50% of the organisms of a particular species.

The comments of **Crow** deserve separate treatment. All of the other commentators concentrate on our hypothesis, and not one questions that brain asymmetries are a general characteristic of the vertebrate brain. Only Crow argues that lateralization is unique to the human species, thus underscoring his hypothesis of a single, major genetic event that produced, in humans alone, brain lateralization, theory of mind, language, and susceptibility to schizophrenia (Crow 2002). Obviously, any scientist would defend his/her own hypothesis but the raw facts cannot be ignored. It is interesting to compare Crow's position in this regard with that of **Corballis**, who in the past has also championed the view that lateralization is unique to the human species, and who now provides a lesson of integrity and scientific fairness. In his commentary Corballis writes (emphasis is ours):

> One of the myths of our time, *propagated by myself*, among others, is that cerebral asymmetry somehow defines the human condition – we are, it has been claimed, the lopsided ape (Corballis 1991). We have been fooled into this myth by a number of factors. [. . .] Some of our lateralized activities may well be distinctive to our own species, *but cerebral lateralization itself is not*.

What more do we need to say? We can only subscribe to Corballis's statements and very much appreciate his intellectual honesty.

In striking contrast, all of what **Crow** states in his commentary is simply not true. Let us consider each of his statements in turn.

Crow says that there is no evidence for population-based asymmetries of paw use in rodents. This is incorrect. As to mice, we certainly do not dismiss Collins's findings and we reported them extensively, but we also noted the reports, which became available after Collins's seminal work, demonstrating that population-level pawedness can indeed be observed in some strains of mice (e.g., Maarouf et al. 1999; Waters & Denenberg 1994). Moreover, if one looks at behavior other than limb use and to neural asymmetries, lateralization appears to be well documented in mice. Mice show, in fact, striking population-level lateralization in recognition of ultrasonic communication calls (Ehret 1987), and striking directional asymmetries have been reported in their brains (Kawakami et al. 2003; Tang 2003).

Contrary to **Crow**'s belief, there is also clear evidence of handedness at the population level in rats (73% of the population; Güven et al. 2003; see also Tang & Verstynen 2002) and, again, a variety of other behavioral and neural asymmetries have been reported in rats (e.g., Adamec & Morgan 1994; Bianki 1988; Crowne et al. 1987; Denenberg 1981; Glick & Ross 1981; LaMendola & Bever 1997).

Crow states that there is no evidence for population-based asymmetries of hand use in primates, in particular in great apes. This is false. To cite Annett and Annett (1991) and subsequently Holder (1999) and Finch et al. (1941) as providing the only data on handedness in apes is a clear example of using the literature in a highly selective way. Crow also quotes Marchant and McGrew (1996) and Palmer

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(2002), ignoring that Hopkins has replied, very convincingly, to the criticisms of these authors (Hopkins & Cantalupo, in press; Hopkins et al. 2005; and see Rogers & Kaplan 1996). Moreover, Hopkins has provided empirical data showing right-handedness in chimpanzees in another two (other than the original Yerkes) very large colonies (Hopkins et al. 2005). Most important, he has shown that handedness in the three colonies is unrelated to the proportion of subjects that had been raised by humans (thus rebutting Marchant and McGrew's hypothesis that handedness in captive chimpanzees is an artifact of being raised by humans in a right-handed environment; we agree here with **Martin & Jones** that our own conjecture that social pressures affect chimpanzees' handedness was incorrect). Crow will have to consider this evidence rather than ignore it. Moreover, Hopkins has recently produced a comprehensive review of the literature on handedness in great apes (Hopkins, in press) showing that there is *very* convincing evidence for population-level right-handedness in chimpanzees. (By the way, such evidence plainly contradicts claims, such as those of **Sainburg & Eckhardt** and **Martin & Jones**, that handedness emerged late in human evolution.)

Crow also ignores all of the literature concerning behavioral asymmetries at the population level in monkeys: to cite a few examples, evidence for asymmetries in face expression published by Hauser (1993) and Hook-Costigan and Rogers (1998), and evidence by Hamilton and Vermeire (1988) that split-brain monkeys recognize faces with the right hemisphere (by the way, all of this literature has been cited in the target article). Also, Crow completely ignores the fact that similar results have been obtained in other mammalian species; for example, there is evidence that the right hemisphere is selectively involved in face recognition in sheep, as demonstrated using both behavioral (Peirce et al. 2000) and neurobiological (*c-fos* expression: Broad et al. 2000) methods. Why does Crow not mention these findings?

