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Executive control of perceptual features and
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Abstract

Studies of executive control often reveal significant limitations in nonhuman primate performance relative to that of humans. In the present study, 24 socially-housed baboons were tested on a computerized version of the Wisconsin Card Sorting Task (WCST) to assess individual differences in executive control. In a second experiment, the same baboons completed a version of the WCST with paired-relational stimuli rather than those that varied on a single dimension to evaluate their set-shifting abilities with abstract relations (*same/different*). All baboons completed the required shifts on the traditional WCST, but only 12 baboons succeeded in making relational shifts. Age was found to be a significant factor in the level of success on both tasks with younger baboons (mean age 4 years) outperforming older, albeit not aged, baboons (mean age 11.5 years). These results implicate an earlier decline in executive control processes for nonhuman primates with more pronounced effects for cognitive flexibility of abstract relations.

Keywords: executive function, cognitive flexibility, primate, WCST, abstract relation

Executive control of perceptual features and abstract relations by baboons (*Papio papio*)

Executive control (EC) essential to everyday human behavior is characterized by an ability to maintain focus by screening out distracters as well as an ability to switch that focus from one set of factors to another [1,2]. A conventional test of EC, the Wisconsin Card Sort Test (WCST, [3]), examines the ability of subjects to attend to a shift in reward contingencies based on stimulus dimension. Berg [3] referred to this capacity as *flexibility* in thinking. Today, it is still considered the definitive test of EC [4, 5]. The WSCT assesses this cognitive flexibility, specifically with respect to an ability to maintain and shift cognitive set according to otherwise unpredictable changes in reward contingency [6, 7]. The WCST requires participants to sort cards on the basis of a rule, and subsequently switch to a new rule as the task contingencies periodically change. This presents the dual challenge of learning new and inhibiting old rules.

As a measure of EC, the WCST provides a means by which two critical functions can be evaluated: the capacity to *attend selectively* to one stimulus dimension and inhibit the disruptive influences from other stimulus dimension, as well as the capacity to *switch* response strategies, inhibiting previously rewarded responses. As the subject learns through trial and outcome which of the several stimulus dimensions must be attended to, the capacities of the central executive are taxed. Additionally, when the task contingencies change without overt indication, the shifting component of the subject's central executive is activated and likely challenged.

In the traditional version of the WCST designed to investigate the ease of human response shifting [3], four target cards are placed before the subject. The subject is then requested to match one of 60 response cards based on color or form, deducing the matching principle from the experimenter's verbal feedback on each trial. Number and type of errors are recorded, with perseverative errors providing the most accurate single measure of an inability to shift. Errors due to the selection of a previously correct response exhibit cognitive inflexibility to adjust to the new matching rule, to inhibit previously correct responses, or an inability to recognize that the rule has shifted [8]. Non-perseverative (other) errors not consistent with previously correct responses represent attempts to shift strategies. Thus, low perserverative/non-perseverative ratios are indicative of high EC and inhibition of prepotent responding. Human subjects on this traditional WCST make approximately 15-30 card-sorting errors after a shift in contingency, with about two-thirds of those resulting from perseveration [8, 9].

In clinical settings, the most common employment of the WCST is for patients with known prefrontal cortex (PFC) damage or traumatic brain injury [10, 6], to assess loss of EC consecutive to frontal lobe lesions [11, 6] but requires converging evidence to serve as a direct marker for damage [12, 13]. Patients with frontal lobe damages make a significantly greater ratio of perseverative errors to non-perseverative errors, implicating frontal lobes as important for task performance on the WCST [14, 15]. Further, functional neuroimaging studies conclude that the WCST utilizes networks involving the PFC consistent with activity during other tests of inhibition, set-shifting and more broadly EC [16, 17].

Converging evidence from neuroimaging studies with nonhuman primates implicate similar activations during WCST and other tests of EC. In tests of set-shifting, Passingham [18] demonstrated that rhesus monkeys with lesions of the PFC made more perseverative, as well as total errors, following a shift. Similar effects were reported on PFC lesioned monkeys tested with a computerized task analogous to the WSCT, suggesting a decline in EC [19, 20].

That the PFC is implicated in EC in both human and nonhuman primates on the WCST and other set-shifting tasks further validates the test, as well as an emergence of these cognitive processes throughout the primate lineage. However, behavioral differences in ability to selectively attend, switch, and inhibit responses remain stark between human and nonhuman subjects. For example, macaques manifest larger Stroop effects, or disruptions from irrelevant but prepotent competing response cues that could not be inhibited, than do humans when both species are directly compared [21]. To the degree that a task requires increasing levels of EC, monkeys tend to have decreasing levels of success.

