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Building the blocks of executive functioning: Differentiating early developing processes contributing to executive functioning skills

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Abstract

The neural processes that underlie executive function begin to develop in infancy. However, it is unclear how the behavior manifested by these processes are related or if they can be differentiated early in development. This study seeks to examine early emerging executive functioning skills in monkeys (*M. fascicularis*) by using an error analysis approach where traditional measures of the tasks, as well as identification of major error patterns are related. Results show that during the infancy and early juvenile period, two processes that help support set-maintenance could be differentiated: modulation of responses to novelty and persistence despite negative feedback. The results suggest that these two aspects of set-maintenance were largely independent. Modulation of responses to novelty was most prominent in the infancy and early juvenile period. The ability to persist with a response set despite negative feedback emerged in the early juvenile period and was related to task performance until the end of the study.

Keywords

M. fascicularis; primates; infant; juvenile; executive functioning; response set maintenance; response to novelty

Executive Functioning (EF) skills have been the subject of a large body of work in the behavioral, developmental, and neuroscience literatures. Despite the large advances that have been made in understanding EF and cognitive control, many questions still remain regarding the overall trajectory and relations between these skills over the course of development. Between the infancy and early childhood period it is especially unclear how early abilities are related to or provide the basis for later skills. Finding correlations between tasks administered during the toddler and early preschool period has been inconsistent (e.g. Carlson, 2005; Miyake, Friedman, Emerson, Witzki, et al., 2000), leading some to conclude that EF skills are not specific early in development but differentiate later (Miyake, et al., 2000). However, this interpretation stands in contrast with the longitudinal research that shows there is continuity and predictability with many EF skills from the early preschool to later preschool years (Carlson et al., 2002; Hughes & Ensor, 2007). An alternative explanation that may help explain both sets of findings is that between infancy and the preschool years, there are qualitatively different skills that are emerging and they serve to generally support the more mature looking EF skills during the late preschool years.

EF skills such as attention regulation, resistance to prepotent responding, and increase in working memory capacity emerge during the late infancy and toddler period (Carlson et al., 2004; Diamond & Doar, 1988; Diamond et al., 1997; Espy et al., 1999). These skills are often common components of the tasks used in the preschool years to assess EF skills (Carlson, 2005). Most studies of EF development utilize a latent construct approach that often summarizes performance on the tasks in single outcome measures. This approach can hide strategy and error patterns that may reveal dissociable skills that are emerging very young.

The EF skills developing during infancy may also be qualitatively different than the ones developing during the preschool years. In particular, response-set maintenance and response to novelty are two changes not well studied in late infancy and the juvenile period. However, both abilities are intrinsically important for performance on many EF tasks.

Within the toddler literature, response to novelty is mainly viewed as an emotional-regulation trait (see Aksam & Kohanska, 2004; Fox, 2010). This research has shown that toddlers with a low approach to novelty are better at EF tasks later in development (Aksam & Kohanska, 2004). However, modulating responses to novelty in non-affective situations may be a developing skill. An infants' ability to break attention from novel stimuli, thus self-regulate attention, has been linked with executive attention skills (Colombo, 2002; Posner & Petersen, 1990; Posner & Rothbart, 1998). Infants' preference for looking at and responding to novel items is the main behavior used to study infant cognition. The preference for responding to novelty persists until toddlerhood (i.e. Diamond, et al., 1994), but substantially declines between the infant and toddler period. It has been proposed that responding to novelty is a prepotent response during this period and the ability to suppress this response has been exploited in inhibition paradigms with toddlers (Diamond & Doar, 1988). However, there is little work on how developmental changes on the preference to respond to novelty during the infancy and early juvenile period are related to other cognitive skills.

The adult literature on novelty detection and response suggest a neural overlap with the networks underlying many EF skills. There is a long literature showing that the medial temporal lobes are important for detecting novelty (see Zeamer, Heuer & Bachevalier, 2010), however this work does not explore what is involved in controlling a response to novelty. Petrides, Alvisato, and Frey (2002) have proposed that the orbital frontal cortex (OFC) is involved in making judgments about the novelty of a stimulus or whether it deviates from expectations. This finding does compliment the medial temporal work given the connectivity between the medial temporal areas and the OFC (Price, 2007). However, this work also shows that ventral lateral prefrontal cortex (vlPFC) is involved in appropriately choosing the response to that stimulus. The shared connectivity between the vlPFC and OFC is thought to facilitate the detection of deviations/novelty and the appropriate response choice to it (Petrides, et al., 2002). The frontal involvement suggests that controlling the preference to respond to novelty would have a protracted developmental trajectory and would emerge later than executive attention, which is modulating the ability to break attention from novel objects.