Crow states that there is no evidence of the cerebral torque from the right frontal to left occipital lobes in nonhuman primates. This is incorrect. In a recent paper on cerebral and cerebellar torque asymmetries (Cantalupo et al., in press), which is a follow up to an earlier study by Pilcher et al. (2001) but with a larger sample size ($N > 50$), Cantalupo et al. describe left-occipital right-frontal asymmetries in cerebral torque in chimpanzees. Moreover, in insisting on the overriding importance of cerebral torque asymmetries, Crow again seems to ignore a basic fact: asymmetries can be observed in human fetuses of only 10 weeks of gestation (before neurons in the brain have connected to the spinal cord): 85% of fetuses move their right arm more often than their left arm (Hepper et al. 1998). This implies that handedness is not solely related to the cortex and language (i.e., with the cerebral torque), but comes from subcortical regions of the central nervous system.

About the issue of brain asymmetries in apes, including the work on the inferior frontal gyrus, **Crow** claims that recent studies report no asymmetries in this region. This too is incorrect, even based on the evidence that Crow cites. Good et al. (2001) did report a leftward asymmetry in the frontal operculum (this would include Brodmann's areas 44 and 45); so why Crow claims they did not do so is unclear to us. Crow quotes Buxhoeveden et al. (2001) but ignores the extensive evidence for brain asymmetries in primates reported in the target article (including recent evidence that species-specific calls evoke asymmetric activity in the superior temporal gyrus; Poremba et al. 2004). No doubt there are likely to be differences in the brain between humans and the other primates, and very likely some of these differences may involve brain asymmetry (an example being the reverse directional cerebellar torque with respect to humans, despite the presence of a cerebral torque in the same direction as humans in chimpanzees; Cantalupo et al., in press), but this is completely different from arguing that there are no brain asymmetries at all in nonhuman primate brains.

Broadfield in his commentary recognizes the evidence of asymmetries in the primate brain, but argues that there is little evidence that relates them to lateralization of function. This is certainly true with respect to the possible functional role of asymmetries in those regions of the brain supposed to be homologues of language areas, but evidence for lateralization of function is clear in primates for functions such as face recognition, head/ear turning responses to the calls of conspecifics, and in the facial expressions of emotions (as discussed above). And in the case of perception of conspecific vocalizations, some relationships of central asymmetries with "language" areas can be postulated (Poremba et al. 2004).

Another point that **Crow** seems to misunderstand is that brain asymmetry is the basic phenomenon and handedness is only one of the several possible manifestations of brain lateralization at the behavioral level. Again **Corballis** seems to be well aware of this when he writes: "Other manifestations of cerebral asymmetry are less obvious than human handedness, but no less present." In some species, the reverse may be the case. It is completely incorrect to argue that a lack of evidence for handedness means a lack of brain lateralization. Several vertebrate species do not have limbs (in the common sense of the term) or they use limbs very little but they exhibit lateralization: one cannot find "handedness" in dolphins, nonetheless there is clear evidence that they are lateralized both in behavior and in the brain (e.g., Ridgway 1986; von Fersen et al. 2000; Yaman et al. 2003). Hand preferences are just one possible expression of lateralization. They may be the easiest behavior to measure in this regard but they do not, and will not, provide convincing evidence in favor of Crow's insistence on the uniqueness of lateralization in humans.

Crow seems to forget the basic principle of logic, as follows. Cantalupo and Hopkins (2001) reported brain asymmetries in chimpanzees, bonobos, and gorillas. Crow argues that these particular asymmetries have not been found in studies of humans and concludes from this that these asymmetries do not exist in chimpanzees, bonobos, and gorillas. This is a *non sequitur*. Another example of this faulty logic is provided by Crow's remarks that some of the asymmetries observed in nonhuman primates are stronger than those observed in humans in the same brain areas and so they cannot be correct. However, these are empirical results and should be accepted as such (or refuted on the basis of other empirical results in which scientists have attempted to duplicate these observations). It is simply illogical to assert that the data cannot be valid *because* the asymmetry observed is stronger than that observed in humans.

