

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?

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**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-relationships 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-*

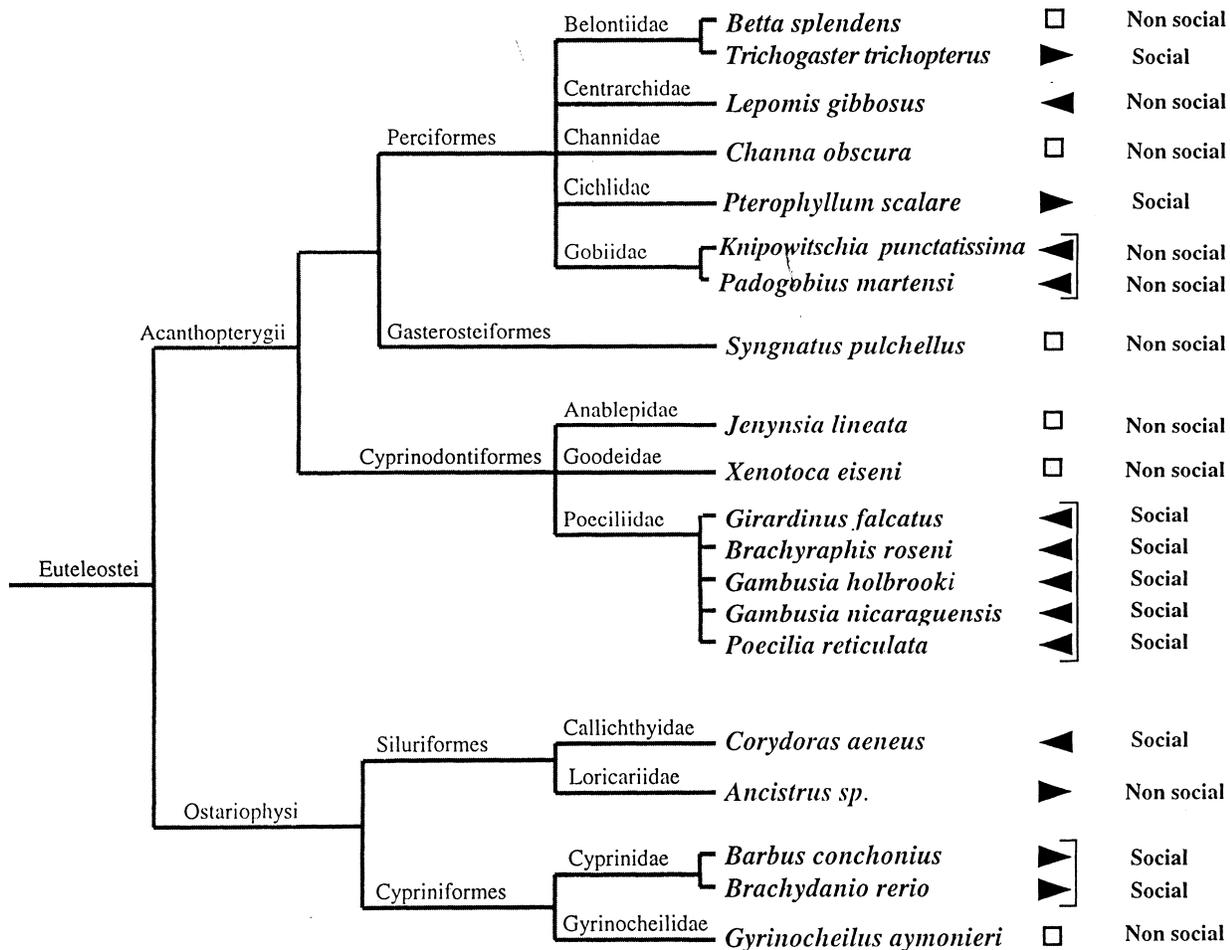


Figure 1 (McManus). Turning tendencies in 20 species of fish. Arrows indicate the direction of bias; squares indicate no bias. Reproduced with permission from Vallortigara et al. (1999).

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 re-

quires 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

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”

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**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 non-lateralized 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

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**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