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Spatial midsession reversal learning in rats: Effects of egocentric Cue use and memory

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ABSTRACT

The midsession reversal task has been used to investigate behavioral flexibility and cue use in non-human animals, with results indicating differences in the degree of control by environmental cues across species. For example, time-based control has been found in rats only when tested in a T-maze apparatus and under specific conditions in which position and orientation (i.e., egocentric) cues during the intertrial interval could not be used to aid performance. Other research in an operant setting has shown that rats often produce minimal errors around the reversal location, demonstrating response patterns similar to patterns exhibited by humans and primates in this task. The current study aimed to reduce, but not eliminate, the ability for rats to utilize egocentric cues by placing the response levers on the opposite wall of the chamber in relation to the pellet dispenser. Results showed that rats made minimal errors prior to the reversal, suggesting time-based cues were not controlling responses, and that they switched to the second correct stimulus within a few trials after the reversal event. Video recordings also revealed highly structured patterns of behavior by the majority of rats, which often differed depending on which response was reinforced. We interpret these findings as evidence that rats are adept at utilizing their own egocentric cues and that these cues, along with memory for the recent response-reinforcement contingencies, aid in maximizing reinforcement over the session.

Spatial midsession reversal learning in Rats: Effects of Egocentric Cue Use and Memory

In order to navigate effectively in an environment, such as in a foraging situation, animals must often learn to use multiple cues to guide behavioral patterns and track reinforcers (Cowie and Davison, 2016; Cowie et al., 2016; Rayburn-Reeves and Cook, 2016). When environmental contingencies change, particularly when they change in predictable or consistent ways, there are often multiple sources of information available both within and outside of the organism to aid in it adaptively responding to these changes (Cowie and Davison, 2016; Cowie et al., 2016). This ability requires attention to relevant sources of information, such as those that predict future reinforcement (Mackintosh, 1975). It also requires the ability to inhibit previous behavior that is no longer profitable and to develop new behavioral patterns by learning new associations in response to changing environmental contingencies. This latter ability requires behavioral or cognitive flexibility, which allows the animal to adjust its behavioral output in response to environmental feedback (Bond et al., 2007; Rayburn-Reeves and Cook, 2016).

The most common method of assessing behavioral flexibility has been to use a serial reversal task in which opposing contingencies between two options repeatedly change over time (Bond et al., 2007). This requires the animal to alter response tendencies toward the stimuli based entirely on feedback provided by recent response-reinforcement contingencies, as the only information that the environmental contingencies have changed is via feedback from recent reinforcement or nonreinforcement. Therefore, in order to adjust quickly to the abrupt change in reinforcement contingencies when a reversal occurs, the animal must be able to retain these recent events in working memory. Arguably the most successful strategy in this task would be to employ a win-stay/lose-shift rule (Levine, 1959; Restle, 1962) based on the animal's memory for the most recent trial, such that responses which are followed by reinforcement should be repeated whereas responses followed by nonreinforcement should produce a shift to the other response option.

A more recent version of a serial reversal task, called midsession reversal, has been used to evaluate both the extent of behavioral flexibility displayed by a given species and the types of cues that appear to mediate the behavioral responses to the two stimuli over the course of a session (See Rayburn-Reeves and Cook, 2016, for a review). In a common midsession reversal procedure, two stimuli that vary along a single dimension (e.g., visual: red vs. green; spatial: left vs. right) are

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presented simultaneously. On each trial, a single response to one stimulus (S1+) is reinforced while a response to the other stimulus (S2−) is not reinforced for the first half of each session (S1+, S2−). At the midpoint of the session, this contingency reverses (S1−, S2+) where responses to the previously correct stimulus are no longer reinforced while responses to the previously incorrect stimulus are reinforced for the remainder of the session. Importantly, the same contingency arrangements are consistent across sessions, with the S1 stimulus always correct for the first half and the S2 stimulus always correct for the last half of each session.

This variation of serial reversal learning increases the number of environmental cues that can be used to predict reinforcement availability over a session due to the consistency with which the reversal occurs within and across sessions. For example, in addition to the information provided by response-reinforcement contingencies from recent trials, the consistent location of the reversal within each session may generate timing or numerical (trial count) estimation information (Roberts and Boisvert, 1998), as well as other internally based information, such as relative amounts of satiety or fatigue. When tested on a spatial midsession reversal task, additional cues in the form of egocentric (self-to-object) cues, which inform the animal of its location relative to stimuli within the environment, may also gain predictive value and discriminative control over behavior (Tamara et al., 2010; Vorhees and Williams, 2014). These potential sources of information also provide relative amounts of predictive value to the animal, depending on the salience, number, and value of other potential cues simultaneously available. This increase in the predictive value of multiple sources of information allows for the assessment of control by these various cues, which may combine to increase, or compete to attenuate, accuracy over the course of the session (Cowie et al., 2016; Davison and Nevin, 1999; Davison and Elliffe, 2010; Rayburn-Reeves and Cook, 2016; Shahan and Podlesnik, 2006).