Many researchers have identified set-maintenance as an important EF skill (Crone, et al., 2004; Davidson, Amso, Anderson & Diamond 2006; Welsh Pennington & Groisser, 1991). However, there is very little work that focuses on the factors or the developmental processes that give rise to set-maintenance. The ability to stay on task despite distraction, to maintain a rule over time, and maintain motivation may all be components of set-maintenance. Resting state connectivity for the network underlying set-maintenance shows qualitative changes until early adolescence (Fair et al., 2007). This network, like detection and response to

novelty, shares connectivity with identified EF networks. Set-maintenance behavior can often be confounded in many measures of switching and inhibition, as one must maintain set in order to perform consistently. Research utilizing error analysis shows developmental improvement until the preadolescent period (Crone et al., 2004, Davidson et al., 2006). Young juveniles and toddlers are capable of set-maintenance as stable behavior can be elicited, but there is substantial variability at these early ages (e.g. Diamond & Doar, 1988; Espy, et al., 1999; Mandell & Sackett, 2009), suggesting this is an early emerging skill with a long developmental trajectory.

The purpose of the current research was to study the longitudinal relations between performance on several EF tasks and assess the common and dissociable components of task behavior. The study covers the 3-month to 12-month range in macaques, which roughly corresponds to the 12-month to 48-month age range in humans. In addition to standard performance measures, errors types were also summarized for each task in order to assess learning, response set-maintenance and response to novelty. The tasks are established measures of working memory, inhibitory control (inhibition of prepotent responding), planning, and reversal ability. Additionally, each requires learning, set-maintenance and several require an ability to modulate responses to novelty. By extracting the behavior associated with these skills through analysis of errors types, we aim to assess the continuity of the behaviors and the relation they have with other EF skills over time.

Methods

Subjects

Subjects were 12 long-tailed macaques (*Macaca fascicularis*, $n = 8$ males). The procedures outlined here, including the conception techniques, were approved by the Institutional Animal Care and Use Committee. All animals were conceived via artificial reproductive techniques including in vitro fertilization, intracytoplasmic sperm injection and embryo splitting. These conception techniques have not been shown to have a substantial impact on infant or juvenile cognitive development in comparison to naturally conceived animals (Sackett, Ruppenthal, Hewitson, Simerly, et al., 2006). Therefore, the animal's conception history was not considered in the analyses.

All animals were born via natural delivery and brought to the nursery within hours of birth. Animals were reared in accordance with standardized nursery protocol (Ruppenthal & Sackett, 1992). This surrogate-peer rearing procedure involves continual access to a cloth surrogate and 24-hour care and hand-feeding until the animal can self-feed (10-15 post-natal days). After 30 days of age, animals receive 20-30 minutes of socialization 4 days a week with same-aged peers. Animals are kept on a formula diet until 60 days of age when they are gradually weaned from formula to solid food. During this time they are also weaned off their cloth surrogate. After 6-month of age, the animals are transferred to social housing with their established peer group. This rearing environment is different and less deleterious than the peer-rearing and nursery-only environment that has been shown to result in a variety of social and cognitive delays (see Novak and Sackett, 2006 for comparison of different rearing environments).

All animals, except two, were full-term (165 days $\pm$ 5). One of the premature animals was not found to be significantly different from the others on any cognitive measure, so was kept in the sample. The other animal was an outlier on age of attainment for A not B but not any other assessment. The medical records of this animal showed that treatments prevented the animal from being tested, thus delaying his age of attainment. Therefore, the animal was kept in the sample because his A not B acquisition was not related to his prematurity.

