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Dynamic cue use in pigeon mid-session reversal

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ABSTRACT

The systematic anticipation and preservation errors produced by pigeons around the reversal point in midsession reversal (MSR) learning experiments suggest that an internal time estimation cue, instead of a more efficient external cue provided by reinforcement, controls behavior over the course of a session. The current experiments examined the role and effectiveness of other external cues in the MSR task. In Experiment 1, providing differential outcomes based on response key location produced fewer errors prior to, but not after, the reversal as compared with a non-differential outcomes condition. Experiment 2a used alternating differentially colored ITIs (*cued* sessions) or dark ITIs (*un-cued sessions*) during each half of the session. The ITI cues improved switch efficiency both prior to and after the reversal. Experiment 2b introduced probe trials around the reversal, testing ITI color cues added to *un-cued* sessions or removed from *cued* sessions. Results showed control by the ITI cues when they were available and control by the time-based cue when they were unavailable. This suggests both cues were being simultaneously processed when available and that the cues could also independently provide sufficient information about future reinforcement. In Experiment 2c, ITI cues were inserted as probe trials in the opposite half of the session (*miscues*). The closer such miscue trials were to the reversal, the more the ITI cues exerted control over behavior. Together, these results indicate that as the utility of internal temporal cues is reduced, the use of external visual cues increases. These results have implications for the way in which cues dynamically shift in controlling behavior over time based on their relative rates of utility, and are discussed in light of an occasion setting perspective.

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Dynamic and complex environments often contain multiple cues that could provide relevant information about biologically significant outcomes. Depending on the particular situation, these cues can independently or jointly provide information about which behaviors might lead to profitable outcomes. When multiple cues are relevant, the extent to which a single cue comes to exert control over behavior depends on a number of factors, such as its saliency, relative utility, history, and redundancy with other available cues. Understanding how various cues come to control behavior at any moment and how this might change over time has been and continues to be an essential element to understanding adaptive behaviors across different species.

Recently, a novel reversal task has been developed that has provided new insight into the cues controlling the sequential and temporal organization of behavior (Rayburn-Reeves and Cook, 2016). In this mid-session reversal (MSR) task, a single discrimination reversal consistently occurs at the midpoint of each session. Thus, responses to one stimulus or contingency are reinforced for the first half of a session, whereas responses to a different stimulus or contingency are reinforced for the second half of the session (Cook and Rosen, 2010; Rayburn-Reeves et al., 2011). Pigeons trained in this task learn to accurately discriminate each of the competing task contingencies. Averaging their data over sessions reveals that pigeons gradually transition from performing the first discrimination to the second discrimination around the session midpoint. This *switching function* reflects how the predictable reversal at each session's midpoint allows the pigeons to learn to respond appropriately during both portions of a session.

The MSR task appears to have two distinct types of cues. The first type is consistent with the traditional meaning of *discriminative cues*. These are the visual stimuli available to the animal during a trial (e.g., red and green key lights) that directly receive choice behaviors and lead to rewarded outcomes as required by simple or conditional contingences. The second type of cue can be thought of as the *switching cue*. This switching cue is a conditional, context-like cue that indicates which discriminative cue(s) the pigeon should differentially select over the course of the session. This switching cue in MSR could be based on estimating the elapsed time within the session (or a count of trials completed) as they can reliably predict when the reversal will occur and when to switch responding. Thus, much like a first-order occasion setter in an associative context (Arnold et al., 1991; Holland, 1992), this switching cue may help to modulate between different competing behaviors to the same discriminative stimuli, although in a temporal or sequential context.

The general finding in the MSR task, at least for pigeons, indicates that the passage of time is the most salient switching cue in controlling response shifts across the session (Cook and Rosen, 2010; McMillan and Roberts, 2012; Rayburn-Reeves et al., 2011). In order to use estimated time as a temporal switching cue, the pigeons must be able to track the time elapsed within the session. The use of elapsed time as a discriminative cue (i.e., interval timing) has been well documented in a number of non-human animal species in operant settings (Buhusi and Meck, 2005; Cheng and Miceli, 1996; Church, 2006; Higa and Staddon, 1997; Staddon and Higa, 1999). Compelling evidence for use of elapsed time as the switching cue for pigeons has come from direct manipulations of time within and across sessions. For example, Cook and Rosen (2010) found that inserting an empty temporal gap of different durations into the middle of the first half of a session resulted in systematic shifts in the onset of subsequent oddity-based behaviors. Additional support for the use of a timing cue in MSR has also been provided by post-acquisition manipulations of the inter-trial interval (McMillan and Roberts, 2012).

An additional alternative cue that is also consistently available in MSR tasks is recent reinforcement history. Given that the task has only one discriminative reversal with the contingencies in a fixed order (e.g., S1+/S2− for the first half, S1−/S2+ for the second half), reinforcement from recent responses can provide sufficiently useful information. Humans, for example, seem to rely entirely on reinforcement cues, responding correctly on every trial except the first reversal trial; behavior indicative of a win-stay/lose-shift rule (Cook and Rosen, 2010; Levine, 1975; Rayburn-Reeves et al., 2011; Restle, 1962). The same appears to be true for rats (Rayburn-Reeves et al., 2013b) and capuchin monkeys (Rayburn-Reeves et al., in prep); when tested under comparable experimental conditions. Curiously, these reinforcement cues appear to be regularly overshadowed by the interval timing cue in pigeons, as well as sometimes in rats (McMillan et al., 2014) and dogs (Laude et al., 2016). This difference suggests that the saliency of time as compared with the saliency of memory for recent response-reinforcement associations may differ importantly across species when organizing competing behaviors over the course of a session.

Whether a given cue exerts control over behavior is dependent on a number of factors beyond saliency, such as the complexity of the situation, the availability of other cues, and their relative utility (McMillan and Roberts, 2013). *Relative utility*, or the degree to which different cues reliably predict outcomes, lies at the heart of cue competition studies. Again primarily in associative settings, the competition among different cues has been extensively studied (Blaisdell et al., 1998; Rescorla and Wagner, 1972). As extended

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