Title
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Permalink
https://escholarship.org/uc/item/9p4925dn

Journal
International Journal of Comparative Psychology, 19(3)

ISSN
0889-3675

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Publication Date
2006-12-31

DOI
10.46867/ijcp.2006.19.03.02

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Peer reviewed

Prospective and Retrospective Learning in Honeybees

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We focus on non-elemental forms of learning in honeybees in order to answer the question of whether retrospective learning can be found in an insect. We analyze three different forms of learning: category learning, rule learning and backward blocking. We provide examples showing that honeybees demonstrate these three forms of learning and propose that causal retrospection underlies them to different extents. We argue that an elemental associative account explains category learning whereas rule learning may require retrospection. Backward blocking, on the other hand, admits interpretations based on prospective learning. Consequently, because animals, including honeybees, solve these three types of problems, distinguishing between species on the basis of these capacities is inappropriate.

Experience-dependent plasticity in animals relies on different forms of associative learning, from elemental to non-elemental ones (Mackintosh, 1994; Pearce, 1997). Such forms of learning allow animals to establish predictions about changes in a complex environment and can therefore be described as *prospective learning*. Prospective learning is considered to be different from *retrospective learning* because they refer, respectively, to the ability to go from causes to effects (prospective learning) and to the ability to go from effects to causes (retrospective learning).

It has been claimed that the very notion of explanation entails retrospective abilities and that only humans are capable of that type of reasoning (Reboul, 2005; Vonk, 2005). It is argued that prospective learning requires extracting predictive relationships between perceptible entities in the world while retrospection allows going beyond the observable and learning about stimuli that are not present. There is a rigorous debate as to whether non-humans animals are capable of causal retrospection (see, for instance, http://www.interdisciplines.org/causality). For instance, the following example, taken from Reboul (2005), compares a dog and a child viewing a rainy day through a glass window, and intends to differentiate between animals and humans based on the distinction between prospective and retrospective reasoning: "Abigaël, the child, is curled in an armchair reading a book; Tolkien, the dog, has sneaked into another armchair and both are casting melancholy eyes at the rain beating on the windows…Abigaël may have a mentalist explanation to the effect that I believe that rain makes one wet and that I don't like to get wet which is why I choose to stay indoors when it rains. This explanation, presumably, is not something that it would make sense to attribute to Tolkien…It seems to me that the difference lies in the fact that Abigaël has an explanation for the association whereas Tolkien is left with the association, naked as it were" (Reboul, 2005).

Here we will focus on experiments on non-elemental forms of learning in honeybees, which will allow discussing whether bees can learn prospectively (A predicts B) and retrospectively (given B, then A occurred). In particular, our objective is to provide experimental evidence as to whether an insect is capable of retrospective learning. We will focus on three different forms of learning: category learning, rule learning and backward blocking. Both category and rule learning imply that subjects learn a predictive relationship between certain stimulus classes, and they then transfer to different, unknown stimuli (recognizing a novel stimulus as a member of a given category or responding to a novel stimulus based on a given rule; see Pearce, 1997, and below). Therefore it could be agued that this ability requires more than simple associative learning and that in order to extract either the category or the rule that has to be learned, the subjects need to build retrospective explanations. Backward blocking, on the other hand, presupposes retrospective learning about a given stimulus that is no longer present. In a typical backward blocking experiment (e.g., Shanks, 1985), a subject is trained with a reinforced compound stimulus AB (henceforth AB+) in a first phase, and then with A reinforced (A+) in a second phase. If backward blocking occurs, the effects of B in a third test phase are reduced due to prior experience with A (in the second phase) because A alone is sufficient to predict the outcome of AB.

We propose that it is not the case that retrospection underlies all of these three forms of learning to the same extent and can be used to distinguish between humans and non-humans. We argue, firstly, that different forms of cognitive processing underlie category and rule learning and backward blocking, despite certain experimental commonalities. Although a pure elemental associative account can explain categorization performances, rule learning may require a different explanation. Furthermore, backward blocking admits alternative interpretations based on prospective learning (see below). Secondly, because animals including honeybees learn these three problem types, distinguishing between species on this basis is inappropriate.

Category Learning in Honeybees: Is Retrospective Learning Required?