To better assess functions of the prefrontal cortex in nonhuman primates, Moore, Killiany, Herndon, Rosene and Moss [19] developed a new computerized analog of the WCST, the Conceptual Set-Shifting Task (CSST). In the task, monkeys were required first to pass a 3-choice discrimination paradigm. Following this phase, monkeys selected a stimulus from a choice of three that was consistent on one dimension (color or shape), but inconsistent for others. For example, if the initial correct response was *green*, selection of a green stimulus regardless of shape was rewarded. Once the monkey chose the correct *green* stimulus on 10 consecutive trials, the program switched contingency without alerting the monkey. The next correct response based on the opposite stimulus dimension (in this case *shape*) then began, requiring the monkey to select *square* (for instance) until criterion was reached and the contingency proceeded to shift again. Perseverative as well as total errors were recorded as measures of EC. Based on patterns of performance, Moore, Killiany, Herndon, Rosene and Moss [22, 19] revealed that aged monkeys expressed significant difficulty in both acquisition and performance on this task, and a higher degree of perseverative errors, therefore validating the CSST as a suitable measure of EC and PFC functioning in nonhuman animals.

New theories of EC note marked similarities with the development of and capacity for analogical reasoning skills in humans [23, 24]. Analogical reasoning is a multi-faceted ability requiring the selection of information that is relevant and rejecting the information that is not. Analogy can be defined as shared structural abstraction [25, 26, 27] or the judgment of relations-between-relations [28]. To possess knowledge of analogy, one must determine a relationship between two or more stimuli and seek out that same relationship amongst a novel set of items. Regardless of the level of representation required, analogy making requires working memory and inhibitory abilities [10]. Additionally, analogical reasoning involves careful attention to and selection of (abstract-relational) information that is relevant to the problem, and the inhibition of responses to that (absolute-physical properties) which is not. Further, in a string of analogies, shifting between relevant relational information would be required. Thus, EC and analogy-making share at the cognitive core many similarities: selective attention, inhibition, and set-switching.

The purpose of the current study was to investigate cognitive flexibility in baboons (*Papio papio*) using an adaptation of the WSCT. Our study marks the first examination of such cognitive abilities in a large social group of animals (n=24), allowing an examination of individual differences in EC in monkeys. With such a large N, important cognitive influences from individual factors such as age at testing and age of task exposure can be more accurately assessed. Further, we present to baboons a novel version of the WCST with an added layer of abstraction (relational stimuli), and perhaps more demanding of maintenance, inhibition, and shifting capacities characteristic of EC. The Relational WCST (R-WCST) aims to address the hypothesized link between EC and the maintenance of relations necessary in analogy. As a more stringent indicator of EC, the R-WCST mirrors the physical dimension set-shifting component required in the traditional WCST, but also requires a shift between relational sets from *same* to *different*. This shift is reminiscent of cognitive flexibility required of relations for employment in analogy. By examining similarities in patterns of performance and individual differences on both tasks, we first show a strong age effect on EC and we provide suggestive evidence for involvement of EC in analogy for nonhuman primates.

Experiment 1: Cognitive flexibility in the processing of perceptual dimension

As a measure of executive control, a computerized version of the WCST was administered to a group of socially-housed baboons. This version of the WCST, adapted from the CSST [19], required the selection of stimuli based on a single stimulus dimension (*color* or *shape*) regardless of the alternate dimension. After criterion was achieved within a condition, the task contingencies changed without indication, requiring a shift of attention to alternative stimulus dimensions. Perseverative errors and trials-to-criterion following a shift were assessed as measures of EC for each member of the group.

Method

Participants

Twenty-four Guinea baboons (*Papio papio*) living in one large social group participated freely on this task. Individuals (16 female, 8 male) ranged in age from 2.2 years to 14.6 years at time of testing. The social group had indoor and outdoor access as part of a new facility of the Centre National de la Recherche Scientifique (CNRS) and Laboratoire de Psychologie Cognitive (LPC) in Rousset, France. At the time of testing, no individual had more than 2 years of experience using computerized test systems, but all had familiarity with basic touch-screen assessments of psychomotor skills and learning paradigms [29, 30]. Of importance to this task, most individuals also had exposure to tests of relational matching-to-sample [31, 32].