The literature reporting the evidence of lateralization in nonhumans, and reviewed by Andrew and Rogers (2002;

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see also Rogers 2002a; Vallortigara et al. 1999), is not "exceedingly meagre" or "rich in anecdotal claims," as Crow says. It reports a substantial body of controlled experiments conducted in a number of laboratories, on a number of species, and using a range of techniques/tasks. Readers who examine this literature in detail will, we believe, see that there is a rather similar pattern of lateralized functions across a range of species.

R3. Some misunderstandings: The ESS hypothesis is *not* a "social learning" hypothesis, *nor* is it a "group selection" hypothesis

Some disagreement (but also some agreement) seems to be based on a misunderstanding of what is meant by saying that directional asymmetries evolved as an evolutionarily stable strategy (ESS). For example, **Miu** attributes to us the idea that "the strength of lateralization is controlled by social learning," and **Concha** says we claim that "genes play no primary function" in determining population level lateralization. This is not correct. Although we also recognize the importance of experience as part of the process determining the expression of lateralization and point out that the manifestation of lateralization (both structural and functional) results from the interaction of genes and experience, the idea of an ESS is a hypothesis that concerns genetic mechanisms and not social learning (Maynard Smith 1982). The misunderstandings seem to have arisen because Miu and Concha might not have realized that one level of explanation (used by evolutionary biologists) is concerned with ultimate, functional explanations (the "why"), whereas the other (used by molecular biologists like Concha and neuropsychobiologists like Miu) aims at proximal, causal explanations. Of course we agree with Concha that genes (or more likely mutants of them) involved in the coordination of visceral organs play a role in the control of brain and behavioral lateralization within a population. And of course we agree with **Deng** that the "direction of the embryo's head rotation [in birds] is determined by asymmetrical expression of several genes (such as *shh*, *Nodal*, *lefty*, and *FGF8*)." The point, however, is not the existence of these genes, but *why* natural selection may have allowed them to persist. If we accept that directional asymmetries in behavior may convey a biological disadvantage, and if we accept (and we certainly do) that these asymmetries are in part determined by genes, then the problem (from the evolutionary biology point of view) is to explain *why* these genes evolved and are maintained in individuals. We argued that they persist because they allow the development of directional asymmetries in the form of an ESS strategy. An ESS hypothesis actually *needs* "directional" genes or a mixture of genetic and epigenetic effects like light stimulation of the embryo in birds in order to align the direction of asymmetries at the population level. Therefore, we are not in disagreement with either Concha or Deng in this respect. Similarly, we agree with **McBeath & Sugar** that some forms of asymmetry depend on arbitrary social trends and reflect social learning, as in the case of those examples associated with experience of reading direction, but our hypothesis was not concerned with these cases of arbitrary social trends in which any alignment of brain lateralization at the level of the species seems to play no primary role. Nevertheless, we agree that it is important to specify which type of lateralization one might be considering, and we do not treat lateralized function as a unified concept.

Miklósi concurs with us on the relevance of "why" questions but contends that we are using a kind of "group selection argument." This is not correct. **Sieratzki & Woll** seem to suggest the same in their statement, "the alignment of the direction of behavioural asymmetries [. . .] serves species survival." The notion of an ESS may resemble group selection, but it is not really the case (cf. Dawkins 1976) because the advantage (the fitness advantage) in an ESS is relative to the individual, not to the group (or the species). The basic idea is that what is advantageous for an asymmetrical individual to do depends on what the majority of the other asymmetrical individuals of the group do. This is completely different from stating that the alignment of asymmetries serves species survival. It actually serves *individual* survival! We did not enter into the mathematical details in the target article, but these can be found in the paper by Ghirlanda and Vallortigara (2004). We agree with Miklósi, however, that the scenario we outlined for the interaction between predator and prey is somewhat unrealistic from an ethological point of view. Yet, the main goal of our work should be considered. We wanted to provide a "proof of existence," so to speak; namely, we wanted to demonstrate mathematically that directional asymmetries may have evolved as "equilibrium conditions" when asymmetrical individuals must interact with each other. As Ghirlanda and Vallortigara (2004) prove, the hypothesis is mathematically sound. Now, more ethologically realistic analyses can be undertaken, even the consideration of other forms of coordination among individuals, as suggested by Miklósi.