Procedures

The assessments used in this study began at 88 days of age and ended at 350 days. Table 1 shows the sequence of the tasks as well as the average age that the animals began testing. Unless otherwise noted, all tasks proceeded in continuous sequence and the next task in the battery was begun after the previous task was completed. The sequence the tasks were administered was determined by previous work (Harlow et al., 1960; Diamond, 1990; see also Sackett, et al., 2006) and was designed so that animals were being tested at an age where mastery of the task was attainable, but where performance would not be at adult levels. This sequencing was designed to maximize variability in the performance measures without creating floor or ceiling effects.

Two of the tasks (A not B and spatial search) were administered manually by experienced testers. The spatial search task was administered in a Wisconsin General Testing Apparatus (WGTA, Harlow). All other tasks were administered with touch screen computers.

Each animal was adapted to the computer-testing environment and trained to use the touch screen after completing the spatial search task (average age = 175 days). The computer-based testing environment and touch screen training procedure has been described extensively elsewhere (Mandell & Sackett, 2008), but will be described briefly here. The apparatus consisted of a 19" capacitive touch screen (3M, Minneapolis, MN) and a Windows based computer (Dell Optiplex, Round Rock, TX). The touch screen was placed flush to a plexiglass template fit on the back of the test cage. The template had 11 square openings that allowed the animal access to 9 test areas and 2 non-test areas on the screen. Applesauce reward was delivered via pneumatic pump (MasterFlex, Cole Palmer, IL) through a stainless steel tube mounted on the bottom of the test cage. The pump was controlled by the testing software via a USB relay (National Instruments, NI USB-9472, Austin, TX).

All trials and tasks were standardized with the following features. Each session began with the animal touching a "start" stimulus that was presented in one of the 2 non-test areas. All tasks, except the list learning tasks, contained 25 trials per session. Each trial had a maximum duration of 60s, visual feedback lasted 2s, and there was a 10s intertrial interval (ITI) between all trials. If the animal did not respond within 60s, the trial was terminated and scored as a "balk". The next trial began after the 10s ITI. If an animal did not respond on 5 trials in a row or on 30% of the presented trials, the session was scored as a "balked" session and performance for that session was not summarized. Feedback was always given when the touch screen registered an on-stimulus touch. Correct choices resulted in the screen clearing, turning from grey to white for 2s, and applesauce being delivered. Incorrect responses resulted in the stimuli clearing and a black X on a white background appearing for 2s where the animal touched. Stimuli used in all tasks were 150 × 150 pixel jpeg images of abstract shapes.

The touch screen training procedure involved training the animal through successive approximation to approach the screen, touch the template surrounding the screen, touch the screen anywhere and touch only the stimulus on the screen (see Mandell & Sackett, 2008 for full training procedure). An experimenter controlled the first three training phases and the last phase was computer controlled. An animal was considered trained when it touched the stimulus 90% of the time in a single 30 trial test session or touched the stimulus 80% of the time for 3 sessions in a row. Animals in this study completed training in an average of 18.3 test days (SD = 14.65).

Cognitive Tasks

A not B—The procedures and apparatus used for A not B (AB) testing has been described previously (Ha, Kimpo & Sackett, 1997; Sackett, et al., 2006). The apparatus consisted of a plastic base with two small wells in which a small toy could be hidden. There were also two identical covers that fit over the wells. Two experimenters that were familiar to the infant administered the AB task. One held the infant wrapped comfortably in a cloth diaper and the other set and scored the trials. The two testers frequently switched between holding the infant and setting the task to minimize testers inadvertently cueing the infant.

The infant was first tested on a series of object permanence tasks then on AB, therefore the animals had already demonstrated object permanence before being tested on AB. In the AB task, the infant was shown the plastic base with the B well covered and the A well uncovered. The experimenter directed the infant's attention towards a juice covered toy, placed it in the A well and covered it. After a short delay of 5s, the infant was given the opportunity to retrieve the toy and suck the juice off it. After the infant successfully retrieved the toy on two trials in a row, the experimenter placed the toy in the B well in full view of the infant for the post-switch trial. The experimenter covered the B well then tapped the lid of the A well. After a 5s delay, the infant was again given the opportunity to search one well. For the next sequence, the toy was again hidden in the B well, then after successful retrieval for two trials in a row, switched to the A well for the post-switch trial. If an animal did not reach criterion for switching within 5 pre-switch trials, the toy was switched to the other well. Infants were tested on 5 switch events in one session. In order to pass AB, the toy had to be correctly retrieved on 8 out of 10 switch events in 2 consecutive test sessions. AB data were summarized into the average number of correct responses on the pre-switch trials (AB_{PreAve}) and the total number of errors made on the post-switch trial ($AB_{PostError}$).