Categorization refers to the classification of perceptual input into defined functional groups (Harnard, 1987). It can be defined as the ability to group distinguishable objects or events on the basis of a common attribute or set of attributes, and, therefore, to respond similarly to them (Delius, Jitsumori, & Siemann, 2000; Troje, Huber, Loidolt, Aust, & Fieder, 1999; Zentall, Galizio, & Critchfield, 2002). Categorization deals, therefore, with the extraction of these defining attributes from objects in the animal's environment. Our use of the term categorization will be restricted to those cases in which animals transfer their learned behavior to novel stimuli that share common features with known stimuli. Recently, the question of whether an insect can categorize visual objects in its environment has been answered affirmatively (Giurfa, Eichmann, & Menzel, 1996). Although this capacity in insect may be surprising, the fact that categorization obeys simple associative rules should demystify this ability.

The honeybee is a good model for addressing questions of visual categorization because of its remarkable ability for learning and memorizing visual stimuli

(Giurfa, 2003; Menzel & Giurfa, 2001). Bees can be easily trained to fly toward a visual target on which a sucrose solution reward is delivered. The associations created in this context link the visual stimuli and the reward, as well as the animal's response (i.e., landing) and the reward. Using this basic paradigm and modifications of it, several studies have demonstrated the visual categorization abilities of honeybees trained to discriminate different patterns and shapes. As noted above, such demonstrations require that the bees transfer their learned responses to novel stimuli belonging to the same (i.e., trained) category.

This type of transfer has been demonstrated for a variety of visual features. For instance, van Hateren, Srinivasan, and Wait (1990) trained bees to discriminate two given gratings presented vertically and differently oriented (e.g. 45° vs. 135°) by rewarding just one of the gratings with sucrose solution (Figure 1). Despite the difference in pattern quality, all the rewarded patterns had the same edge orientation and all the non-rewarded patterns also had a common orientation that was perpendicular to the rewarded one. In these tests, the bees had to extract and learn the
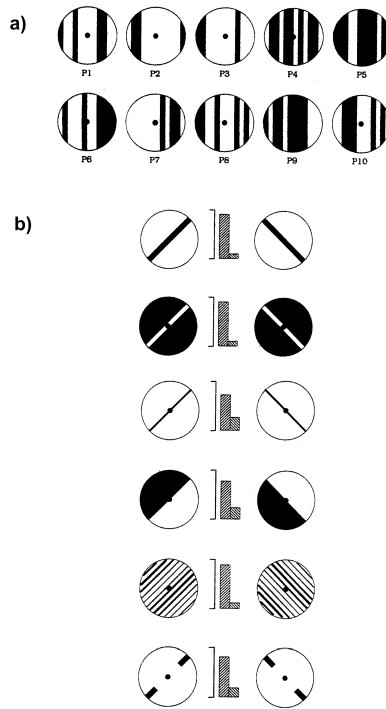
Figure 1. Categorization of edge orientation by honeybees. *(a)* Training stimuli (P1 to P10) used in van Hateren et al.'s experiments (1990). Pairs of stimuli were presented in a random succession to the bees. Within each pair, one was oriented at 45° and the other at 135°. In this case, gratings oriented at 45° were rewarded with sucrose solution while those at 135° were non-rewarded. *(b)* Tests performed with stimulus pairs not used during the training. In each case, there was a significant preference for the pattern presenting the orientation rewarded during the training. Bars indicate the proportion of choices for each stimulus. Bees transferred their choice from the known to the novel patterns and classified them according to their orientation (from van Hateren et al., 1990).

common orientation of all the rewarded patterns to solve the task, and they could apply this knowledge to novel patterns. These results led to a model of orientation detection, based on the existence of three types of orientation detectors, each with defined, preferred orientations (Srinivasan, Zhang, & Witney, 1994), analogous to those in the mammalian visual cortex (Hubel & Wiesel, 1962). Such detectors were found later by means of electrophysiological recordings in the visual areas of the bee brain (Yang & Maddess, 1997).