R4. The interactive roles of genes and environment in the determination of cerebral lateralization

Up to this point we have concentrated on questions concerning the evolution of lateralization. These ideas need to be juxtaposed to questions, and experimental evidence, about the development of lateralization. As **Denenberg** reinforces very clearly, our gene-based evolutionary hypothesis is not deterministic since experience around the time of hatching or birth can markedly influence the pattern of lateralization. In any given individual, lateralization develops as an interaction between genetic expression and the effect of experience, as shown clearly in three experimental models, the chick, the pigeon, and the rat. As we discussed in the target article, lateralization of the visual pathways and of some important types of visual behavior develops as a result of exposure of the chick or pigeon embryo to light (see also the commentary by **Casey** for an interesting discussion of hatching behavior itself affecting lateralization). Denenberg reminds us that handling of the neonatal rat has a similar role in ensuring the development of asymmetry. His commentary takes our thinking on this process a step further by proposing the interesting hypothesis that environmental stimulation is needed in order to develop a lateralized brain and that the level of stimulation must be above a threshold. According to this hypothesis, failure to receive stimulation above the threshold leaves the brain in a state of being prepared for a world of little vari-

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ability or one with little complexity, and in such an environment with fewer demands on the brain, the basal (fall-back) brain state of symmetry develops and may be sufficient for survival. The converse also holds: above-threshold stimulation, in terms of complexity, novelty, and so on, causes the development of asymmetry and such a brain has increased functional capacity. It is, therefore, able to cope with the multiple demands of a more complex world/habitat. We note Denenberg's suggestion that the fall-back condition is one of symmetry and not reversal of the direction of lateralization, and here he is speaking of lateralization at the individual level, not the population level. Reversal of direction is possible in the chick, following experimental manipulation that exposes the embryo's left eye to light at the same time that the right eye is occluded. Both **Andrew** and **Deng** rightly stress that such reversal is abnormal, the normal variation being one of degree of lateralization and not direction of lateralization. On this point Andrew, Denenberg, and Deng are in agreement, and so are we.

According to **Denenberg**, and we also agree here, the early experience that leads to the development of lateralization does not itself have to be lateralized, as the example of handling of the rat demonstrates. The findings of **Brown** support this hypothesis since he showed that those members of a poeciliid fish species that were exposed to higher levels of predation were more lateralized than ones living in environments with fewer predators. Quite obviously, exposure to high levels of predation would provide a complex and highly stimulating environment and, hence, one demanding the efficiency and capacity of a lateralized brain. Moreover, we might consider that stress in early life may be an ingredient for development of a lateralized brain. Brown deduces from his data that predation pressure may have played a key role in the evolution of lateralization. We do not disagree with this, for other reasons outlined in our target article, but here we raise the possibility, based on Denenberg's hypothesis, that the presence or absence of lateralization in the species studied by Brown may have resulted from experience during development. This could be tested experimentally.

Inconsistent with the above suggestion that stress during the early stages of development may enhance the likelihood of developing a lateralized brain, Rogers and Deng (2005) have shown that elevation of the levels of the stress hormone, corticosterone, in the chicken egg just prior to the sensitive period when light stimulation has its effect (in the last few days before hatching) prevents light from causing the development of asymmetry in the visual pathways. In fact, the effect of corticosterone seems to be one of randomization at the individual level so that no population bias is present, although some individuals are lateralized in one direction or the other, and others are not lateralized. Hence, whereas experience may not be able to reverse the direction of lateralization, at least at the individual level, this hormone can reverse the direction in some individuals. The fall-back condition at the level of the population, however, remains one of no asymmetry. In fact, the corticosterone-treated group appears to have platykurtic asymmetry (see Fig. 1.2 of Møller & Swaddle 1997). Tang and Verstynen (2002) found a somewhat similar effect of stress on paw preference in rats: whereas control rats showed a significant population-level right-paw preference, handled rats (i.e., those subject to a certain degree of stress in neonatal life) showed no such population bias. These results considered together with the prior findings of **Denenberg** (above) would suggest that the experience of stress, or complexity, in early life may enhance the development of (or generate) some lateralizations and inhibit the development of others. This indicates a clear route by which individual-level lateralization may be modified to cause variation within a population or, conversely, to establish similar degrees of lateralization within a population (provided all individuals have the same critical experience) or within a subpopulation of a species.