One of the first midsession reversal tasks tested pigeons for 50 sessions using a simultaneous red/green discrimination where, for example, responses to red and not green were reinforced for the first half of each session and responses to green and not red were reinforced for the last half of each session (Rayburn-Reeves et al., 2011). Across the last ten sessions, pigeons displayed systematic errors near the reversal location that suggested they were being controlled by time-based information for the reversal event and were not using the information afforded by working memory for the most recent response-reinforcement contingency. Further evidence of time-based control over responding in midsession reversal tasks by pigeons has been found repeatedly when they are tested with visual discriminations or with spatial discriminations with ITI durations longer than 1.5 s (McMillan and Roberts, 2012, 2014; Rayburn-Reeves et al., 2013a,b; Rayburn-Reeves and Cook, 2016).

Rayburn-Reeves et al. (2011) found that humans showed a markedly different behavioral pattern when tested on the midsession reversal task. They showed almost no anticipation and almost no perseveration, especially when tested with varying reversal locations across sessions. These results indicated their responses were being guided by the information from the previous trial, indicating use of the win-stay, lose-shift rule and control by recent trial information. Recent research has also found a similar pattern of behavior in rhesus macaques on a visual midsession reversal task, suggesting control by recent response-reinforcement reinforcement contingencies (Rayburn-Reeves et al., 2016). Therefore, humans and rhesus macaques show markedly different patterns of behavior in midsession reversal learning as compared with pigeons, suggesting control by qualitatively different environmental cues in this task.

In an attempt to assess qualitative differences in control by these various environmental cues in pigeons and rats, Rayburn-Reeves et al., (2013a,b) trained both species on a spatial midsession reversal task using left and right white key lights for pigeons and left and right levers for rats. Both species were tested for 50 sessions at 80 trials per session

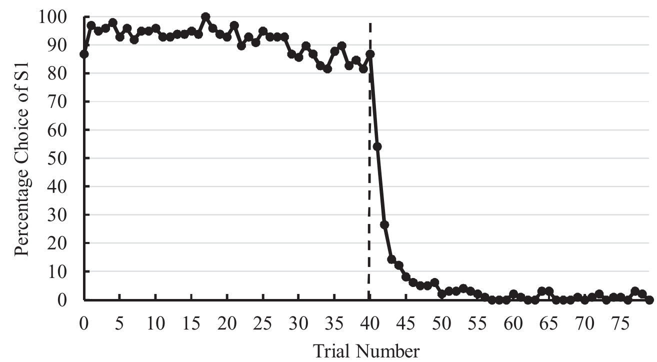

Fig. 1. Percentage choice of the first correct stimulus as a function of trial number averaged across rats for Sessions 31–38. The reversal event is indicated by the vertical dashed line.

and with 5-s ITI durations. Results showed a clear difference between rats and pigeons in the patterns of behavior that emerged during Sessions 11–20 that were sustained throughout training (Rayburn-Reeves et al., 2016, Fig. 1a and b). Pigeons showed the same anticipatory and perseverative errors as was found when they were tested on the visual task (Rayburn-Reeves et al., 2011) which indicated that they were being controlled by time-based information. Rats, however, showed virtually no anticipatory errors and very few perseverative errors, which mirrored the behavior of humans more so than that of pigeons. The lack of errors in anticipation indicated rats were not estimating the time within the session to the reversal, but that their responses were likely being guided by feedback from the most recent trials.

Smith et al. (2015) assessed whether the nature of the response could play a role in performance on the spatial midsession reversal task in rats. The authors argued that lever pressing may afford better use of proprioceptive cues, such as pawedness, to bridge the gap during the ITI, thereby requiring little to no use of memory-based cues. In an attempt to make the task more similar to how pigeons would be required to respond in a spatial midsession reversal task, they trained one group of rats to make nose-poking responses and another to press levers, as in Rayburn-Reeves et al., 2013a,b) study. Results showed that, although the two groups differed in both the rate of learning and in the number of errors produced after the reversal, both showed little evidence of control by time-based cues. Therefore, the nature of the response does not appear to be a major factor in the differences in performance seen by pigeons and rats on spatial midsession reversal tasks.

The finding that rats, humans, and primates differ in the types of cues that guidebehavioral patterns as compared with pigeons revealed an interesting interpretation of the differences between species to use memory for the most recent response-reinforcement contingencies as a predictive cue. McMillan et al., (2014) assessed the effect of visual and spatial information on midsession reversal performance in pigeons and rats. When given a visuo-spatial discrimination where these cues were confounded (e.g., red left, green right), pigeons showed near optimal performance on the task, producing few errors around the reversal location. These cues were then separated in a follow-up study where red and green hues were randomly presented on the left and right keys. Pigeons tested with visual-relevant cues, which required ignoring spatial information, made many anticipatory and perseverative responses, suggesting they were using the time into the session as a predictor of which response to make. In contrast, pigeons transferred to a spatial-relevant task, which required ignoring visual information, showed minimal errors, which were comparable to when both visual and spatial information were relevant. Other research has found similar improvement in pigeon midsession reversal performance when spatial information is relevant and ITI durations are minimal (Laude et al., 2014; McMillan and Roberts, 2012, 2014; Rayburn-Reeves et al., 2013a). The results also contradicted previous research showing little improvement by pigeons when tested on a spatial midsession reversal task with 5-s ITI