



Original Articles

Cognitive flexibility and memory in pigeons, human children, and adults

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ABSTRACT

This work examines cognitive flexibility using a comparative approach. Pigeons (Experiment 1), human children (Experiment 2a), and human adults (Experiment 2b) performed a task that required changing responses to the same stimuli twice across the experiment. The results indicate that all three groups demonstrated robust memory for learned information. In addition, pigeons showed comparable and substantial perseveration following both response shifts. In contrast, both children and adults exhibited some perseveration following a first response shift, while exhibiting no cost following the second response shift. These findings are discussed in relation to memory-based theories of cognitive flexibility, according to which perseveration occurs as a result of competition between long-term and working memory, revealing important differences in memory and cognitive flexibility between species.

1. Introduction

Cognitive flexibility is an important aspect of executive function that may be defined as the ability to efficiently adapt to changing task demands. As the environment, needs, and goals change frequently for both non-human animals and humans, cognitive flexibility is often critical for survival. The current work examines one form of cognitive flexibility – changing responses to the same stimuli – using a comparative approach. Specifically, we examined the role of memory in this process in pigeons as well as human children and adults.

One aspect of cognitive flexibility is responding differently to the same stimuli, depending on the current situation. For example, the Wisconsin Card Sorting Test (Berg, 1948) provides a measure of cognitive flexibility by requiring participants to learn to sort cards by different dimensions (i.e., shape, color, or number) based on feedback. Crucially, the sorting rule periodically changes without warning, such that participants must learn to switch responses to the same stimuli based on shifting rules. This task is commonly used as a clinical measure of frontal lobe functioning; patients with frontal lobe damage have greater difficulty shifting between sorting rules (Robinson, Heaton, Lehman, & Stilson, 1980).

Variants of this task are commonly used to investigate the development of flexibility. For example, in the Dimension Change Card Sort (DCCS) task, young children are asked to sort cards according to shape or color (Zelazo, 2006). After a number of trials of sorting cards according to one dimension, children are told to shift and sort by the other

dimension. Three-year-old children have substantial difficulty shifting to the second dimension; they perseverate by continuing to sort by the prior dimension (Zelazo et al., 2003). Five-year-olds, in contrast, succeed at shifting to the new rule in the standard task, but struggle in an advanced version of the task, in which they are required to shift between sorting rules on a trial-by-trial basis conditional on a contextual cue, such as the color of a border surrounding the object (Hongwanishkul, Happaney, Lee, & Zelazo, 2005).

Why does perseveration occur? And what factors account for developmental change? One account stipulates that perseveration occurs due to “attentional inertia” (Kirkham, Cruess, & Diamond, 2003). According to this theory, participants learn to attend to a particular aspect of stimuli, such as shape; perseveration happens when the contingencies change and participants struggle to inhibit the now-irrelevant dimension and shift attention to another, now-relevant dimension. Hence, the primary locus of developmental change is inhibition of established attentional patterns.

An alternative account (Morton & Munakata, 2002) stipulates that perseveration occurs due to competition between latent (or long-term) memory and active (or working) memory. Specifically, participants first learn (over multiple repetitions) a given contingency, which eventually becomes part of their long-term memory. Then, after the shift, the contingencies change, yet the stimuli do not. As a result, these old stimuli re-activate the learned contingencies in long-term memory, thus triggering the learned response. At the same time, the new contingency has to be actively maintained in working memory. This co-existence of

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conflicting memory traces creates competition between the re-activated contingencies and the new contingencies. Any failure to inhibit the old contingency, while maintaining the new one, results in perseveration. Therefore, according to this memory-based account, perseveration stems from young children's working memory limitations (Gathercole, Pickering, Ambridge, & Wearing, 2004); previously learned contingencies overwhelm children's ability to maintain new contingencies in working memory.

The current work attempts to contribute to understanding of cognitive flexibility by using a new task in which participants learn to make different responses to the same stimuli (with no changing dimensions) across different experimental phases. In contrast to dimensional shift tasks (such as the Wisconsin Card Sorting Test or DCCS), shifts in the present task pertain only to the assignment of stimuli to responses, not to the dimensions of stimuli. Therefore, because neither stimuli nor dimensions of interest change across the phases, attention should not differ across the phases. As a result, perseveration on this task would present a challenge to the attentional inertia theory. At the same time, because working and long-term memory traces conflict across the phases, the memory competition theory has a natural way of explaining such perseverations. Specifically, participants would remember the pre-shift stimulus-response mappings, and, when contingencies change, these "old" mappings interfere with the current mappings that need to be maintained in working memory.

To increase the probability of high within-phase learning coupled with response perseveration, we decided to address these issues using a comparative approach. In addition to including human children and adults in the study, we also included pigeons. We did so because avian species (and pigeons in particular) exhibit remarkable learning and memory abilities (Castro & Wasserman, 2016; Emery, 2006; Güntürkün & Bugnyar, 2016; Kirsch, Güntürkün, & Rose, 2008; Wasserman, Brooks, & McMurray, 2015), despite possessing rather limited (compared to humans) working memory capacity (Gibson, Wasserman, & Luck, 2011). Therefore, examining these organisms and comparing their performance to that of human children and adults might prove to be especially informative.