Spatial Search—Following a 2-month average delay, during which time animals were habituated to the WGTA testing environment, they were tested on a spatial search task (see Ha, Mandell, & Gray, 2011). The animal was presented with 4 identical boxes with spring-loaded tops, enabling the lid to close on its own. A food reward was randomly placed in 1 of the 4 boxes out of view of the animal. The subject was allowed to search through the boxes until the fruit piece was retrieved or until 60s had passed. Animals were tested for 5 test days with 25 search problems per session.

Data from this task were summarized into the average number of searches needed to find the reward ($Search_{Ave}$). This outcome measure was only calculated for the problems in which the animal found the reward within the 60s time limit. Additionally, the average number of repeated searches per problem was also calculated ($Search_{Repeats}$). This score was calculated even for problems where the animal did not retrieve the reward

2-Object Discrimination and Reversal Learning—After each animal completed touch screen training, it was tested on 2-object discrimination and reversal learning. The task presented the animal with two images that differed only in color. The images were a purple or orange square with a simple two-tone checkerboard pattern. On each trial, these objects appeared randomly in two of the nine test locations. In the 2-object discrimination phase, the animal learned to associate one of the objects with reward (A+), whereas the other did not (B-) result in reward. Once this initial contingency was learned, it was reversed the following test day (A-B+). The animal was tested until it learned the new contingency. Criterion for passing both phases was set at performance above 80% correct in a test session. Over half the animals were above 90% correct when they passed each phase.

Both 2-object discrimination and reversal learning were summarized into the number of errors until criterion (2-object_{Error}, Reversal_{Error}, respectively). In keeping with the error

analysis established by Jones and Mishkin (1972), the reversal learning data were summarized into the number of sessions the animal's performance was less than 30% correct. It was also discovered that animals were balking excessively on this task. Balking on occasional trials is not unusual for animals in this environment; however, balking on entire sessions or for multiple sessions in a row is rare. We suspect that the balking on this task may be a sign of frustration with the reversal phase of the task as has been reported with human children (Overman, et al., 1996). This suspicion was anecdotally confirmed by the testers, who reported increases in emotionality during this phase for some of the animals. In order to capture this behavior, the number of balked sessions while in the perseveration phase of the learning curve was combined into an overall balk/perseveration measure ($\text{Reversal}_{\text{Perseverate}}$). These sessions were defined as a balked session preceded by a session where the animal was less than 30% correct.

Delay Response—Delay response (DR) testing was begun after the animal completed reversal learning. The computerized version of DR is equivalent to a delay match to location task. The reward location was indicated by a single place-holder image (a white square containing 2 black circles) displayed on the screen in one of the nine designated response locations. Once the animal touched this location, the screen cleared for 2s then two placeholders were displayed; one in the previously presented location and one in a different location. Responses to the previously presented location were rewarded. Testing proceeded until performance was above 80% correct in a session.

The main outcome measure for this task was errors to criterion (DR_{Error}). This task also required a modulation of novelty responding because the animal must respond to the same location as seen before. In order to assess preference for responding to novelty, data were also summarized into a nonmatching bias measure ($\text{DR}_{\text{Novelty}}$), defined as the number of sessions the animal spent with a performance level of less than 40% correct.

Nonmatch to Sample and List Learning—After reaching criterion on delay response, animals were tested on nonmatch to sample (NMS) and list learning. For NMS the animal was presented with a single image in the middle of the test screen. Once the animal touched the image, it cleared for 2s, then the sample and a novel image were presented. The spatial arrangement of these 2 images was constrained so that neither image could appear in the middle location and both were the same visual distance from the middle location. Responding to the novel image resulted in reward. Mastery of this task was performance above 80% correct for 3 days. Performance on this task was summarized by the number of errors to criterion ($\text{NMS}_{\text{Error}}$).