Apparatus

The task was administered via the Automated Learning Device for Monkeys (ALDM) which consists of automatic operant chambers controlled via touch-screen computer interfaces [29]. Baboons had 24-hour access to the ALDM from the outdoor enclosure, thereby no removal from the social group for testing was necessary. The ALDM consists of a 70 x 70 x 80 cm test chamber that remains open during testing. Therefore, animals could enter and exit freely, completing trials voluntarily. Access to a 19-inch LCD touch monitor was granted via view and hand ports, around which antennas read the forearm embedded microchip identifier tag of the animal. Upon passage of the forearm in the hand port, identification triggered the initiation of the appropriate task program, also retaining the last stopping point in trial presentation. Thus, animals had the opportunity to complete trial sequences of varying lengths and continue the session later from the point at which it was suspended in their absence. All correct responses resulted in the delivery of grains of dry wheat as reward.

Stimuli

Stimuli presented in our computerized variation of the WCST were 3 simple geometric shapes (circle, triangle, star) of 3 different colors (green, violet, gold) for a total of 9 stimuli. Each monochromatic stimulus measured 200 x 200 pixels presented on a black background.

Testing procedure

Upon the initiation of a trial, three stimuli were displayed within three (one each) quadrants randomly selected from 9 possible quadrants (from an invisible 3X3 matrix) on the computer monitor (see Figure 1A). This randomization of locations reduced the possible confound of selection of stimuli based on spatial arrangement. Each stimulus was unique in its shape and color within a trial presentation. Four conditions were presented in succession. In all conditions, touches to the correct stimulus resulted in the delivery of reward, whereas touches to either incorrect stimulus resulted in an increased inter-trial interval and the presentation of a blank green screen before the next trial. The four conditions sequentially required that the monkeys learned to select the circle shape (Condition 1), gold color (Condition 2), triangle shape (Condition 3) and violet color (Condition 4), regardless of the shape or color of the two foils.

For instance, in the first condition, the correct (target) stimulus was the circle, regardless of its color. The alternate (foil) stimuli were a triangle and a star both drawn with a color not used for the target. Once the target stimulus was chosen with 80% accuracy within a 60-trial block, the computer program automatically switched the rule and proceeded to the next test condition, until test condition 4 had been accomplished. Because the stimulus sets were indistinguishable in the four test conditions, the correct selection of the target required a determination of a rule by trial and outcome, which had to be updated following a shift considering the reward contingencies. Altogether, our test procedure allowed for shifts of two kinds: shape-to-color and color-to-shape.

Insert Figure 1

As measures of EC, we analyzed perseveration and learning speed. Perseveration, as defined in many previous studies [22, 33] was scored as the ratio of errors due to the selection of a previously rewarded stimulus dimension in a set of trials immediately following a shift in condition. In this experiment, the perseveration ratio was calculated from the first set of 50 trials in the condition. Learning speed was computed as the number of 60-trial blocks required to meet a criterion of greater than 44% correct in two consecutive trial blocks (significantly greater than chance responding, $p < 0.05$).

Results

All 24 baboons successfully completed 4 learning conditions and the 3 required shifts. These results confirm with a large number of participants that old-world monkeys have a requisite level of EC to solve set-shifting tasks on perceptual dimension [19, 33]. Baboons required an average of 178 trials to meet an 80% criterion in each condition before a shift was initiated. Comparable to levels of perseveration observed in humans (about 2/3, [3]), baboons made perseverative errors ranging from 52.22% (*SD* = 12.99) during the first 25 trials performed after a shift in reward contingency to 68.06% (*SD* = 12.61) for the entire condition.

Significant differences in learning speed and perseveration between shape and color were observed, wherein shape seemed more salient a dimension. A one-way ANOVA revealed that baboons took significantly fewer trials to reach 44% correct (i.e., chance level for a 60-trial block, $p < 0.05$) in two consecutive blocks for shape than for color $F(1, 46) = 26.17$, $p < 0.01$. For shape, the group of baboons required an average of 1.44 60-trial block (*SD* = 0.62). For color, 3.15 trial blocks (*SD* = 1.52) were required to perform above levels of chance. In addition, perseverative errors in the color condition following a shift from the shape condition, by choosing the previously rewarded shape regardless of its color, were more prevalent. Ratio of perseveration was higher for shape (*M* = 55.92, *SD* = 13.99) than for color (*M* = 44.83, *SD* = 21.23), $F(1, 46) = 4.56$, $p = 0.038$ (one-way ANOVA).