Under natural circumstances the avian embryo may be exposed to higher levels of corticosterone because it suffers stress (e.g., resulting from lowered temperature of the eggs) during the later stages of incubation when this hormonal system of the embryo becomes functional or because the hen has deposited corticosterone in the egg yolk before the egg is laid. Social stress or stress from predation suffered by the hen might elevate the levels of this hormone in the egg yolk (see Elf & Fivizzani 2002; Schwabl 1999) and lead to modified lateralization of her offspring (discussed in more detail by Rogers & Deng 2005). We think that this would be worth investigating.

Experiences in early life other than those already mentioned may play a role in the development of different types of lateralization, as **Harris & Almerigi** point out for the holding of infants by humans. As these commentators discuss, it remains an open question whether the adult (mother) influences the lateralization of her offspring by carrying the infant on her left side or whether she carries the infant on her left side in response to lateralization of head turning already present in the infant. In either case, the left-side carrying may enhance, or modulate, lateralization in the developing infant. **Sieratzki & Woll** also refer to the left-side bias for cradling infants in humans and note its possible importance for parent-infant communication, especially for communication by touch and soothing vocalizations. Although these observations and measurements of lateralized behavior in humans are interesting in their own right, at the present time they provide little evidence to support (or indeed refute) our hypothesis, since nothing is known of whether or not the left-side cradling does influence the development of a lateralized brain. Furthermore, we do not adhere to the view advanced by Sieratzki & Woll that the left hemisphere is specialized for "the self" (control) and the right for "the species" (adaptation), or any discussion on the interaction between these two postulated alternatives. Although the right hemisphere does appear to be specialized for controlling rapid, species-typical responses, it is foolhardy to extrapolate that to say that this hemisphere is specialized for species adaptation, or to go so far as to say that the left hemisphere is for the self and, were it in sole control, the individual "would have no reason for procreation," as Sieratzki & Woll say. Quite apart from the fact that it is doubtful whether reason has anything to do with procreation in humans, such wild extrapolation is fanciful and dangerous both from the position of science and logic, as well as from the social perspective.

Deng takes issue with our hypothesis that population-level lateralization occurs when lateralized individuals have to interact socially with each other. Deng points out that lateralization of the nuclei that control the production of song in songbirds would not be predictable, or rather detectible, by other birds. This is correct, but perhaps the perception

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of song involves lateralized mechanisms or perhaps the singing bird uses lateralized visual communication (eye preference) in conjunction with singing. Just as **Manns** suggests for asymmetry of the Mauthner cells in amphibians, asymmetry of the motor control system may be a secondary consequence of lateralized sensory input.

Miu is interested in the trade-off between corpus callosum development and intrahemisphere neuroplasticity, and discusses some very interesting evidence showing that a functioning corpus callosum inhibits intrahemispheric neuroplasticity. Based on this, he suggests that eutherian mammals have a much shorter time window, in early life, during which "evolutionarily relevant behavioral asymmetries" can be implemented, than would be available to vertebrates without a corpus callosum. It may be true that a functioning corpus callosum reduces synaptogenesis, although the evidence so far shows only that these two processes are associated – and that in itself does not prove a causal connection – but neural plasticity continues to occur at other levels of organization (e.g., modulation of neurochemical transmission) and that could modify lateralization quite effectively. We do, of course, recognize that stimulation in early life is more effective than in later life in modifying or enhancing brain development, including lateralization, as the work of **Denenberg** has shown. In fact, Miu seems to be unaware that Denenberg has shown that the corpus callosum of the rat is important for the expression of cerebral lateralization and that the handling procedure influences the size of the corpus callosum. This fact alone is sufficient to refute Miu's idea that our hypothesis can apply only to vertebrates without a corpus callosum. Although the corpus callosum may assume an important role in the development and expression of lateralization in eutherian mammals, this would be an addition to a process that has already been well established in early vertebrates. Whether the corpus callosum enhances or suppresses cerebral laterality is a matter of debate (Filgueiras & Manhaes 2004) and may be function-/task-specific. Two extra points are relevant here: (1) lateralized functions occur also at subcortical levels in eutherian mammals (Nordeen & Yahr 1982) and so are independent of the corpus callosum, and (2) two of the commissures that occur in the avian brain (the tectal and posterior commissures) do have a role in the expression of at least some types of lateralization, as revealed by sectioning them (Parsons & Rogers 1993). Therefore, we are of the firm opinion that Miu's attempt to confine our hypothesis to vertebrates lacking a corpus callosum is incorrect on a number of grounds.