Following mastery of this task, the animal moved to the list-learning task. This task was presented in the same way as NMS except 2, 3, 4, 5, or 7 samples were presented in a row before advancing to the test phase. Each sample was presented for 10s or until the animal cleared it by touching it. In the test phase, the test pairs were presented in the same order as the samples were presented. Only one list length was presented in a session and an animal was not tested on a longer list length until demonstrating mastery of the shorter one by responding correctly to at least 80% of the trials in a test session.

The NMS task and each list length were summarized into the number of errors to criterion. Only the data from the 5-item ($\text{5-List}_{\text{Error}}$) lists were used in the analysis. The 5-item list was the longest list length all animals could master. The 7-item list emerged as a challenging list length. One animal did not master this list length and half of the animals required more than 2 sessions to pass.

Data Analysis

None of the outcome measures were normally distributed. In order to maximize the degrees of freedom and power in these analyses, all the data were transformed in order to bring them in line with the assumptions of normality. The purpose of all analyses was to assess the relation between early-administered tasks and later-administered tasks. Therefore, regressions were conducted to investigate these partial relations. While there is temporal priority for the tasks, this design does not allow for causal or meditational inferences to be made. The partial correlation from the regressions will be interpreted and presented as this study is mainly concerned with the independent relations the performance measures have with each other.

The following specific hypotheses, which are derived from previous work with children and monkeys, were tested. First, the relation between AB and DR was tested. As has been shown in infant children and monkeys, it was expected that $AB_{PostError}$ would be related to DR_{Error} (Diamond & Doar, 1988; Diamond et al., 1997; Espy et al., 1999). We also believed that the $AB_{PostError}$ measure would be positively related to the $DR_{novelty}$ measure, which would suggest that good switchers on AB were also biased to respond to novelty. A relation between Spatial Search and 2-object reversal was also directly tested. It has been proposed that perseverative behavior on search tasks are related to perseverative behaviors on reversal learning (see Ha et al, 2011 for a discussion), but with little data to support this assertion (Diamond, et al., 1997; Ha et al., 2011). The $Reversal_{perseveration}$ measure has not been previously used in studies assessing this relation, therefore, if the relation exists, it was expected to be between $Search_{ave}$ and $Reversal_{perseveration}$. Finally, it was expected that all the tasks would show some relation with 5-item List performance. This task is the most advanced EF task used in the study and contains a working memory component that is present in all of the tasks. If there is a general relation between this task and the others, but dissociable relations between the other tasks, then this would support the hypothesis that early skills are dissociable but generally support performance on EF tasks at a later age.

Results

Overall Performance Levels

Table 1 shows the descriptive statistics of the measures as well as which transformation was applied to the data. Performance on AB, search and reversal learning is in-line with performance levels reported by others on these tasks using comparable aged animals (Ha, et al., 2011; Mandell & Sackett, 2009; Sackett et al., 2008). The DR procedure used here is a departure from manual procedures because the animal does not see the hiding event. However, the performance levels observed in this study are not out of line with what has been reported with the manual version of the task with animals of a comparable age (Diamond, 1990; Harlow, et al., 1960). Performance on the NMS task (Bachevalier & Mishkin, 1984) and the list task was in-line with previous work that reported good, but variable performance on a 5-item list, but difficulty on a 10-item list with 2-year-old monkeys (Malkova, et al., 2001).

The bivariate correlations between the transformed scores of all outcome measures are shown in table 2. One consequence of this type of sequential testing design is that animals that are poor performers on early tasks will be older on later tasks than the animals that performed well. This effect results in age being confounded with all of the outcome measures. Therefore, all of the following regressions were conducted controlling for age at the time of the dependent variable.

Predictive Relations

The expected relation between AB performance and DR was significant after controlling for age at DR testing. $AB_{PostError}$ was significantly related to DR_{Error} , $r_{partial} = .60, p = .049$ and not significantly related to $DR_{Novelty}$, $r_{partial} = .45, p = .161$. However, AB_{PreAve} was a marginal predictor of $DR_{Novelty}$ after controlling for age, $r_{partial} = -.55, p = .072$. These results suggest that there are two distinct error types on the two tasks that are related. Animals who had difficulty consistently choosing the correct hiding location on the pre-switch phase of AB were more biased to choose the novel location on DR. However, as expected, animals who were good at switching to the B location on AB also made fewer errors on DR.