Individual differences. Upon examination of individual differences in performance (Table 1), both learning speed and perseveration were found to be highly correlated with age, with the youngest individuals excelling in each case. Age of the baboons ranged from 2.2-14.6 years. The learning speed was 1.5-3.5 60-trial blocks (approximately 96-210 trials to reach significance). A significant positive correlation between age and learning speed ($r = 0.81$, $p < 0.001$ *two-tailed*) was observed. Baboons younger in age also scored lower ratios of perseverative errors in the 25 trials following a shift in reward contingency. The range of perseveration scores was 32.00-66.66%. Pearson product coefficient reveals a significant positive correlation between age and perseveration ($r = 0.506$, $p = 0.012$ *two-tailed*). See Figure 2 for plots depicting these relationships.

Insert Figure 2

In sum, this first experiment confirms two critical aspects of Moore et al. [19]. First, it confirms that set shifting can be efficiently assessed in monkeys. Second, it confirms that monkeys exhibit frequencies of perseverative errors in the same range as humans tested with similar tasks. However, one new contribution of this first research is that set shifting was assessed in a much larger set of subjects (N = 24) than Moore (N = 8). Further, these data suggest an effect of age on set shifting that seems to happen earlier in the life of the baboon.

Experiment 2: Cognitive flexibility in the processing of abstract relations

To examine further individual difference in cognitive flexibility, Experiment 2 introduces a newly-devised version of the WCST in which target and foils are pairs of stimuli rather than single stimuli. The Relational Wisconsin Card Sort Task (R-WCST) provides an even more stringent measure of EC than the perceptual WCST task of Experiment 1, because attention is required to a stimulus dimension that is not absolute, but rather relational and therefore more abstract. Further, a shift from one abstract rule to another (e.g., *same* to *different*) may require a more sophisticated level of cognitive control similar to analogy-making [24].

Method

Participants and Apparatus

The same 24 baboons (socially-housed) participated and the identical ALDM computerized testing apparatus was utilized as described in Experiment 1.

Stimuli

Stimulus pairs were composed of two 100 x 100 pixel geometric shapes. A total of 20 different shapes of 20 different colors were used to draw a total of 400 individual novel stimuli and 160,000 possible unique pairs. To control for confound of within-pair symmetry, pairs were constructed with each stimulus randomly staggered a distance of 0-30 pixels from a vertical plane. The horizontal distance between two shapes of a pair also varied randomly from 10 to 20 pixels.

Testing procedure

The same core procedure was followed as in Experiment 1, but the conditions were no longer one-dimensional in nature. The conditions displayed in the R-WCST sequentially required detection of a target pair which was defined by two identical shapes (regardless of their color, Condition 1); two different shapes (regardless of their color, Condition 2); two different colors (regardless of their shape; Condition 3) and two identical colors (regardless of their shape; Condition 4). Thus, two different types of shifts were also made possible: *featural* (from condition 2 to condition 3) and *relational* (from condition 1 (*same-shape*) to condition 2 (*different-shape*) and condition 3 (*different-color*) to condition 4 (*same-color*).

Upon the initiation of a trial, three pairs were displayed within three (one each) of four randomly selected invisibly drawn quadrants on the computer monitor. Of these four possible stimulus locations on the screen (from a 2x2 matrix), three were filled with stimulus pairs on any given trial (See Figure 1B).

In the first of four conditions, the correct (target) stimulus pair was determined as *same-shape*, regardless of the color of either stimulus comprising the pair. The alternate (foil) stimulus pairs were one each of *different-shape* and *different-color*. Thus, the target pair was the only one that contained the target relation. Correct selection of the target stimulus pair required a determination of rule by trial and outcome. Once the target stimulus was chosen with 80% accuracy within a 60-trial block, the computer program switched to the next rule without any visible notification. The presentation of the subsequent condition followed, visually indistinguishable from the previous set. Alternatively, if the animal did not reach criterion after 4800 trials, the condition was marked as a failure and the subsequent condition was initiated to examine possible learning of an alternate stimulus dimension. Only the determination of the target stimulus pair changed following a shift.

As measures of EC, we analyzed the number of shifts and the learning speed. A shift was tabulated only if the animal met a criterion of greater than 44% in two consecutive 60-trial blocks (significantly above chance, $p < 0.05$) in one condition, prior to a shift in contingency and subsequently performed to the same criterion following the shift. A perseveration score was not possible due to limitations in methodological design with paired stimuli wherein many trials presented the animals with more than one possible incorrect perseverative choice. Learning speed was computed as the number of 60-trial blocks required to meet a criterion of greater than 44% correct in two consecutive trial blocks (significantly greater than chance responding, $p < 0.05$).