Recently, the demonstration that bees can categorize visual stimuli based on orientation has been expanded to show that different coexisting orientations can be considered simultaneously and integrated in a global stimulus representation that is the basis for the category (Stach, Benard & Giurfa, 2004). Thus, besides being able to focus on a single orientation, honeybees were shown to assemble different features to build a generic pattern representation which could be used to respond appropriately to novel stimuli sharing the basic layout (Stach et al., 2004). Honeybees trained with a series of complex patterns sharing a common layout comprising four edge orientations simultaneously remembered those orientations in their appropriate positions, and transferred their response to novel stimuli that preserved the learned layout (Figure 2). Honeybees also transferred their learning to patterns with fewer correct orientations depending on the degree to which the novel stimulus matched the original layout. These results showed that honeybees extracted regularities in their visual environment and established correspondences among correlated features such that they generated a large set of object descriptions from a finite set of elements.

Consequently, because honeybees' learned behaviors are consistent with the definition of visual categorization, the ability is not restricted to certain vertebrates. In our opinion, this type of categorization does not reflect any retrospective analysis of events; rather, it results from simple associative learning. To explain this view, the neural mechanisms underlying categorization in the honeybee need to be considered.

If we admit that visual stimuli are categorized on the basis of specific features such as orientation, the neural implementation of category recognition could be relatively simple. The feature(s) allowing stimulus classification could activate orientation-specific neuronal detectors in the optic lobes (the visual areas of the bee brain; e.g., Yang & Maddess, 1997; also see above). Consequently, responding to grating orientation would be trivial since they would activate the same set of orientation detectors despite their structural differences. In category learning, however, the activation of an additional neural element would be needed. The activity of such an element would be both necessary and sufficient to represent the reward and would be integrated with the activity of the visual feature detectors in order to assign value (or valence) to their activity. This kind of neuron has been found in the honeybee brain related to olfactory learning. The neuron, VUMmx1, receives its name from its location in the bee's brain ("ventral unpaired median neuron of the maxillary neuromere 1"). The dendrites of VUMmx1 arborize symmetrically in the brain and converge with the olfactory pathway at different sites (Hammer, 1993).The essential property of VUMmx1 is that it responds to sucrose solution delivered both at the antennae and the proboscis of the bee with long lasting spike activity (Hammer, 1993). Furthermore, the activity of this neuron apparently con-

stitutes the neuronal representation of reward in the case of olfactory learning as shown by the fact that bees learn to associate an olfactory stimulus that is paired with an artificial depolarization of VUMmx1 rather than an actual sucrose reward (Hammer, 1993). Other VUM neurons with unknown functions are also present in the bee brain. It could be conceived that one or more of them underpin reinforcement in associative visual learning. Category learning would then be the result of progressive reinforcement (through Hebbian rules, for instance) of an associative neural circuit relating visual-coding and reinforcement-coding neurons, similar to that underlying simple associative (e.g., Pavlovian) conditioning. Consequently, even if viewed as a higher-order cognitive performance, categorization may simply rely on elemental links between conditioned and unconditioned stimuli and be based on prospective/predictive learning rather than on retrospection.
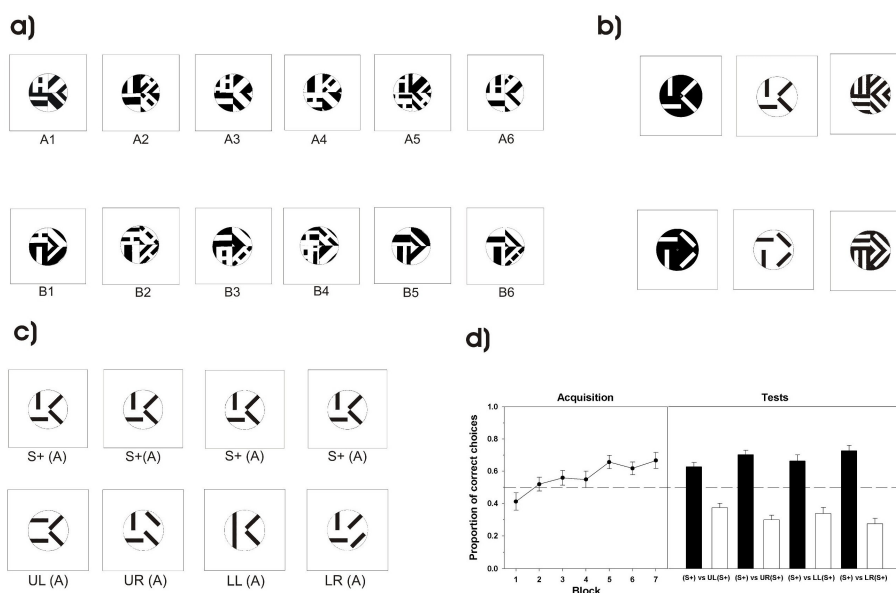
Figure 2. Categorization based on sets of multiple features. *(a)* Training stimuli. A patterns (A1 to A6) differed from each other but shared a common layout defined by the spatial arrangement of orientations in the four quadrants. B patterns (B1 to B6) shared a common layout perpendicular to that of A patterns. *(b)* Test stimuli. Bees transferred appropriately their choice to these novel, non rewarded patterns preserving the basic layout of the trained ones. *(c)* Test stimuli used to determine whether bees extract or not the simplified layout of four bars from the rewarded A patterns. The four test pairs shown correspond to the honeybees trained with A patterns. Equivalent tests were performed with the honeybees trained with B patterns (not shown). S+, simplified layout of the rewarded training patterns; UL, upper-left bar rotated; UR, upper-right bar rotated; LL, lower-left bar rotated; LR, lower-right bar rotated. *(d)* Left panel: acquisition curve showing the pooled performance of bees rewarded on A and B patterns. The proportion of correct choices along seven blocks of six consecutive visits is shown. Bees learned to discriminate the rewarding patterns (A or B) used for the training *(a)* and improved significantly their correct choices along training. Right panel: proportion of correct choices in the tests with the novel patterns. Bees always preferred the simplified layout of the training patterns previously rewarded (S+) to any variant in which one bar was rotated, thus showing that they were using the four bars in their appropriate spatial locations and orientations (from Stach et al., 2004).