There was also a relation between the search and reversal tasks. $Search_{Ave}$ was a significant predictor of $Reversal_{Perseveration}$ after controlling for age at the beginning of reversal testing, $r_{partial} = .63, p = .04$. The relation between spatial search and reversal learning was specific to the perseveration measure as it was not significantly related to $Reversal_{Error}$, $r_{partial} = .38, p = .25$. Additionally, the relation between the perseveration measure on reversal learning and spatial search was specific to the average number of searches needed to find the reward, as $Search_{Repeat}$ was not related to $Reversal_{Perseveration}$, $r_{partial} = .40, p = .219$, after controlling for age. Given the nature of the relations between spatial search and reversal learning, an exploratory analysis was conducted to determine whether the relation could stem from a general learning process. This hypothesis was tested by regressing 2-object $_{Error}$, $Search_{Ave}$, and age onto $Reversal_{Perseveration}$. 2-Object discrimination and spatial search had substantial overlapping variance as the model with both variables explained significant variance, $R^2 = .56, p = .023$, yet neither emerged as a significant unique predictor of the perseveration measure on reversal learning.

There was also a surprise relationship between $Reversal_{Perseveration}$ and $DR_{Novelty}$ that emerged from the correlations. Given that AB_{PreAve} was also related to $DR_{Novelty}$, a regression was conducted to investigate whether some shared process between AB and reversal performance could explain these relations. Both remained significant predictors of $DR_{Novelty}$ after controlling for each other and age, AB_{PreAve} : $r_{partial} = -.70, p = .026$; $Reversal_{Perseveration}$: $r_{partial} = -.75, p = .013$. In contrast, neither emerged as a significant predictor of DR_{Error} . The direction of these results is interesting. Animals with a bias to respond to the novel location on DR were the animals that perseverated less on reversal learning. This relation was independent of the relation that showed animals that were worse on the pre-switch phase of AB were also more biased to the novel location on DR.

Given this relation with novelty, another exploratory analysis was conducted to determine whether animals biased to respond to novelty were faster learners on NMS. Neither $DR_{novelty}$ ($r_{partial} = -.02, p = .95$) nor AB_{PreAve} ($r_{partial} = -.24, p = .48$) were significantly related to NMS_{error} after controlling for age. There was also no significant bivariate relation between this measure and any of the other outcome measures (see table 2).

Performance on list learning task showed correlations with almost all tasks, as predicted. However, when entered into a regression, only the relation with $Reversal_{Perseveration}$ remained significant after controlling for age, $r_{partial} = -.79, p = .012$. Age was also significantly related to performance after controlling for the other performance measures, $r_{partial} = .85, p = .004$. This result pattern shows that animals that perseverated to a greater degree on reversal learning made fewer errors on the 5-item list.

Discussion

The main purpose of this study was to assess the level of continuity and differentiation among EF skills early in development. Additionally, the study sought to determine whether set-maintenance and response to novelty could be identified as a common but dissociable component of EF. The data do show that set-maintenance underlies many EF tasks during this young age. However, the results also show that there are two routes through which set-maintenance can be expressed. One is through the ability to modulate responses to novelty and the other is through the ability to persist with a response-set despite negative feedback. There is evidence that these two routes overlap, but are independent and that modulation of responses to novelty may recede in importance as the animal ages.

The relation that is often found in other studies between AB and DR performance (e.g. Diamond, 1990; Diamond & Doar, 1988; Espy, et al., 1999) was replicated in this study. The results from this study also suggest that the relation between AB and DR appears to extend beyond working memory functioning, as the delays for both tasks were short. These results lend further support to Diamond's assertion that the common thread between the two tasks is not just working memory, but rather flexible encoding and execution of rules that go against prepotent responding (Diamond & Doar, 1988). In the AB task this prepotent responding is built up through the repeat searching of the A location. Diamond (1990; Diamond & Doar, 1988) has argued that the inhibition component of DR is due to the young subject's preference to respond to novelty.