Results

Shifting between relations proved to be a significantly more difficult task than shifting between perceptual dimensions, as only half of the baboons (12 of 24) succeeded in achieving criterion (80% in all four conditions) following a shift. Four of twelve baboons that failed to successfully complete a shift did meet criterion in the initial learning condition, but failed to succeed at levels above chance after a change in reward contingency. The remaining baboons who failed to complete shifts (N = 8) never met criterion in Condition 1.

The following analyses refer only to the 12 individuals who successfully completed the 3 required shifts. Differences in learning speed following the perceptual and relational shifts were observed. From Condition 1 to Condition 2, a relational shift was required. One-way ANOVAs revealed that baboons required significantly more blocks of trials (M = 15.67, SD = 8.34) in Condition 2 (*same-shape* pair target), than in Condition 1 (M=7.75, SD = 3.59; *different-shape* pair target) to meet an above chance criterion on 44% in two successive 60-trial blocks, $F(1, 22) = 9.123$, $p = 0.006$. A similar switch cost was observed from Condition 3 (M = 4.75, SD = 1.60; *different-color* pair target) to Condition 4 (M = 14.17, SD = 3.81; *same-color* pair target), $F(1, 22) = 62.308$, $p < 0.01$. Alternatively, a significant saving was observed when shifting across physical dimension from Condition 2 (*different-shape* M = 15.67, SD = 8.34) to Condition 3 (*different-color* M = 4.75, SD = 1.60), $F(1, 22) = 19.843$, $p < 0.01$. These results indicate a high switch cost for cognitive flexibility of relations, relative to physical stimulus dimensions. See Figure 3 for a depiction of learning speed by condition illustrating these switch costs.

Insert Figure 3

Individual differences. As in Experiment 1, individual differences in performance were observed wherein the youngest individuals in the group exhibited the capacity to shift and older individuals did not. A two-tailed Pearson product coefficient at the group level reveals a significant negative correlation between age and number of successful shifts made (r = -0.74, p < 0.01, see Figure 4). Further evidence from a median-split of the group reveal that the younger individuals, ranging in age from 2.2-5.8 years (mean age of 4.08 years) completed on average 2.75 shifts (*SD* = 0.87) whereas the older individuals ranging in age from 5.9-14.6 years (mean age of 11.56 years) completed on average only .42 shifts (*SD* = 0.99) with most succeeding to make none at all, $F(1, 22) = 37.50$, $p < 0.01$.

Insert Figure 4

WCST vs. R-WCST. In comparison to the results from Experiment 1, we observed significant differences in both learning speed and ability to shift (EC). In Experiment 1, all baboons succeeded in making the 3 required shifts whereas in Experiment 2, the group succeeded in making an average of 1.58 shifts (*SD* = 1.5), $F(1, 46) = 21.50$, $p < 0.01$. Further, baboons succeeded in achieving above-chance performance (44%) in two consecutive 60-trial blocks in significantly fewer blocks of trials for Experiment 1 (*M* = 2.29, *SD* = 0.87) than for Experiment 2 (*M* = 10.58, *SD* = 3.35), $F(1,34) = 132.638$, $p < 0.01$. See Figure 5.

Insert Figure 5

Learning speed for the 12 successful animals in Experiment 2 was also found to be correlated positively with the perseverative ratio (low score = better EC) of those animals in Experiment 1 (r = .509, p = .046 one-tailed), implicating higher levels of EC with more rapid relational learning. Finally, both perseverative ratios and learning speeds from Experiment 1 were found to be correlated negatively with the number of successful shifts in Experiment 2, (r = -0.515, p = .01; r = -0.668, p < 0.01, respectively) further validating the R-WCST as a good indicator of executive control.

Discussion

The findings from the current study provide three critical developments to the comparative study of EC. First, we provide evidence that old-world monkeys perform a task (computerized WCST) of EC at levels similar to humans. Second, with the juvenile baboons far out-performing young adults on both conventional levels of EC and ability to succeed on the relational variant, we better characterize how EC develops in monkeys from childhood to adulthood. Finally, with the relational variant of the task (R-WCST), we demonstrate a link between EC and knowledge of relations as used in processes similar to analogical reasoning.

