

Spotlight

Flexible Planning in Ravens?

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Across two different contexts, Kabadayi and Osvath found that ravens preferentially selected items that could be used to obtain future rewards. Do these results demand a rethink of the evolution of flexible planning, or are there leaner alternative explanations for the performance of ravens?

Many complex and highly adaptive human behaviors can only be understood through our capacity to imagine, flexibly plan for, and actively shape future events. It has been proposed that this capacity is unrivaled by any other species and is a key adaptive strategy that enabled humans to fundamentally transform and control ecological niches across the planet [1,2]. Exactly how unique our powers of foresight are, however, is controversial [3]. Evidence for the presence of flexible planning in non-human animals would raise profound questions about the evolution of the capacity and what precisely is distinct about human foresight.

In an apparently breakthrough study, Kabadayi and Osvath [4] recently reported that ravens (*Corvus corax*) can flexibly plan for future events in domains where they have no natural behavioral predispositions (tool use and bartering). If correct, this conclusion would indicate that the capacity must have evolved at least twice in distinct phylogenetic lineages separated by 320 million years of evolutionary history. Over a series of four experiments (E1–E4), five ravens were given the opportunity to select a tool or token that could be used to obtain a

future food reward. The birds selected the correct tool or token significantly more than distractor items in conditions in which the reward became available 15 minutes (E1) or 17 h (E2) later. They also selected the correct item significantly more often than a small food reward (E3–E4), suggesting that they could inhibit a current preference for food so as to obtain a greater amount of food in the future.

Although the birds clearly preferred the appropriate items in these experiments, it is premature to conclude that ravens can flexibly plan. Before the first experiment the ravens learned how to use the functional tool and token to obtain food over five and 35 training trials, respectively, and they also had the opportunity to learn that distractor items were non-functional. All the ravens then selected the trained items on the first experimental trial, even though they had not experienced a predictable return of the reward situation and therefore had no reason to expect a specific future episode in which to use them. Thus, a lean alternative hypothesis is that the learned reward associations simply made the functional items more attractive than the distractors, given that the functional items had been associated with food more than the distractors.

One could test associative explanations, for instance, by pairing distractors and functional tools equally with reward before test, or by visibly destroying the reward apparatus to check if ravens continue to prefer the previously functional tool over the small food reward even when there is no future utility. One could examine flexibility by making the same objects functional in one future context and useless in others. Instead, throughout the studies the ravens were tested for selection of the same objects.

The authors infer flexibility because the ravens selected the target object more when there was an immediate opportunity to use the items (E4) than when there

was not (E3), but this may reflect carry-over effects because these experiments were not counterbalanced. That is, the birds could have learned to choose the functional object more often because of their experience in E3, leading to their increased performance in E4. This could have occurred in two ways: (i) memory-mediated reinforcement [5] during E3, where birds remembered their prior object choice when they were presented with the apparatus 15 minutes later, and paired this memory with the subsequent outcome (functional item leads to reward; small food leads to no reward), or (ii) the association between functional item and reward could have been stronger in E4 as a result of repeated pairing of reward and tool in E3, meaning that the functional object was more attractive in E4 than E3, and was therefore chosen more often. In fact, E3 was the second experiment in the series and occurred before E2 (see supplementary materials of [4]), and the ravens therefore had even more opportunity to learn the association between functional item and reward before E4. One way to test if the behavior of the ravens was truly affected by temporal distance would be to run E3 and E4 twice such that temporal distance does not change in a linear fashion that correlates with experience.

Although the authors suggest that the capacities of ravens parallel those of great apes, it is important to acknowledge that the evidence for animal foresight remains very controversial [3]. Methodological criticisms [1,6] have been leveled at the positive findings they cite [7,8], and other studies have failed to find evidence of even elementary components of planning in great apes, such as preparation for two alternative event outcomes [9] or for two sequential and causally linked events [10]. Thus far animal studies have failed to match the conservative criteria used to demonstrate competence in children [11], namely the use of (i) single trials, to prevent consistent exposure to the same stimulus–reward relationships, and

demonstrate memory of a past problem that can be solved at a particular future occasion; (ii) multiple problems from different domains, to demonstrate flexibility and domain-general competence, (iii) different temporal and spatial contexts for exposure to the problem and the crucial future-directed action, to prevent cuing and demonstrate a capacity to link past and future events; and (iv) novel problems, to preclude the effect of learning histories and necessitate the use of future-directed cognitive processes.

Studies of great apes and other primates are of particular relevance to the evolutionary history of human capacities, and studies of corvids and other phylogenetically distant taxa have potential to shed light on the ecological factors supporting the emergence of shared traits. However, before equating cognitive traits between species and drawing conclusions about homologies and convergent evolution, comparative psychologists must carefully rule out alternative explanations for the observed behaviors.

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Forum

Associative Learning Should Go Deep

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Conditioning, how animals learn to associate two or more events, is one of the most influential paradigms in learning theory. It is nevertheless unclear how current models of associative learning can accommodate complex phenomena without ad hoc representational assumptions. We propose to embrace deep neural networks to negotiate this problem.

Associative learning describes how two or more events (be they stimuli or responses) become associated (Box 1 and Figure 1). This deceptively simple idea is one of the fundamental pillars in the study of learning

and cognition. It has been proven to operate at both behavioural and neural levels, with a wide range of procedures and organisms, and to underlie higher-order cognitive processes (rule learning and concept formation). The rules of association formation may be simple but the world upon which they operate is not necessarily so. We argue that whereas models of associative learning often assume an arbitrary connectionist architecture, using deep networks to learn stimulus representations would allow for biologically plausible, hierarchical representations, better model comparison, and ultimately more accurate predictive models of learning. Although there is an on-going debate on the explanatory power of associative learning theory [1], recent studies on the neural bases of trial and error learning [2], and the role of associative learning in evolutionary biology [3] and social interaction [4] seem to bolster the status of associative learning as one of the cardinal paradigms in behavioural neurosciences. The crux of the controversy nonetheless does not question experimental evidence, of which plenty exists, but whether such evidence is supported by current models within the terms of reference of traditional associative learning theory.

The past decade has seen a surge of increasingly sophisticated computational models of association formation, stemming from both neuroscience and artificial intelligence [5,6]. For instance, reinforcement learning algorithms have been remarkably successful in modelling the role of dopamine in reward learning [7] and are at the heart of cutting-edge

Box 1. A Classical Conditioning Example

When a stimulus is perceived a central representational node becomes active. Pairings of two stimuli engender concurrent activation of their internal nodes. In a typical procedure, a stimulus A is paired with an outcome (O, also known as unconditioned stimulus or reinforcer), a stimulus able to elicit an unconditioned response (UR). A, however, is said to be neutral to that response. With pairings, a link is progressively formed between the stimulus nodes; as a result of which A becomes a conditioned stimulus for the outcome. Thereupon, presentations of A alone will activate the central representation of O, eliciting a conditioned response (CR) (top panel). The strength of the association (w) between A and O increases with the number of pairing trials as the error, that is the difference between the value of the prediction of O by A and the actual value of the occurrence of O, is reduced (bottom panel).