These data support that argument but also expand upon it by showing that a novelty response bias, in addition to adding an inhibition component to DR, could also be interfering with response set-maintenance on the pre-switch trials of AB. While post-switch AB errors were related to total errors on DR, pre-switch AB errors were related to the bias the animal showed towards using a nonmatch-to-location rule on DR. This pattern suggests there is a cognitive component in the task related to flexible execution of responses and another component that is related to maintaining a response set that requires modulating responding to novel locations. A strong preference for responding to novelty can tax not just inhibition but also response-set formation. This assertion also compliments and extends Espy, et al.'s (1999) data, who also found evidence for a dual process underlying the relation between AB and DR but were unable to identify the second process.

Aksam and Kohanska (2004) have shown that young toddlers who are reticent to approach novelty are better at inhibition tasks as preschoolers. These results are interpreted in terms of social modulation of emotional reactions; therefore an approach to novelty is seen as affective regulation (Fox, 2010). The results from this study expand upon those results by showing that modulating novelty responses in non-affective situations is also related to better EF functioning. However, this relation in the non-affective domain may be developmentally time limited as we see this aspect have little bearing on task performance at 12-months. If novelty preferences had persisted, monkeys with a high preference for novelty should have performed better on the NMS and list-learning tasks because they utilized a novelty rule. However, the relation did not persist in these data, suggesting that this is a developmentally relevant behavior in the transition between infancy and the early juvenile period. More work should be done relating these seemingly different manifestations of novelty modulation in order to better characterize their relations with the development of EF and emotional self-control skills.

Persistence in light of negative feedback was another common ability that emerged from the analysis. Animals that perseverated more on reversal learning let go of a novelty bias quicker on DR and had the least amount of errors on the 5-item list. Therefore, this behavior

manifested itself in both maladaptive and adaptive ways. Maintenance of response set, even in the face of negative feedback, is important for consistent behavior. Errors can occur because of inhibition, memory or distraction failures (Crone et al., 2004). However, these errors should not be grounds for abandoning a response set, such as using a nonmatching rule. In these situations, one must persist with the response set despite the negative feedback. The results of this study show that this persistence can be expressed in maladaptive ways. Animals that perseverated more on reversal learning, therefore had maladaptive persistence on the previously learned rule, showed consistently better performance on subsequent tasks. This pattern suggests that their early maladaptive persistence was adaptive on later tasks.

Persistent responding showed the greatest relationship on late administered tasks, suggesting that this aspect of response-set maintenance has a long developmental trajectory. This protracted development is consistent with human developmental work showing that response-set maintenance continues to develop into late childhood (Crone et al., 2004, Davidson et al., 2006). The relation between perseveration and response-set maintenance is novel, however. We know of no behavioral work that has assessed the relation between perseveration and persistence, but there is neurological work in adults that point to a route through which they could be related. Independent lesions to the anterior cingulate cortex (ACC) or to the OFC will produce impaired performance on reversal learning and list learning, although not equally in magnitude (Meunier, Bachevalier & Mishkin, 1997). Connectivity between the OFC and amygdala is thought to underlie perseverative behavior on reversal tasks (Jones & Mishkin, 1972) and has been implicated in detecting deviations from expectations (Petrides, et al., 2002) and changes in reward contingencies (see Ghahremani, et al., 2010 for a discussion). The ACC is involved with maintaining response-set and is particularly involved in error detection, feedback processing, and performance adjustment (see Bush, Luu, & Posner, 2000; Ridderinkhof, Ullsperger, Crone & Nieuwenhuis, 2004 for reviews). Importantly, the ACC and OFC share connectivity both directly and indirectly (Bush et al., 2000; Medalla & Barbas, 2010) and both structures have protracted development (Gogtay et al., 2004). Adult work suggests that the OFC is involved with flexibly switching when the reward contingency changes and the ACC is mainly involved with post-switching adjustments (Ghahremani, et al., 2010).

The behavioral data in this study suggests that the ability to differentiate between negative feedback that signals a change in reward contingency from feedback that signals an error may be a developmental process that occurs in the early juvenile period and promotes set-maintenance. The neurological work in adults suggests that developmental changes between the OFC and the ACC related to judging the meaning of the feedback and appropriate action-selection may underlie this relation. The relation between perseveration and persistent action selection should be investigated to understand how developmental changes in these domains promote set-maintenance in this early juvenile period.