Converging evidence from humans and monkeys provides support for the frontal lobe, and more specifically PFC, as a common locale for EC (i.e., [5,6,11,20]). Moreover, the present results, along with those of Moore and colleagues [19,22] implicate levels of responding indicative of EC on the WCST and similar tasks on par with humans [3,8,9]. Whereas we do not conclude that EC operates under identical cognitive mechanisms in human and nonhuman primates, we note here the similarities in performance as further validation of the task in monkeys as measure of EC, and support for a nonhuman primate model for behavioral investigations of EC.

Regarding the effects of age, two research teams have addressed the issue of EC in monkeys with conflicting conclusions. Using a task very similar to the WSCT task of Experiment 1, Moore and colleagues [22,34] (see also [35]) reported an EC decline at 12 years in rhesus monkeys (i.e. in the mid-adulthood). Opposite results were obtained in Weed, Bryant and Perry [36], who found reduced EC and set-shifting abilities in 2 year-olds relative to adult macaques (10 years). Our study provides greater support to Moore et al. [34] than Weed et al. [36], but suggests that the decline in EC occurs earlier in baboons (approximately 6-8 years) as evidenced from trends reported in Experiment 1. Further, as evidenced in Figure 4 on R-WCST, there seems an even more stark contrast in performance between individuals less than and greater than 6 years of age. The conclusion of an early EC decline in baboons is reminiscent of recent data showing that, in humans, age-related changes in cognition, EC in particular, may occur much earlier than previously thought [37,38], further supporting the sharing of EC functions by humans and monkeys. In fact, on the WCST in humans, deficits in EC appear as early as middle age. Changes begin in the 40s and 50s, an age range comparable with the middle-aged monkeys in this study. These latter studies further suggest similarities in the EC of monkeys and humans, but conclusions regarding this early decline in baboons might be premature at this point.

In our study, all baboons tested had approximately two years of extensive exposure to computerized tasks. Therefore, the youngest baboons were first exposed to these tasks during their early childhood, whereas the oldest individuals received their first exposure to the tasks when adults. This difference in training may have enhanced the cognitive flexibility of the youngest subjects, in comparison to adults, therefore leading to an apparent early decline of EC with increasing age. Future ontogenetic studies will indicate whether our group of young monkeys will show similar EC declines as they progress to adulthood over the years. Although as a trend, younger baboons showed better EC than the more mature members of the group, we observe upon close examination of data from Experiment 1, that the two youngest individuals (2.2 and 2.3 years) have a fairly high rate of perseveration compared to the average young. Also, in Experiment 2, the youngest individual (2.2 years) in the group was not able to complete any shifts. In support of Weed et al.'s [36] conclusion, it is perhaps the case that while significant effects of declining EC with age are observed, these trends are driven largely by data from individuals beyond infancy.

Our innovation of the relational variation of the Wisconsin Card Sort Test (R-WCST) in Experiment 2 provides important evidence for a connection between EC and the processing of abstract relations. When processing an abstract relation, such as *sameness* or *difference*, the animal must refrain from responding to the first layer of perceptual cues to focus on more conceptual dimensions [39,40]. The processing of such abstract relations was required in the R-WCST task, when the animal was required to select the stimulus pair illustrating a *same* or *different* relation considering cues (color or shape) that may change over sessions. Interestingly, performance in that task correlated with the performance in our non-relational WSCT (Experiment 1), although a reduced number of baboons could solve the R-WCST task. We found in particular that the learning speed of the 12 successful animals in the R-WCST correlated positively with the ratio of perseverative responses in Experiment 1. The perseverative ratios from Experiment 1 also correlated negatively with the number of successful shifts in Experiment 2. These relations between the two experiments suggest that EC is required when processing abstract relations. This conclusion might be relevant for study on analogy making in both humans and nonhuman primates.

When making a shift between conditions on the R-WCST from *different* to *same* (shape or color), monkeys were required to use flexibly their knowledge of relations, inhibiting responses to previously rewarded relations, and seeking out a novel relationship in a fashion similar to the flexible employment of relations in analogy. Although a direction comparison of base-to-target relations is not required in the R-WCST as it typically involved in analogy and relational matching, we posit that similar processes are involved in seeking out a new relation following a shift in contingencies, in support of similar theories of EC's involvement in analogy [41]. The increased difficulty in making a relational shift in this task when compared to a dimensional shift (e.g., *different-shape* to *different-color*) supports our claim that switching from the selection of one relation to another is akin to computations required in analogy, and requires a level of EC higher than that required for typical dimensional switch in the WCST. Future research with infant nonhuman primates may help to further explore the similarities and intertwined developmental trajectories of executive control, abstract processing and analogy-making.

