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Executive control and task switching in pigeons

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ABSTRACT

Flexibly adjusting one's behavior depending on the task at hand is a hallmark of executive function. In two experiments, we explored pigeons' cognitive flexibility to concurrently perform two complex categorization tasks: a numerosity discrimination (where number was the relevant dimension and variability was the irrelevant dimension) and a variability discrimination (where variability was the relevant dimension and number was the irrelevant dimension). The flexibility of pigeons' behavior was evidenced by their rapid, on-demand switching between tasks within training sessions. In addition, in Experiment 1, pigeons more accurately performed the numerosity task with arrays of different stimuli than with arrays of same stimuli and they more accurately performed the variability task with arrays of 16 stimuli than with arrays of 6 stimuli. In Experiment 2, when the magnitudes of the relevant and irrelevant dimensions were congruent, pigeons' accuracy was higher than when the magnitudes were incongruent. Thus, the irrelevant dimension facilitated target discrimination performance when its magnitude matched the magnitude of the correct choice. These cross-task interactions suggest that a common computational mechanism underlies both discriminations. Pigeons' cognitive complexity and flexibility—even in the absence of a prefrontal cortex—indicates that other avian brain areas can support behaviors emblematic of executive functioning.

1. Introduction

In 1637, René Descartes famously proposed that human reason is a *universal instrument* that can be adaptively applied in all kinds of problem-solving situations (Wheeler, 2008). Today's researchers still embrace the essence of Descartes' universal instrument, while now invoking the operation of *executive functions* in human abstract thought, flexible problem solving, and attention to relevant task attributes (O'Reilly, 2010).

There has, however, been a profound change in the longstanding belief that only humans possess such executive functions. Researchers currently posit that nonhuman primates too possess a comparable ensemble of executive functions, which control and regulate complex cognitive activities. This change follows from both behavioral and neuroscientific evidence indicating that the prefrontal cortex (PFC)—an area of the brain common to humans and primates—is vitally important for executive functioning (Moore, Schettler, Killiany, Rosene, & Moss, 2009; Stoet & Snyder, 2009).

Birds do not have a brain structure homologous to the PFC; nevertheless, the avian nidopallium caudolaterale (NCL) and the mammalian PFC share several anatomical and physiological features (Güntürkün, 2012). Perhaps if birds were tested under suitably demanding conditions, then they too might exhibit behaviors emblematic of executive functioning (Emery, 2006).

Executive control and executive functioning are rather vague terms that may include a variety of different behaviors. Typical tasks that target human executive function require the individual: to learn abstract rules to guide behavior, to create an attentional set based on those rules, and to switch their attentional set depending on task demands (Banich, 2009). Indeed, flexibly adjusting one's behavior when the prevailing task changes is a hallmark of executive function; this is the aspect that we will investigate, in pigeons, in the current study.

To study cognitive flexibility in nonhuman animals, researchers have used several different paradigms that preserve the essential properties of human tasks. For instance, Stoet and Snyder (2003) had rhesus monkeys concurrently perform two choice tasks: a color discrimination (red vs. green lines) and an orientation discrimination (vertical vs. horizontal lines). The task to be performed was specified at the beginning of each trial by different background colors: yellow (cueing, for example, the color discrimination) or blue (cueing, for example, the orientation discrimination).

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Monkeys readily switched their behavior from one task to another, reaching global accuracy levels over 90%.

Veit and Nieder (2013) explored executive function in carrion crows by using a delayed matching/nonmatching-to-sample task. A sample picture was presented and, after a 2-s delay, two comparison pictures were presented: one the same as and one different from the sample. The match rule required the birds to choose the identical picture, whereas the nonmatch rule required the birds to choose the nonidentical picture. The rule in force was specified during the delay between the sample and the comparison stimuli by different (auditory or visual) cues. Crows reached high accuracy levels (about 90% correct) on both match and nonmatch trials, and they flexibly switched between tasks. Critically, as was true for neurons in primates' PFC (e.g., Bongard & Nieder, 2010; Wallis, Anderson, & Miller, 2001), the response pattern of the neurons in the birds' NCL was significantly different depending on the prevailing task.

Here, we explored the flexibility of pigeons to concurrently perform two complex categorization tasks: a numerosity discrimination and a variability discrimination. These tasks would be said to involve abstract computational capacities if people or nonhuman primates were to perform them (e.g., Beran, 2008; Cantlon, Platt, & Brannon, 2009). Specifically, in the numerosity task, pigeons had to discriminate arrays of pictorial stimuli containing few (6) items vs. arrays containing many (16) items. The birds had to peck the 6-item or the 16-item array depending on the color of the background screen. Several studies have reported that rhesus monkeys can readily solve this task (e.g., Beran, 2007; Cantlon & Brannon, 2005, 2006). In the variability task, pigeons had to discriminate low-variability arrays (containing items that were all the same as one another) vs. high-variability arrays (containing items that were all different from one another) involving the same pool of stimuli used in the numerosity task. The birds had to peck the low-variability or the high-variability array depending on the color of the background screen. Castro, Kennedy, and Wasserman (2010) found that pigeons can readily solve this task (reaching accuracy levels over 90%; see also Castro & Wasserman, 2011; Castro, Wasserman, & Young, 2012). At issue was whether pigeons could flexibly and accurately perform *both* tasks. Note that concurrently learning these two tasks—with different sets of rules in each—is highly demanding, especially when, from the outset, all of the various types of trials were randomly intermixed.