In conclusion, a relation between tasks did emerge that suggests that two dissociable aspects of cognition may be important in the early development of EF skills; namely, the ability to modulate responses to novelty and the ability to persist with a response set despite negative feedback. Given the pattern of behavioral results in this study, it appears that modulation of response to novelty and the ability to maintain the appropriate response set are important skills that contribute to other EF skills. The developmental trajectories of these abilities and their underlying neural networks should be the subject of more research to help understand the early development of EF skills. Understanding these trajectories may give insight into the roots of developmental disorders that show EF dysfunction and are thought to originate in infancy or earlier.

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Works Cited

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Table1

Descriptive statistics for all outcome measures

Males = 8, Females = 4	Mean	SD	Range
<i>1. A not B: Age (days) = 88.8 (34.3)</i>			
Number of post-switch errors ^{Cr}	5.1	4.5	1-14
Average correct on pre-switch trials ^{Sq}	.86	.12	.58-1
<i>2. Spatial Search: Age = 167.2 (25.7)</i>			
Average number of searches per problem ^{Cb}	2.6	.3	1.9-3
Average number of repeat searches per problem ^{Cr}	.4	.2	.1-.7
<i>3. 2-Object Discrimination: Age = 185 (34.7)</i>			
Number of errors to criterion ^{Ln}	41.3	21.4	16-93
<i>4. Reversal Learning: Age = 194.9 (39.3)</i>			
Number of errors to criterion ^{Ln}	102.8	35.9	60-168
Number of balk/perseverative sessions ^{Ln}	6.3	5.8	1-21
<i>5. Delay Response: Age = 237.2 (51.1)</i>			
Number errors to criterion ^{Sr}	206	142.1	22-415
Number of sessions below 40% ^{Sr}	2.8	2.3	0-7
<i>6. Nonmatch to Sample: Age = 272.8 (65.9)</i>			
Number of errors to criterion ^{Ln}	252.3	162.9	94-638
<i>5-Item List: Age = 337.5 (92.4)</i>			
5-Item: Number of errors to criterion ^{Ln}	12.4	12.9	2-39

Note: Tasks are ordered to reflect the order they were presented to the animal. Age is the average age of the sample when they began a task. For data transformations: Cb = values cubed; Cr = cube root transformation; Sq = values squared; Sr = square root transformation; Ln = natural log of the value

Table 2

Correlations between transformed outcome measures

	2	3	4	5	6	7	8	9	10	11
1. AB _{PreAve}	-.58*	.14	.10	-.05	.31	.21	-.49	-.58*	-.17	-.04
2. AB _{PostError}		-.47	-.24	-.17	-.47	-.46	.61*	.49	.20	.44
3. Search _{Ave}			.62*	.65*	.47	.67*	-.21	-.23	-.06	-.70*
4. Search _{Repeat}				.82**	.44	.56	-.10	-.16	.03	-.33
5. 2-object _{Error}					.68*	.79**	-.16	-.32	.25	-.51
6. Reversal _{Error}						.92**	-.44	-.58*	.45	-.54
7. Reversal _{Preseveration}							-.53	-.62*	.38	-.68*
8. DR _{Error}								.89**	-.04	.57*
9. DR _{Novelty}									.01	.59*
10. NMS _{Error}										.09
11. 5-List _{Error}										

Note: A not B-preswitch average correct (AB_{PreAve}); A not B-postswitch errors (AB_{PostError}); Average number of searches per problem (Search_{Ave}); Average number of searches to a previously searched location per problem (Search_{Repeat}); Number of errors to criterion on discrimination (2-object_{Error}); Number of errors to criterion on reversal learning (Reversal_{Error}); Number of sessions spent balking or perseverating (Reversal_{Preseveration}); Number of errors to criterion on delay response (DR_{Error}); Number of sessions biased towards a nonmatching rule on delay response (DR_{Novelty}); Number of errors to criterion on nonmatch to sample (NMS_{Error}); Number of errors to criterion on the 5-item list length (5-List_{Error}).

* $p < .05$;

** $p < .01$