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Acknowledgments

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Figure Captions

Figure 1. Sample trials from Experiment 1and 2. (A) In the computerized version of the WCST, baboons viewed trials in succession from top to bottom in this figure. The correct pair is noted by a white square outlining the stimulus. In the trials on the left, baboons should select the color gold, regardless of shape. Following a shift in contingency, baboons should learn to select triangle, regardless of its color (right-hand trial succession). For grayscale reproduction, stripes denote stimuli green in color in the actual task. (B) In the R-WCST, baboons viewed trials in succession from top to bottom in this figure. Correct selections are noted by a white square outlining the stimulus pair. In the trials on the left (Condition 1), baboons should learn to select the pair containing the same shapes, regardless of colors. Following a shift, baboons should learn to select the pair containing different shapes, regardless of color.

Figure 2. Age differences in learning speed and perseveration in Experiment 1. Plots of Age on Learning Speed (A) and Perseveration (B) depict the significant trend observed wherein younger individuals excel with faster learning speeds (lower scores frequencies and trials to criterion) and fewer perseverative errors. Learning speed measured as the number of 60-trial blocks required to meet a criterion significantly above chance (33%) for two consecutive blocks. Perseveration measured as a percentage of errors within the first 25 trials performed after a shift in task contingency/condition.

Figure 3. Learning speed by condition for WCST and R-WCST tasks. Learning speed (LS) measured as the number of 60-trial blocks required to meet a criterion of 2 consecutive blocks above chance (33%). Whereas similar trends are observed in both the WCST and R-WCST tasks, learning speed is significantly slower for R-WCST. Differences in LS reflect shift costs and savings when shifting from one condition to another. For example, when completing a relational shift in R-WCST from Condition 1 (*same-shape*) to Condition 2 (*different-shape*), a significant shift cost is observed where learning speed is significantly slower following the shift.

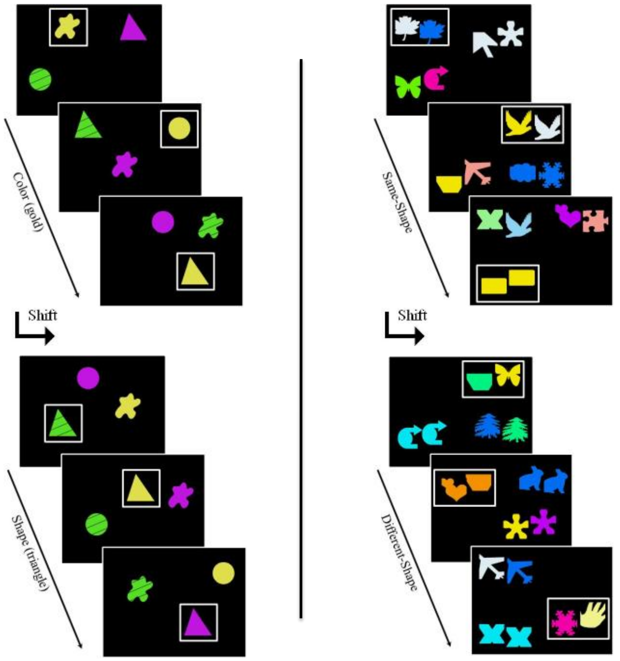
Figure 4. Age differences in the number of shifts completed in Experiment 2, R-WCST.

Figure 5. Comparison of the average number of successful shifts by all individuals in the group on the WCST and R-WCST.

		Experiment 1		Experiment 2	
Subject	Age	Learning Speed	Perseveration	Learning Speed	Shifts
ANG	5.3	2.25	54.67	8.75	3
ARI	4.9	2	41.33	8.25	3
ART	4.9	1.75	45.33	7.75	3
ATM	12.5	2.75	58.67	N/A	2
BAR	4.3	1.5	48.00	9.25	3
BOB	4.1	1.5	38.67	8	3
BRI	14.6	3.5	88.00	N/A	0
CAU	3.4	1.5	33.33	13	3
CLO	3.6	1.5	42.67	13.25	3
DAN	2.5	1.75	65.33	19.25	3
DOR	2.2	2.25	65.33	N/A	0
DRE	2.3	1.5	48.00	8.75	3
KAL	15	3.25	56.00	N/A	0
LEA	14.6	3.25	65.33	N/A	0
MIC	14.6	5	62.67	N/A	0
MON	13.5	2.5	57.33	N/A	0
PET	11.5	2.5	56.00	N/A	0
PIP	11.1	3.5	66.67	N/A	0
ROM	10.4	2	32.00	N/A	0
TAR	8.3	2	56.00	N/A	0
URA	6.7	2	44.00	N/A	0
VAN	5.8	2	46.67	10.75	3
VIO	5.7	1.75	45.33	11.75	3
VIV	5.9	1.5	36.00	8.25	3

