

experiences. However, most experimental studies of this phenomenon have induced negative emotions in subjects after a learning experience. Work presented at the recent Annual Meeting of the Society for Neuroscience suggests that moderate positive experiences can also improve memory. Nielson and Bryant presented three groups of subjects with word lists to learn. After testing their memory of the words one group were simply thanked, one group were praised and thanked and the third group were given a dollar and thanked. At an unexpected recall test a week later the group who were paid performed better than the other two groups. This suggests that moderate unexpected rewards strengthen memories and, as Nielsen explains, that 'financial reward produces significantly better effects than social reinforcement'. *HJB*

Criminal past influences bird behaviour

Certain cognitive abilities are often considered to be uniquely human, or at least, restricted to primate species. These include 'mental time travel' (using past experience to guide future behaviour) and 'theory of mind' (ascribing beliefs or

intentions to another individual). However, new research suggests that hallmarks of these traits are present in the behaviour of the humble scrub jay [Emery and Clayton, (2001) *Nature* 414, 443–446]. Jays bury their own food for later retrieval and are notorious for stealing each other's food if they see it being buried. Emery and Clayton set out to test whether the birds modify their behaviour to avoid their buried food being stolen. They set up an artificial environment in which jays hid food either in private, or while being watched by another bird. The birds' subsequent behaviour did indeed depend on whether it had been watched, and on whether it had a personal history of stealing. Birds who had stolen food in the past, and who were watched hiding their own food, returned later to hide it in a different place. Birds who were not watched, or who did not have a criminal past, left their food in its original hiding place. Emery reported that, 'we're not saying that scrub jays have the same cognitive abilities as humans, but what they do seem to possess is a close approximation... the projection of their own experience (pilfering) to the intentions of another bird demonstrates many of the hallmarks of theory of mind'. *HJB*

Broca goes ape

Broca's area in human brains is known to play a key role in speech production. Brodmann's area 44, which is part of Broca's area, is larger in the left than in the right hemisphere and until now, this asymmetry has been considered to be a uniquely human trait. But Cantalupo and Hopkins [*Nature* (2001) 414, 505] have now shown that a similar asymmetry exists in mankind's three closest relatives. Studying the brains of bonobos, chimpanzees, and gorillas using MRI, these authors have concluded that all three species have an asymmetry in the area analogous to area 44. As they point out, this might seem puzzling, given the very primitive vocalizations in these apes. However, their observations support a recent theory that the origin of language is not vocal but instead tied to a capacity to imitate and interpret manual gestures. In monkeys, it is precisely area 44 that contains 'mirror neurons', which are active when the animal both performs particular movements, and when it is observing them in others. *MW*

In Brief articles written by
Heidi Johansen-Berg and Mark Wexler.

Letters

'Neuroecologists' are not made of straw

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.

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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Everything in neuroecology makes sense in the light of evolution

Response from Bolhuis and Macphail

We are grateful to Hampton *et al.* [1] for their thoughtful comments on our critique [2]. It is gratifying to see that we seem to have correctly identified a mode of research that can be called 'neuroecology'. We feel that the authors' comments do not detract from the main thrust of our critique. We will reply to their various points in order:

(1) Explanation

We use the word 'explain' in the same way that Shettleworth did [3]. Sherry and Schacter's proposals [4] regarding the evolution of multiple memory systems might provide interesting clues, but by themselves they can of course never give us insight into the mechanisms of memory. This is the essential message of our critique, which Hampton *et al.* seem to have missed – function cannot explain mechanism. That is, functional (or evolutionary) speculation