Indeed, in humans, switching between concurrently performed tasks comes with a cost: people in this case are slower and make more errors than when repeating the same task (see Monsell, 2003, for a review). This "switch cost" is said to be the consequence of the time needed to reconfigure the task set (Rogers & Monsell, 1995) or to overcome interference from the prior task (Wylie & Allport, 2000). So, we also examined whether pigeons showed any costs when switching between the numerosity and variability tasks.

On another matter, studies of both humans and nonhuman animals have found that some abstract concepts may be understood as quantitative dimensions; as such, they should be affected by the same factors that affect physical dimensions like size, orientation, and brightness (e.g., Piazza, Izard, Pinel, LeBihan, & Dehaene, 2004). This is true of numerosity. In accord with Weber's Law (1834/1996), the accuracy of humans' and monkeys' numerosity judgments rises as the disparity between the amounts to be compared increases; furthermore, accuracy is systematically affected by the ratio of the numerosity values being compared, so that as the ratio (smaller/larger) decreases, accuracy increases (Cantlon & Brannon, 2006).

Now, consider the 16-item Low-Variability (Low-V, containing items that are all the same) and High-Variability (High-V, containing items that are all different) arrays depicted in Fig. 1. These displays actually represent the endpoints along a continuum of variability or *entropy*. Low-V arrays entail the lowest possible entropy (0.0, all 16 items are the same), whereas High-V arrays entail the highest possible entropy (4.0, all 16 items are different; see Wasserman & Young, 2010, for details on computing entropy). Castro and Wasserman (2011) trained pigeons with multi-item arrays located at the extreme values along this entropy continuum (0.0 vs. 4.0) and later tested them with arrays involving intermediate levels of entropy. As the disparity in entropy between the arrays increased, pigeons' choice accuracy progressively rose. In addition, equivalent disparities in entropy were more discriminable at the lower end of the entropy scale (where there is less variability) and less discriminable at the upper end of the entropy scale (where there is more variability). These results comport with the idea that distinguishing different levels of variability also follows Weber's Law.

Finally, interactions between numerical and temporal judgments have been reported for decades in both humans (Moyer & Landauer, 1967) and nonhuman animals (Church & Meck, 1984). So, too, have interactions between space and number (Adachi, 2014; Dehaene, Bossini, & Giraux, 1993; Drucker & Brannon, 2014), and between time and space (De Long, 1981; Merritt, Casasanto, & Brannon, 2010). These interactions have led authors to hypothesize a single *general magnitude system* that underlies all three domains: space, time, and number (Gallistel & Gelman, 2000; Walsh, 2003). Given the above parallel between numerosity and variability, one might suspect that a common mechanism is involved in each; perhaps variability is yet another *magnitude* that is computed by this general computational system.

If so, then pigeons' concurrent attention to the demands of the numerosity and variability discrimination tasks may "cross over" and affect their performance on the other task. To examine this possibility, we assessed pigeons' numerosity (6 vs. 16) discrimination when the items in the arrays involved low variability and when they involved high variability; plus, we assessed pigeons' variability discrimination (low vs. high) when there were 6 items and when there were 16 items in the arrays. In Experiment 1, the value of the irrelevant dimension was constant for the two arrays (for example, when given the numerosity discrimination, items would display either low or high variability in the two arrays; see Fig. 2). In Experiment 2, both values of the irrelevant dimension were presented on a given trial, so all of the trials included two arrays containing 6 and 16 items, as well as low- and high-variability arrays.

Note that whether the items in the arrays display low or high variability is irrelevant when the pigeons must select the array that contains 6 or 16 items; correspondingly, whether the array contains 6 or 16 items is irrelevant[1] when the pigeons must select the array that contains low or high variability. The birds could ignore the irrelevant attributes or they could be affected by the irrelevant attributes of the displays.

2. Experiment 1

2.1. Method

2.1.1. Subjects

The subjects were four pigeons (*Columba livia*) maintained at 85% of their free-feeding weights. They had earlier served in

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[1] We should mention that, in order to compute the entropy of an array, the number of items in the array is one of the factors that enter the computation. Nonetheless, we consider number to be an irrelevant dimension when the task to be performed is variability because paying attention to the number of items in the arrays is not necessary for the birds to choose the correct response. In that sense, number is irrelevant for the variability discrimination.