To conclude this section, we reiterate that lateralization of brain and behavior results from the interaction of gene expression, the action of certain hormones on neural tissue, and environmental stimulation. **Manns** interpreted our target article as implying that genetic and epigenetic factors are opposing factors for aligning lateralization at the population level, but this was not our intention. The important role of light stimulation in the development of certain important types of lateralized visual function in the chick and pigeon is, we agree, crucial and not a minor facet of the process. The same is the case for the motor behavior associated with hatching, as **Casey** discusses, and for the stimulation caused by handling neonatal rats. Likely, other examples will emerge: we expect investigation of the effects of sensory stimulation on the development of lateralization to be a rich field for future research.

R5. Further data and ideas in support of the hypothesis that directional asymmetries developed as evolutionarily stable strategies

Some authors are basically in agreement with our hypothesis and add further data in support of it. This applies to **Schirillo & Fox**, whose research agrees with our premise (not Maynard Smith's premise actually: Maynard Smith developed the mathematical concept of an ESS, but he did not work on lateralization) that the alignment of the direction of lateral biases in most individuals in a population may have evolved as an evolutionarily stable strategy to coordinate behavior among asymmetric individuals. Schirillo & Fox provide interesting new data relating asymmetries in face portraiture to sex differences in humans. **Tommasi** and **McBeath & Sugar** also independently suggest a role of sexual selection in the development of lateralization. However, as recognized by Tommasi, in animals with laterally placed eyes courtship and mating displays are usually unilateral, and thus estimation (by the animal being courted) of symmetry on the basis of face-to-face presentation is unlikely to occur. It is also unclear whether unilateral displays can be aligned at the population level by sexual selection alone. For instance, during courtship behavior in several species of poeciliid fish, the large intromittent organ of the male (gonopodium) is angled to the right or to the left; females too have a genital opening only on one side, so that dextral males must mate with sinistral females and vice versa (reviewed by Bisazza et al. 1996). Usually textbooks report that there are roughly equal numbers of the two types of animals; however, it has been claimed that there is a small preponderance of dextral males and sinistral females (see Bisazza et al. [1996] for a discussion). The issue deserves further investigation.

Brown suggests that "non-lateralised individuals may have enhanced fitness within the context of the group and may play some pivotal role in maintaining group cohesion." The idea is interesting, but we see a bio(logical) difficulty. In order to maintain non-lateralized individuals in the population, we must suppose that there are fitness advantages (for the individual) in being non-lateralized. We can see the advantage for the group as a whole in Brown's hypothesis, but we do not see the individual advantage. If natural selection operates on individuals (so far, evidence for group selection is unconvincing), we need to specify an advantage in terms of fitness of non-lateralized individuals. The story is different for animals that represent the minority group in the population (the "left-handed" ones, so to speak). In this case we can see that there is an advantage at the individual level in maintaining a bias opposite to that of most of the other ("right-handed") individuals (a frequency-dependent advantage; see Ghirlanda & Vallortigara [2004] for mathematical details), but the condition of non-lateralized individuals is puzzling to us. Perhaps we can think of them as sort of "cheaters," but their existence would cause some problems of explanation. In principle, having both sides identically able to detect predators would be an advantage. However, such a lack of lateralization is likely to convey costs – for example, in terms of efficiency (speed) of response to predators or ability to perform other tasks simultaneously (Rogers et al. 2004). Yet, if these types of individuals develop as an alternative strategy within groups in which strongly lateralized animals already exist, they can perhaps compensate for these costs with the benefits of oc-

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cupying the central position of groups (e.g., fish shoals). They would have the further advantage of not taking part in any competition for the "best position" in the shoal (because in contrast to lateralized companions they have no side preferences) and they could be treated as a sort of useful parasites by the lateralized individuals within a shoal.

