

Cognitive Learning Abilities in Capuchin Monkeys (*Cebus apella*)

Michelline Coutinho de Resende,¹ Maria Clotilde Tavares,¹ Carlos Tomaz^{1,2}

Se ha sugerido que en los monos del mundo antiguo, así como en humanos, existen dos sistemas de memoria distintos que sustentan la memoria de hábitos y reconocimiento. Estos dos circuitos neurales tienen diferentes momentos de maduración. Mientras que el circuito del sistema del hábito está presente temprano en la vida, el sistema de memoria cognitivo se desarrolla después. En este reporte investigamos las habilidades cognitivas de monos capuchinos del nuevo mundo (*Cebus apella*) jóvenes y adultos para desarrollar un Aprendizaje de Discriminación Concurrente (ADC) y un ensayo único de pruebas Delayed Non-Matching to Sample (DNMS) tasks a través de intervalos de retardo entre 8 s a 10 min. Nuestros resultados indican que todos los sujetos fueron aptos para aprender la prueba ADC con 20 pares simultáneamente después de un intervalo de 24 horas. En contraste, mientras los puntajes de los adultos estuvieron más allá del azar a través de todos los retardos en la prueba de memoria DNMS, los monos capuchinos jóvenes desarrollaron la prueba por el nivel del azar. Consecuentemente, demostramos que los monos capuchinos tienen una disociación ontogénica de estos sistemas de memoria. También, los monos capuchinos adultos son capaces de desarrollar una prueba de alta demanda cognitiva, desde que una capacidad de formación de conceptos es requerida para resolver el problema del DNMS. Debido a las similitudes encontradas en el comportamiento de *C. apella*, los humanos y los monos del mundo antiguo en estas dos pruebas de memoria, asumimos que los monos capuchinos pueden ser un valioso modelo alternativo para las investigaciones de las bases neurobiológicas de la memoria. *Salud UIS 2002; 34:162-169*

Palabras Clave: Habilidades cognitivas, DNMS, CDL, *Cebus apella*

It has been suggested that in Old World monkeys as in humans there are two distinct memory systems that support habit and recognition memory. These two neural circuit have a different time maturation. Whereas the habit system circuit is present early in life, the cognitive memory system develops later. In this report we investigated the cognitive abilities of the young and adult New World capuchin monkeys (*Cebus apella*) in performing a Concurrent Discrimination Learning (CDL) and a trial-unique Delayed Non-Matching to Sample (DNMS) tasks across delay intervals ranging between 8 s to 10 min. Our results indicated that all subjects were able to learn the CDL test with 20-pairs simultaneously after a 24-hr interval. In contrast, while adults' scores were above chance across all delays in the DNMS memory test, the young capuchin monkeys performed the task by chance level. Consequently, we demonstrated that capuchin monkeys have an ontogenetic dissociation of these memory systems. Also, adult capuchin monkeys are capable to perform a high cognitive demand task, since a capability of concept's formation is required in order to solve the DNMS problem. Due the similarities found in the performance of *C. apella*, humans and Old World monkeys in these two memory tasks, we assumed that capuchin monkeys can be a valuable alternative model for investigations of the neurobiological basis of memory. *Salud UIS 2002; 34:162-169*

Key Words: Cognitive abilities, DNMS, CDL, *Cebus apella*

INTRODUCTION

Higher-order cognitive learning permits a construction of differentiated actions and perceptions in order to create more complex and highly variable behavioral.¹ The generalization of concepts and rules learnt from previous experience allows the subject to deal efficiently with new situations and more complex challenges.² Memory is the manner in which all

of these important information are store, making possible their later retrieval and utilization in order to reconstruct a behavior more adaptive and qualified.³ Although there are several classifications,^{4,5} it is well defined that memory can be divided in two principal systems: a cognitive memory system, that seems to be impaired after diencephalic and medial temporal lobe (MTL) lesions,^{6,7} and a habit system (or non-cognitive memory system) that utilizes a corticostriatal circuit that is not affect by lesions in MTL.^{8,9}

¹ Primate Center and Department of Physiological Sciences, Institute of Biology, University of Brasilia, CEP 70910-900; Brasilia, DF, Brazil.

² Corresponding author: Tel/Fax: 55-61-274-1251.

E-mail: ctomaz@unb.br

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In order to assess the cognitive system, which mediates both recognition and recall, researchers have used the delayed non-matching to sample test (DNMS). In a typical DNMS procedure, trials comprise of an acquisition (sample) phase separated from a test phase

by a delay. During the acquisition phase, subjects are presented to a sample stimulus, whereas in the test phase they face two stimuli, one of which is the original sample. The subject is rewarded if chosen the new stimulus. Stimuli vary randomly from trial to trial, such that no single stimulus is associated with the reinforcement.⁸ Success in these tasks has been interpreted as “conceptual” learning, since the rule that allows subjects to make a correct choice has to be generalized in each single trial. Memory can be assessed by increasing the delay between sample and test trials.^{8,9}

In the other hand, the habit system seems to mediate stimulus-response retention, skill and habit learning. In monkeys, the Concurrent Discrimination Learning task (CDL) is believed to be suitable for evaluating this type of memory, as subjects solving the test progressively over many trials.^{8,9,10} In this kind of task, subjects are required to learn a list of pairs of objects concurrently, in which each pair has only one rewarded stimulus.^{8,9,11} The subject has to learn specific characteristic of the objects and associate them with the reward.

