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Coding of stimuli by animals: Retrospection, propection, episodic memory and future planning

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ABSTRACT

When animals code stimuli for later retrieval they can either code them in terms of the stimulus presented (as a retrospective memory) or in terms of the response or outcome anticipated (as a prospective memory). Although retrospective memory is typically assumed (as in the form of a memory trace), evidence of prospective coding has been found when response intentions and outcomes are particularly salient. At a more abstract level is the question of whether animals are able figuratively to travel back in time to recover memories of past events (episodic memory) and forward in time to predict future events (future planning). Although what would constitute adequate evidence of episodic memory and future planning is controversial, preliminary evidence suggests that animals may be capable of both forms of subjective time travel.

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When animals use past experiences to make current decisions, the memory is sometimes referred to as retrospective. If they use those past experiences to anticipate future responses, it is often called prospective memory. A distinction between retrospective and prospective memory can be made in principle by asking, when animals are required to delay a response, what do they remember during the retention interval. Do they remember the characteristics of the preceding event, retrospectively, or do they remember what response they will make at the end of the retention interval, prospectively? This question, first clearly articulated by **Honig and Thompson (1982)**, has important implications for the nature of coding processes in animal memory. Specifically, if animals have the capacity to encode prospectively it suggests that they have the ability to represent future events.

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Retrospective versus prospective memory

Pavlovian conditioning

The simplest case of the anticipation of future events is Pavlovian conditioning. In Pavlovian conditioning, when a neutral stimulus (a conditioned stimulus, CS) is paired with a biologically important event (an unconditioned stimulus, US) that produces an unconditioned response (UR), one often sees evidence of the anticipation of the US in the form of a response (a conditioned response, CR) made to the CS. Although Pavlovian conditioning has often been thought of as a process involving simple reflexive responses, and thus having few cognitive implications, recent evidence suggests that the nature of what is learned can be quite complex (see e.g., Miller & Matzel, 1988). Nevertheless, the response measure used in Pavlovian conditioning is typically a reflexive response similar to that produced by the US. Better evidence for a prospective memory process would be obtained if a future event could serve as a cue for an instrumental choice response.

Simple versus conditional delayed discriminations

Honig and Wasserman (1981) tested pigeons for prospective memory using an instrumental go/no-go procedure. They trained one group of pigeons on a delayed conditional discrimination (or successive matching task) in which an initial stimulus (or sample) indicated which terminal stimulus (or comparison) would be followed by food. Thus, a red or green sample stimulus indicated whether pecking the single stimulus that followed (vertical or horizontal lines) would be reinforced. If the sample was red, then pecking the vertical lines but not the horizontal lines would be reinforced. If the sample was green, then pecking the horizontal lines but not the vertical lines would be reinforced.

A second group of pigeons was trained on a delayed simple discrimination involving the same stimuli but the contingencies of reinforcement were different. In the delayed simple discrimination, the same red or green sample stimulus was presented at the start of each trial but it indicated whether reinforcement would follow or not (independent of the stimulus that followed the color). Thus, for example a red sample indicated that pecking either line orientation would be reinforced, whereas a green sample indicated that pecking neither line orientation would be reinforced.

Honig and Wasserman (1981) argued that once the tasks had been well acquired and a delay was introduced between the hue sample and the line-orientation comparison stimulus, if the pigeons were remembering the samples during the delay (i.e., they were coding the samples retrospectively) the retention functions for pigeons performing the delayed conditional discrimination and those performing the delayed simple discrimination should look quite similar. That is, memory for the samples should decline similarly with increasing delay. On the other hand, if the pigeons were remembering a response intention—what they were going to do at the end of the retention interval (i.e., they were coding the comparisons prospectively) then the task for the pigeons performing the delayed simple discrimination should be easier (a decision to peck or not peck) than for pigeons performing the delayed conditional discrimination (e.g., a decision to peck if the comparison stimulus was vertical lines but to refrain from pecking if it was horizontal lines).

Honig and Wasserman (1981) found that the retention functions for the pigeons that had acquired the delayed simple discrimination were quite shallow, whereas those for the pigeons that had acquired the delayed conditional discrimination declined more rapidly with increasing delay (see Fig. 1), and they concluded that the pigeons were prospectively coding their response intentions.

However, Urcuioli and Zentall (1992) noted that the difference between the delayed conditional discrimination and the delayed simple discrimination involved more than a difference in response intentions. In the case of the delayed simple discrimination, the pigeons could not only develop an intention to peck or refrain from pecking, they could also develop an expectation of getting fed if the sample was red and of not getting fed if the sample was green. During acquisition, the pigeons may have learned that if they expected to get fed they should peck and if they expected not to get fed they should refrain from pecking. Thus, the fact that there were differential outcomes associated with the two samples may have mediated responding to the comparison stimuli.

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