Previous research suggests that pigeons display many cognitive similarities, and some key differences, compared to humans. Pigeons have excellent visual abilities (Gibson, Wasserman, Gosselin, & Schyns, 2005; Levenson, Krupinski, Navarro, & Wasserman, 2015; Watanabe, Sakamoto, & Wakita, 1995) and are able to memorize and categorize a wide range of visual objects (Soto & Wasserman, 2014). For example, Fagot and Cook (2006) found that pigeons could memorize 800–1200 different images associated with different responses learned over a period of 3–5 years. Pigeons are not limited to memorizing individual items; they also show clear evidence of category learning (Lazareva & Wasserman, 2010; Wasserman, 2016) and even relational learning (Wasserman & Young, 2010). In addition, these birds exhibit primacy and recency effects in memory (Wright, Santiago, Sands, Kendrick, & Cook, 1985), as well as episodic-like memory (Zentall, Clement, Bhatt, & Allen, 2001), long-term memory (Cook, Levison, Gillett, & Blaisdell, 2005), and working memory (Diekamp, Kalt, & Güntürkün, 2002).

Although pigeons display impressive memory abilities, there are some critical differences in working memory between pigeons and humans. Perhaps not surprisingly, pigeons have lower working memory capacity than human adults (Gibson et al., 2011). More importantly, these capacity differences may stem from differences in how pigeons and humans bind visual features in visual working memory. In a change detection task (Lazareva & Wasserman, 2016), pigeons were sensitive to the total number of changed *features* rather than the number of changed *objects*, suggesting an absence of feature binding. In contrast, human adults did exhibit evidence of binding: namely, they were as likely to detect change in a single *feature* within a single-feature object as they were to detect change in any of multiple features within a multi-feature object (Vogel, Woodman, & Luck, 2001).

These results suggest that humans may possess object-based

working memory, whereas pigeons' working memory may be feature-based; this disparity may explain the lower working memory capacity in pigeons compared to humans, especially when multi-feature objects are involved. If cognitive flexibility depends on working memory, then pigeons should exhibit substantially poorer cognitive flexibility than humans.

Yet, prior work does suggest that pigeons, at least under some circumstances, can exhibit impressive cognitive flexibility. In one recent study (Castro & Wasserman, 2016), pigeons were trained to categorize sets of multi-item visual stimuli according to two dimensions: numerosity and variability. Impressively, pigeons were able to shift back and forth between these categorization tasks on a trial-by-trial basis, using the same set of stimuli, with only the color of the background indicating which task and response rule should be performed on any given trial.

It should be noted, however, that, because the categorization tasks were presented in an interleaved manner, these pigeons had received extensive training (144 trials per day for 50 days), which resulted in extensive practice *shifting* between tasks from one trial to the next. Therefore, these findings attest more strongly to the impressive ability of pigeons to *learn* to shift from one task to another based on an external contextual stimulus than to their spontaneous (i.e., not requiring training) cognitive flexibility. This kind of training regimen is likely to have established strong long-term memory representations for each stimulus-response contingency, thus obviating the need to maintain the current contingency in working memory. This idea is similar to considerable work in human learning showing that attentional processes which at first must be highly controlled can eventually become automatic through extensive experience (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977).

An earlier study also found evidence of cognitive flexibility in pigeons (Cook & Rosen, 2010); in this study, pigeons were trained in a task-shifting procedure in which it was necessary to change response strategies halfway through each session. Without the support of external discriminative stimuli, pigeons ably learned to shift from a match-to-sample task to an oddity-from-sample task, suggesting that they used temporal cues to flexibly change their behavior. Here too, pigeons were trained over many daily sessions, again suggesting that pigeons can demonstrate flexible task-shifting behavior supported by long-term memories. In contrast, in the current work, we examine *spontaneous* cognitive flexibility when: (1) little training to shift is provided, and (2) long-term memories are likely to compete with new information that must be maintained in working memory.

In addition to pigeons, we also studied 5-year-old human children and adults. We included 5-year-olds because this age group demonstrates flexible task-shifting behavior in the DCCS task reviewed above, although they struggle with an advanced version of the task in which they are required to shift between tasks on the basis of contextual cues differing between trials (Hongwanishkul et al., 2005). Finally, we included adults as a comparison group to examine any developmental differences in humans.

To examine the role of memory in cognitive flexibility, as well as potential species differences in this domain, we used a new variant of a task previously used to measure proactive and retroactive interference in human memory across development (Darby & Sloutsky, 2015a, 2015b). In the original task, participants learned to associate *pairs* of objects with cartoon characters across three phases. In the first phase, participants learned one set of contingencies; in the second phase, a different set of contingencies was learned; and in the third phase, the original set of Phase 1 contingencies was again presented. In the prior version of this task, the second set of object pairs (presented in Phase 2) was a recombination of the same objects that had been presented in Phase 1. This recombination of objects required *new learning* in Phase 2 that was subject to proactive interference and *retrieval of previously learned* information in Phase 3 that was subject to retroactive interference.

In contrast, in the current version of the task (schematically

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