2002

'Neuroecologists' are not made of straw

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Letters

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In the October issue of *Trends in Cognitive Sciences*, Bolhuis and Macphail criticized the functional/evolutionary approach to the neural mechanisms of learning and memory, and concluded that the approach is 'often misleading and might provide us with the wrong answers' [1]. Their critique touches on a number of interesting issues, and provides a useful prompt to examine the role of an adaptationist approach to the study of cognition. In their effort to stimulate discussion, however, Bolhuis and Macphail have overstated positions they attribute to 'neuroecologists'.

(1) Bolhuis and Macphail state that 'evolutionary or functional considerations cannot explain the neural mechanisms of behaviour' (pp. 426, 432). Various interpretations of the word 'explain' can cloud this issue. Sherry and Schacter ([2] cited on p. 426) proposed that 'functional incompatibility' might predict the occurrence of distinct memory systems. Their argument is that when different types of memory place distinct functional requirements on biological storage mechanisms, independent storage systems are likely to evolve because no one system can meet the disparate demands. The contrast between the kind of memory that supports the gradual acquisition of habits, and that supporting memory for specific episodes in an animal's life, is offered as one example where functional incompatibility might arise. It is important to be clear that the prediction of the evolution of multiple memory systems is not a prediction about the specific neurobiological mechanisms that would instantiate these systems.

(2) Bolhuis and Macphail imply that *de novo* creation of unique cognitive mechanisms or modules is the only way that adaptive specializations in cognition can occur (p. 426). This is clearly incorrect. It should not be controversial that brain and cognition have evolved, and done so by small steps. Small differences in traits are the very grist of evolution [3]. Thus the application of an adaptive framework will encompass quantitative and qualitative variation. Although most students of cognition hypothesize distinct memory systems, neuroecology does not depend on the existence of entirely distinct memory systems. The neuroecological approach begins by hypothesizing that evolution has shaped cognition, and then tests various subordinate hypotheses about specific instances in which this might have occurred (as in food-storing birds). The success of neuroecology does not rest on the success of particular subordinate hypotheses.

(3) Bolhuis and Macphail 'suppose that memory is a central system that is not domain specific' (p. 427, Box 1). They question the existence of multiple memory systems generally and argue that only perceptual systems, which provide input to *the* central memory system, can adapt to specific information processing needs.

 1364-6613/02/$ – see front matter PII: S1364-6613(00)01821-0

This is a difficult position to defend given the many dissociations of memory systems reported in the literature [4]. Additionally, it should be again emphasized that neuroecology is not tied to particular hypotheses about the specific form of adaptive specializations. However, natural selection may have selectively enhanced or diminished the function of specific memory processes in ways that cannot be accomplished using traditional neurobehavioral approaches [5]. Whether this has occurred, and how many distinct memory systems or processes exist, is an empirical question. It is too early to provide a definitive answer.

(4) Neuroecology is subject to the difficulties inherent to any scientific endeavor. Bolhuis and Macphail seem to regard the fact that specific neuroecological hypotheses have been discarded or refined as a weakness. The suggestion that neuroecology is misguided for this reason is akin to suggesting that physiological analysis of memory is a forlorn effort because of the difficulty in connecting long-term potentiation (LTP) to memory [6]. For example, based on the well-documented finding that the hippocampus is relatively large in food-storing birds, Hampton and Shettleworth tested the simple working hypothesis that food-storing birds would perform better than other birds on cognitive tasks that were impaired by hippocampal damage [5]. They found that sensitivity to hippocampal damage *by itself* did not predict the direction of species differences in each task, and advanced some testable refined hypotheses. It seems reasonable to suspect that the enlargement of the hippocampus in food-storing birds has *some* functional consequence [7]. What that functional consequence is can be revealed only if we do not give up on the effort prematurely because the problem is not easy. The fact that the results of lesion studies and comparative studies do not easily map onto each other in all cases suggests that the comparative approach might indeed provide insights not readily garnered with traditional approaches.

(5) By focusing solely on the relationship between food storing and hippocampal enlargement, Bolhuis and Macphail provide an overly simplistic view of the contribution of the comparative approach to an understanding of brain–behaviour relationships. Neuroecologists are the first to admit that volumetric changes are a crude measure of neural function [5]. They are also well aware that selection for a given neural property is not uniformly the result of a single behavior. For instance, enlargement of the hippocampus has been associated not only with food storing in several families of birds [8,9], but also with migration in garden warblers [10], homing in pigeons [11], and with brood parasitism in cowbirds [12]. There are thus multiple instances of a coincidence between hippocampal enlargement and an increased demand for spatial information processing. Neuroecologists, in the true spirit of evolutionary biology, find such coincidences worthy of investigation.

The criticisms of neuroecology offered by Bolhuis and Macphail create an opportunity to clarify areas in which there is confusion and disagreement, such as in the *kinds* of explanation that can be generated by a given approach, and whether there are distinct memory mechanisms susceptible to species-specific selective pressures. It is certain that neuroecologists will often be misled, hypotheses will be discarded and refined, but the science of neuroecology will stagger forward. As Bolhuis and Macphail suggest, filial imprinting and olfactory learning are excellent systems in which to study the neurobiology of learning and memory. However, alone they are insufficient for addressing questions concerning the evolution of brain and behavior. Neuroecologists believe that the universe of phenomena worth explaining is greater than the universe of immature domestic fowl and inbred mice.

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  PII: S1364-6613(00)01829-5