Rule Learning in Honeybees: Is retrospective Learning Required?

Like categorization, rule learning also presupposes positive transfer of an appropriate response from a known to a novel set of stimuli. However, despite this common experimental basis, we maintain that these processes do not rely on common mechanisms. In rule learning, the animal does not base its choice on any perceptual similarity between the novel and the known stimuli but rather on properties that transcend the training stimuli such as "*larger than*" or "*on top of*" that may apply to stimuli which do not share any common feature, per se. We propose that simple, elemental associative links cannot account for success in this type of rule learning and that retrospection may be necessary to solve this kind of problem.

An example of rule learning is the learning of the so-called principles of "sameness" and "difference." These rules are usually uncovered through the delayed matching to sample (DMTS) and the delayed non-matching to sample (DNMTS) experiments, respectively. In DMTS, animals are presented with a sample and then with a set of stimuli, one of which is identical to the sample and is reinforced. Because the sample is being changed regularly, the subjects have to learn the sameness rule "*always choose what is shown to you (the sample), independently of what is shown to you.*" In DNMTS, the animal has to learn the opposite, i.e., to choose the stimulus that is different from the sample previously shown. The interesting point concerning these protocols is that predictive analysis based on stimulus or feature generalization does not necessarily hold as the rule is ideally independent of the physical nature of the stimuli used. To discover the rule, the animal has to operate on the set of examples known such that retrospection and different forms of heuristics can be applied to solve the problem. Neural accounts based on simple associative networks such as that proposed for visual categorization (as explained above) may not be valid in this case. Although reinforcement can still be represented by a specific neural pathway or element (such as the VUMx1 neuron or its equivalents), the novel, differing sample (e.g., a color) will not activate the same network components responding to a previous sample (e.g., an odor). Extracting the rule in a changing learning set means, therefore, going beyond stimulus modality and performing a form of retrospection based on the problem faced.

Honeybees foraging in a Y-maze (Figure 3) learn to solve both DMTS and DNMTS tasks (Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001). For example, if bees are trained in a DMTS problem in which they are presented with a changing non-rewarded sample (i.e., one of two different color disks) at the entrance of a maze and are rewarded only if they chose the stimulus identical to the sample, they will learn and apply this sameness rule to transfer tests using gratings. Similarly, bees can transfer sameness rules from gratings to colors (Figure 3). Transfer is not limited to different kinds of modalities (pattern vs. color) within the visual domain but can also operate between very different domains such as olfaction and vision (Giurfa et al., 2001). Furthermore, bees can also master a DNMTS task, showing that they can learn the principle of difference between stimuli (Giurfa et al., 2001). In both DMTS and DNMTS, win-stay/lose-shift (or win-shift/lose-stay) strategies can not account for the performances of the bees. These results demonstrate that bees can learn rules that describe relationships between stimuli in their environ-

