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COMMENTARY

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On the usefulness and limits of functional analogies

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Comparison is the essence of science. But before any comparison can be made one should extend one's knowledge of the subjects to be compared. We should be grateful to Bshary, Wickler, and Fricke (2002) for their comprehensive review of cognitive processes in fish because despite its long history, this field has faced serious neglect in recent years. This lack of interest in fish cognition is even more striking if one considers that all ethologist Nobel Prize winners had some interest in fish behaviour during their career, and much of this work is still cited in textbooks for students [e.g. von Frisch (1941): fright pheromons; Ter Pelkwijk and Tinbergen (1937): recognition of sign stimuli)]. Unfortunately too many researchers interested in cognitive processes in animals have turned to the study of mammals, despite the fact that the laboratory environment for the study can be made more natural for fish than for most mammals. Primates, especially, have received much attention from the scientific community, and although there are debates about the interpretation of many experimental results, primate cognition research is flourishing, and comprehensive reviews are published on a regular basis (e.g. Köhler 1925; Byrne and Whiten 1988; Tomasello and Call 1997).

Given the present situation, Bshary et al. (2002) did the best they could by comparing many different skills in fish that are thought to depend on cognitive processes with similar traits described for primates. They argued that fish cognition can and should be used as a null hypothesis for understanding primate cognition since most phenomena can be found in both taxonomic groups, suggesting that the difference is only of a quantitative nature.

However, apart from knowing our "subjects", for any evolutionary comparison we should clarify the supposed relationship between them. In comparative ethology, as in other biological sciences, such evolutionary comparisons are based on the concept of homology and analogy (or convergence). By homology we mean that there is some detectable evolutionary relationship ("continuity") among these traits - in other words, one trait was presumably the antecedent of the others (in two different species). Analogies always describe the functional value of the traits of two species. In other words, it is supposed that similar ecological constraints may lead to similar behavioural traits in a function, since this enables both species to survive in a given environment. Since in evolution species-specific traits change over time, the detection of homologies is getting more and more difficult. The opposite is true for functional analogies, where a longer time on the evolutionary scale means an increased chance to develop similarity. It should be noted, however, that functional analogy does not mean that the behaviour is served by similar underlying mechanisms. Nobody thinks that the bee dance informing companions about distance and direction of a food source is driven by the same behavioural/neural mechanisms used by humans when transmitting the same information using language. Nevertheless, in a sense bee dance and language can be regarded as functional analogies. The main question therefore is how far one should stretch such a comparison, given that one's interest lies in the underlying mechanisms that govern the behaviour.

In the present case of animal cognition one might suppose that the building blocks of such abilities are strongly tied to the neural characteristics of neurons and are well modelled by the forms of associative learning. The question, then, is whether such similarity at the basic level of neural organisation is enough to warrant a comparison between these distantly related taxa. In other words, what can we gain by such comparative analysis?

Part of my argument against this proposition relies on Bshary et al.'s (2002) observation that in the primate group one could pick many single species that have been shown to have most of the traits investigated. In strong contrast, in fish for many or most cases different species had to be used as the subjects of comparison. Although

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this also might be problematic from a more general point of view of comparative research (the compared taxa are at different levels of the systematic categorisation: "Pisces" are a class; "Primates" are an order), it also suggests that the behavioural mechanisms are tied to neural systems of different structures and levels. To express it more crudely, the primate brain is not only composed of many fish brains stuck to each other but is very likely equipped with additional organisational levels that are needed to synchronise the many cognitive processes that are "confined" to single fish species. Moreover, it is likely that these additional structural organisations contribute to the fact that primate behaviour is regarded as being more flexible.

In my view the comparison of taxa or species that are more similar in their complexity but have a different evolutionary history is of more interest in this respect. For example, our work on dogs (i.e. Miklósi et al. 1998; Topál et al. 1998; Soproni et al. 2001) is one small step in this direction, in which we explore how this domesticated species in a new niche (human social environment) evolves functional behavioural analogies comparable to some traits in humans (see also Csányi 2000).

Although it could be treated as a separate field of interest, communication bears some relation to cognitive abilities in general. Bshary et al. (2002) did not list communication as a trait of comparative interest but it is clear that there are immense differences between the two taxa. In primates functionally referential and intentional communication has been described (e.g. Zuberbühler 2000), and some individuals could even attend to passive (comprehensive) communication with humans based on language sings (Savage-Rumbaugh et al. 1993). In contrast there seems to be little or no learning involved in the production of communicative signals in fish. Nor are there convincing reports on play in fish, an activity that is also supposed to reflect complexity of cognitive abilities.

All this does not suggest, however, that fish should not be used in comparative research. On the contrary, fish could be very useful if one does comparisons within this class. There are many distantly related fish species that live in similar ecological environments. The investigation of such behavioural analogies could lead to a better understanding of evolutionary processes that operate under constraints of the species. In this regard there is even more prospect for comparative fish research on cognition since there are more species at hand for the researchers to compare.

To understand the organisation of functional analogies primates should be compared with species of more similar complexity. Here I see more prospects in research based on comparative investigations of dogs, dolphins, or parrots.

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