We thank **Reggia & Grushin** for providing us with literature on simulated evolution of lateralization using neural networks. We think this may be indeed a very useful complement of the game-theoretic approach used by Ghirlanda and Vallortigara (2004). It seems to us, however, that current neural network models that lead to directional asymmetries are too simple (as Reggia & Crushin recognize) and miss a crucial aspect – that of the potential disadvantages of directional biases in behavior. Of course, these simulations can produce directional asymmetries without social interactions between the individuals, but they do that because only the computational advantages (task performance/accuracy) associated with lateralization are considered (i.e., there are no selective pressures *against* directional asymmetries). In this condition, individual-level or population-level lateralization would be quite similar in terms of individual fitness. Nevertheless, Reggia & Grushin's observation that directional asymmetries may have arisen simply as a result of the convergence property of genetic algorithms remains very interesting.

Heuts & Brunt have added further evidence from their own work on fish that aligning of behavioral asymmetries may be beneficial in shoaling species, whereas ground-dwelling species that do not profit from shoaling show no lateralized swimming. Moreover, Heuts & Brunt have pointed out that behavioral lateralization at the population level may not be unique to vertebrates. They provide novel, extremely interesting evidence for directional asymmetries in spiders and ants. At least some of the asymmetries seem to be specific to arthropods, and not to vertebrate species that predate them. Lateralization has been reported in octopus (Byrne et al. 2004), but only at the individual level, which is perhaps expected, given that this is a very solitary species. Intriguingly, however, lateralization has been reported in fruitflies (Pascual et al. 2004) and in *C. elegans* (Hobert et al. 2002). Given that there are advantages to asymmetries of the functioning of the central nervous system, and that there is a left/right axis that is strongly and conservatively specified in Metazoan development, lateralization is very likely to have evolved in some advanced invertebrates. The common ancestor had so simple a nervous system that it could not have had much in the way of lateralization of the vertebrate type, but it would of course be interesting to know a lot more about invertebrate lateralization, particularly in arthropods.

We concur entirely with **Dräger**, **Breitenstein & Knecht** (**Dräger et al.**) that although some aspects of brain lateralization for language are likely to be unique to our species, lateralization is not specific to language or human speciation. Left hemispheric language dominance may be the result of pre-adaptation for language (for a discussion, see Vallortigara & Bisazza [2002] and Rogers & Bradshaw [1996]). Dominance of the left hemisphere for vocal production or processing has been demonstrated in several different species of passerine birds (reviewed in Williams 1990), in monkeys (Heffner & Heffner 1986; Petersen et al. 1978), mice (Ehret 1987), frogs (Bauer 1993), and catfish (Fine et al. 1996). However, since lateralization for language in humans is striking, in particular with respect to phonology, it is unclear to what aspects the species-invariance could refer. One possibility is that control by the left hemisphere occurs for all stimuli having species-specific communicative relevance. However, a right-ear advantage has been reported by O'Connor et al. (1992) in male rats for discriminating two- and three-tone sequences (but not single tones). Fitch et al. (1993) also reported that male rats show significantly better discrimination of tone sequences with the right ear than with the left ear. These stimuli have no communicative relevance. A crucial finding seems to be that Japanese macaques rely on temporal information (frequency peak position) in making the "coo" vocalization and that they show a right-ear advantage (May et al. 1989). This suggests a left-hemisphere specialization for the processing of temporal acoustic information, which could represent an evolutionary precursor to lateralized speech perception and language processing in humans. MacNeilage (in press) has developed the interesting hypothesis that this may be associated with a more basic left hemisphere specialization for whole-body control under routine circumstances.

Matsushima has provided thoughtful comments on the possible role of (individual-level) brain lateralization in reducing the probability of delaying the emission of response due to behavioral conflict when attending to different targets simultaneously. In fact, direct evidence for this has been obtained in the domestic chick (Rogers et al. 2004). We would like to stress, however, that the problem of processing incompatible functions may have played a key role in the evolution of lateralization, not only for response emission, but also for encoding of different types of information. We have argued elsewhere (Vallortigara 2000; Vallortigara et al. 1999) that the segregation of functions of the separate halves of the brain may represent a solution to a problem of "functional incompatibility." Once again, however, this can provide a rationale for the evolution of individual-level lateralization, but not for its alignment at the population level.

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Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

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