ment. The capacity of honeybees to solve DMTS tasks has been verified in other contexts (e.g., Zhang, Srinivasan, Zhu, & Wong, 2004; Zhang, Bock, Si, Tautz, & Srinivasan, 2005). In particular, introducing longer delays between the offset of the sample and the onset of the comparison stimuli yielded a decay in matching performances which suggests that honeybees retrospectively code the samples in delayed matching-to-sample tasks (Zhang et al., 2005).

Retrospective Revaluation in Honeybees

Associative learning theories account for causal and predictive learning but cannot account for retrospective learning because associations can only occur when the stimuli are present. As noted in the Introduction, the case of *backward blocking* (Shanks, 1985) is interesting in that it implies training an animal with a compound reinforced stimulus (AB+) in a first phase, and then with reinforced A (A+) in a second phase. If backward blocking occurs, the effects of B in a third test phase are reduced (retrospectively) by the subject's experience with A in the second phase.

Backward blocking has been recently studied in free-flying honeybees trained to collect sucrose solution from grey targets labeled with two different odors, peppermint and geraniol (henceforth A and B; Blaser, Couvillon & Bitterman, 2004). Bees trained with AB+ and then with A+ showed reduced responding to B in a subsequent test phase, which shows backward blocking. It was also shown that responding to B after AB+ training was less in animals that also had A+ training than in control animals that were equally often reinforced in the absence of A. Furthermore, in an experiment in which an odor C (hexanol) was introduced, responding to B was less after AB+ followed by differential training A+C- than after AB+ followed by C+A- training. In the first case (AB+, A+C-), retrospective revaluation would decrease the value of B as A is a reliable cause or predictor of the outcome during the compound training. In the second case (AB+, A-C+), retrospective revaluation would have the opposite effect, i.e., it would enhance the value of B as a reliable cause or predictor of the outcome during the compound training.

