

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-*

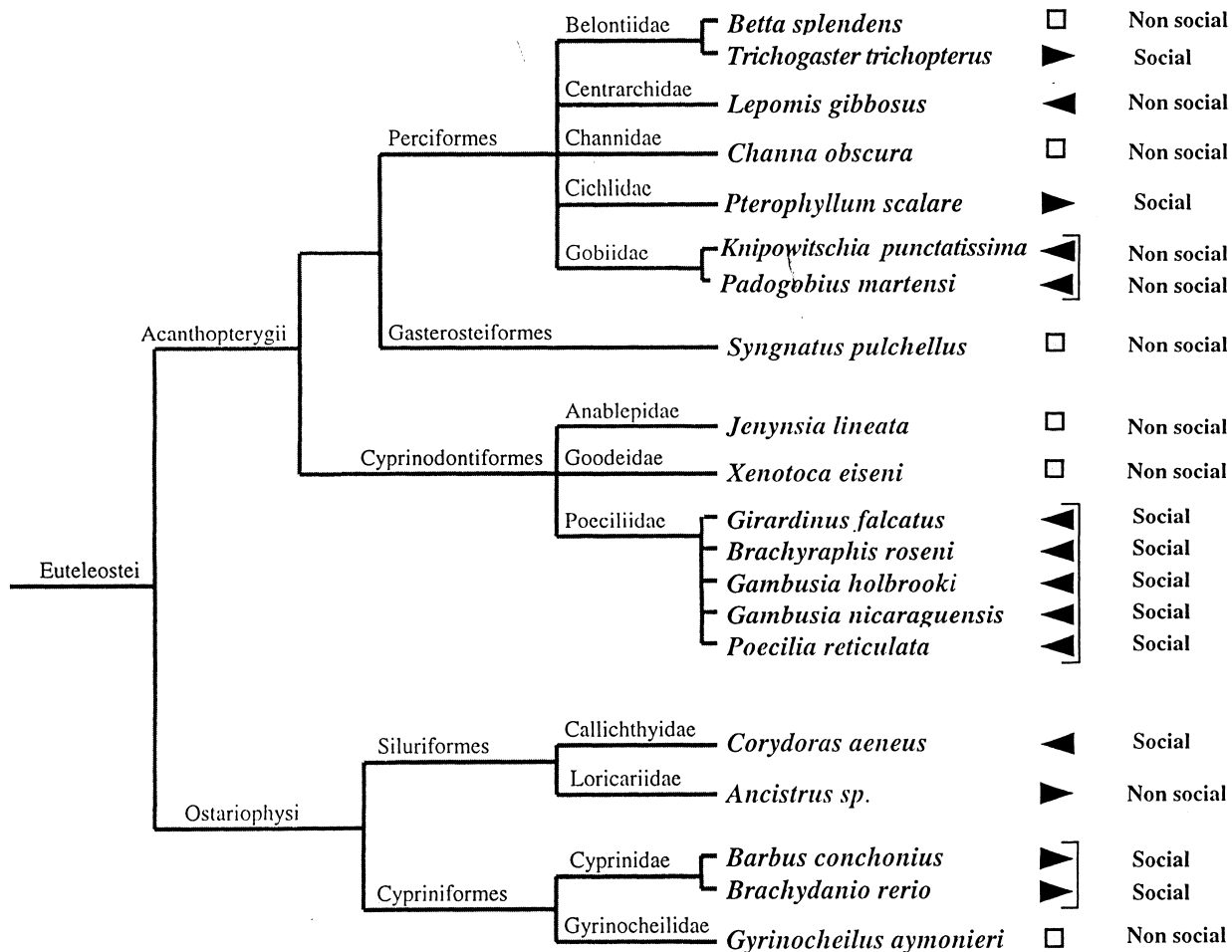


Figure 1 (McManus). Turning tendencies in 20 species of fish. Arrows indicate the direction of bias; squares indicate no bias. Reproduced with permission from Vallortigara et al. (1999).

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.

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.