Table 1. Summary of the performance and executive control findings of Experiments 1 and 2. That table provides (from left to right) the participant’s name, its age (in years), the learning speed (blocks to criterion) and perseveration ratio (ratio of errors due to the selection of a previously rewarded stimulus) of Experiment 1, and the learning speed and number of successful shifts observed in Experiment 2.

Figure 1.



A. WCST: Experiment 1

B. R-WCST: Experiment 2

Figure 2.

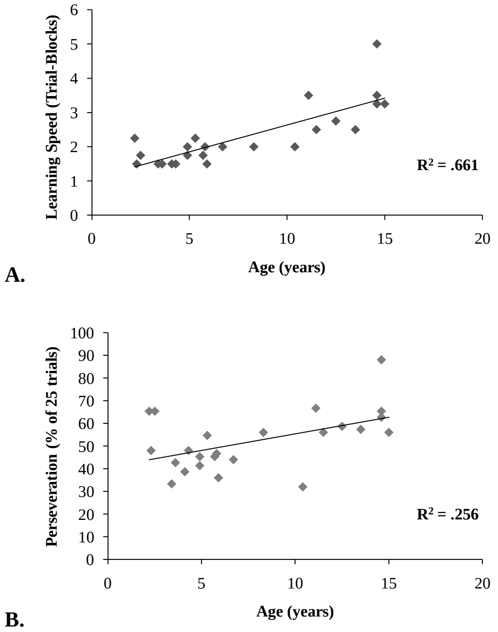

6
5
4
3
2
1
0
Learning Speed (Trial-Blocks)
0
5
10
15
20
Age (years)
R² = .661
A.
100
90
80
70
60
50
40
30
20
10
0
Perseveration (% of 25 trials)
0
5
10
15
20
Age (years)
R² = .256
B.

Figure 3

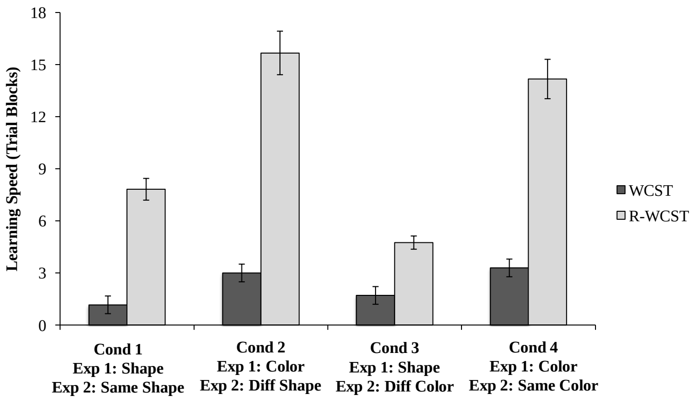
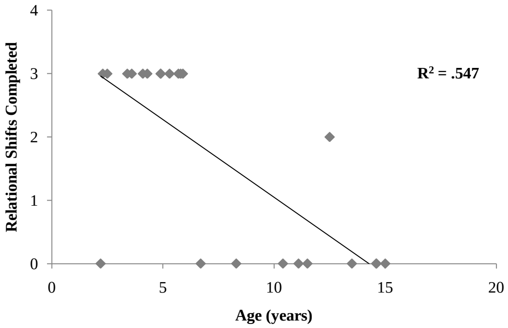

Learning Speed (Trial Blocks)
18
15
12
9
6
3
0
WCST
R-WCST
Cond 1
Exp 1: Shape
Exp 2: Same Shape
Cond 2
Exp 1: Color
Exp 2: Diff Shape
Cond 3
Exp 1: Shape
Exp 2: Diff Color
Cond 4
Exp 1: Color
Exp 2: Same Color

Figure 4.



4
3
2
1
0
0
5
10
15
20
Relational Shifts Completed
Age (years)
R² = .547

Figure 5.