Caution is nevertheless needed when analyzing these data in the light of a possible dichotomy between prospective and retrospective learning. Firstly, Blaser, Couvillon, and Bitterman (2004) trained bees with both a backward blocking and a forward blocking design (e.g. A+ in the first phase, AB+ in the second phase and test of B in the third phase). Their results were similar in both cases and they concluded that the effect of experience with A+ on the response to B after AB+ training seems, at least in honeybees, to be largely independent of the sequence of the A+ and AB+ trials. Secondly, it is worth mentioning that associative, prospective accounts have been provided to explain retrospective revaluation. For instance, Van Hamme and Wasserman (1994) suggested that when A and B are paired with
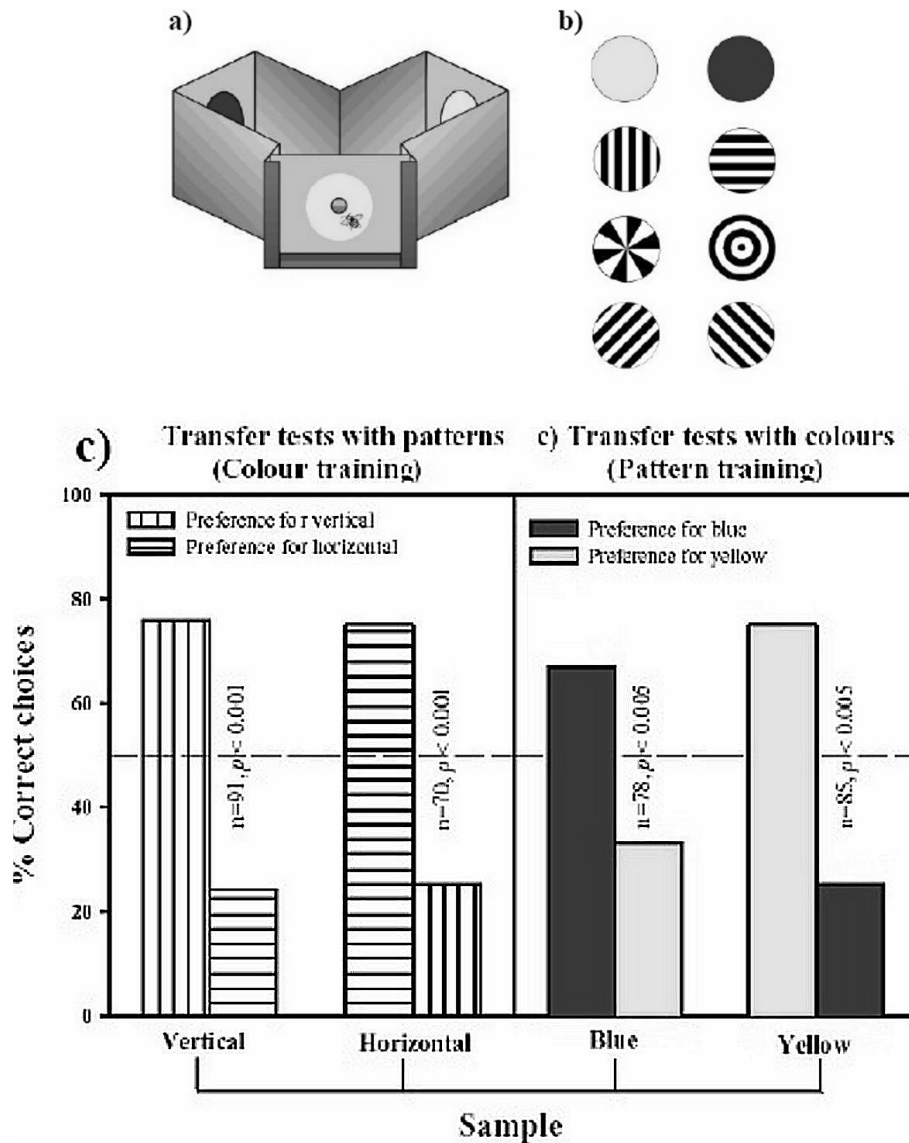
Figure 3. Bees were trained in a delayed matching-to-sample procedure to study whether they could build a concept of sameness between stimuli, independently of the stimuli used. In such a task, animals were presented with a sample and then with a set of stimuli, one of which was identical to the sample. The animals had to learn to choose always that stimulus that was identical to the sample despite the fact that the sample was being changed regularly. *(a)* Y-maze used for training and testing the bees. The sample was presented at the entrance of the maze and bees passed through it without being rewarded on it. The bee was rewarded with sucrose solution if it chose the stimulus presented on the back walls of the maze that was identical to the sample. *(b)* Visual stimuli used for training and testing the bees. Bees were trained with colored disks or with achromatic patterns; bees trained with colors were then tested with patterns and vice versa in transfer tests. *(c)* Performance of the bees in the transfer tests; in both cases bees solved the problem and chose the novel stimulus corresponding to that of the sample at the maze entrance (from Giurfa et al., 2001).

the outcome in Phase 1, a within-compound association is formed between them, which then allows the presentation of A in Phase 2 to activate the representation of B. The predictive strength of an expected but absent cue decreases. Therefore, when A alone is followed by the outcome in Phase 2, the associative strength for A increases while the associative strength for the absent cue B simultaneously decreases. In this case, the proposed distinction between associative learning, which allows extracting predictive relationships between perceptible stimuli in the world, and causal learning, which allows learning about stimuli that are not present, may not be so straightforward.

Conclusions

Although honeybees exhibit simple forms of associative learning, they also learn non-elemental problems for which simple associative accounts are not straightforward (Giurfa, 2003). Bees operate on associations between events in their environment in order to extract rules and retrospectively evaluate stimuli and their outcomes. Therefore it seems that bees have expectations based on associative, predictive learning but that such learning is not the whole of honeybee cognition (Giurfa, 2003).

The extent to which different forms of learning depend on retrospection learning needs to be studied in a deeper way using an across-species comparative approach. Clearly, research articulated on categorization and rule learning may be useful to distinguish between different levels of complexity of cognitive processing but not to determine what is or is not unique to humans. Backward learning, on the other hand, may not be useful to assess retrospection as long as its mechanistic basis has not been determined and prospective explanations based on elemental associative theories cannot be excluded. Debates on differences between humans and non-humans are certainly useful but species differentiation cannot be made based on the ability to solve non-elemental problems or employ retrospective learning.

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