Whereas the corticostriatal system is believed to be functionally mature at the birth, the corticolimbic circuit seems to develop later in life.^{8,12} This ontogenetic dissociation in these two memory systems occurs not only in monkeys, but also in humans.^{13,14,15} For instance, Overman (1990) tested children in DNMS task using a rate of 15 trials/day to a criterion of 87% correct response for two consecutive test days. He found that the youngest group of children (12-15 months old) only attained the criterion after 20 weeks of continuous training and it had the lowest rate of learning compared with the other four studied groups. By the other side, the performance of the two oldest groups (18-20 month-old and 22-32 month-old) was above chance since the beginning of the test. Whereas children were able to solve a concurrent discrimination task, 12 month-old children needed 8.7 days to reach the learning criterion and 18-20 month-old attained the criterion in 6 days.¹⁴ Studies with rhesus monkeys also showed the ability to perform CDL as early as 3 months of age.⁸

Research on the neuropsychology of memory has a long tradition in using non-human primates as experimental subjects. They are the preferred choice of experimental animal, due to the fact that their cognitive capabilities and brain functions are comparable to those of humans.¹⁶

However, most part of studies employ Old World monkeys and few studies have used New World monkeys in this sense, the genus *Macaca* for example,

is largely used in procedures of delayed comparison memory tasks. Among the neotropical primates the New World capuchin monkey, genus *Cebus*, has been suggested as a good candidate for studies concerning high-cognitive abilities. This assumption comes from several lines of evidence in which capuchins are able to show: tool-using capacities,^{17,18,19} sharing food between group members outside the parent-offspring context and attitudinal reciprocity in food-sharing, a characteristic well described in chimpanzees;^{20,21} spatial knowledge to solve foraging problems;^{22,23,24} and learn by imitation, indicating some degree of social learning.²⁵ At the same time, some results indicate a lack of comprehension of cause-effect relations for this specie.^{20,26}

D’Amato and co-workers in the 1980’s reported that capuchins monkeys are able to process identity matching and conditional (or symbolic) matching, although they fail to transfer the matching rule from static to dynamic visual stimuli or from visual to auditory modality.^{27,28,29} In this version of delayed memory task, Delayed Matching to Sample/DMS, the subjects is rewarded when chooses the same object showed in the sample phase and not the new one.

Oddity concept learning has also been demonstrated in *Cebus albifrons*.³⁰ In a typical oddity task the subject is faced with three stimuli, two of which are identical and one different. The subject is reinforced for choosing the stimulus that is different. As with the matching concept, the critical test for assessing concept formation is the presentation of new stimuli items.

Although these data suggest that the capuchin monkeys seems to have a sophisticated level of cognitive abilities, little is known about how young versus adult capuchins perform in memory tasks mediated for both memory systems mentioned before. Therefore, the aim of this study was to investigate the cognitive capabilities of young and adult capuchin monkeys in performing a concurrent object discrimination learning task with 24-hr intertrial interval and a delayed non-matching to sample test with different delays.

MATERIALS AND METHODS

Procedures

Capuchin monkeys (*C. apella*) were tested in their own home cages in the Primate Center – University of Brasilia. The animals (were not food or water deprived, however food was removed from the cage during the experimental session. The experiment was carried out in a version of

the Wisconsin General Test Apparatus (WGTA) containing a mobile test tray with three food wells of 5 cm in diameter and 12 cm apart. The stimuli were "junk" plastic objects that differed in shape, size, color and texture. Pieces of grape were used as reward.

This present study was approved by the Animal Ethics Committee of the Institute of Biology, University of Brasília.

Behavioral Tasks

Two visual discrimination memory tasks were used to evaluate the performance of young and adult monkeys:

Concurrent Discrimination Learning task (CDL)

Ten animals were tested in this task. The young group was composed of five monkeys (two females and three males, 1 – 3 ½ years). The adult group had five adult monkeys (three females and two males) with estimated age between 6 - 10 years. One young and one adult subject had previous experience in visual discrimination tasks, but not in this specific task.

The CDL task consisted in the presentation of 20 different pairs of objects to the subjects (Set A). For each pair only one object was baited with food reward. Each object of the pair was present simultaneously over the lateral wells of the test tray. After the monkey had gotten its reward by displacing one of the objects, a new trial was presented with the second pair of stimuli and so on until all 20 pairs had been displaced. The same list of objects was then repeated after a 24-hr intertrial interval (24-hr ITI). The objects of the pairs and the serial order of the pairs remained constant, except for the left-right position of the baited object that varied pseudorandomly across the sessions.

The test was performed every day until the subject had attained the learning criterion setting at 90% (i.e., 18 correct responses in 20 trials) at the same session. A second set of new objects, Set B, was presented in the same way nine days after completing Set A. We analyzed the number of sessions (days), errors and trials that each monkey took to reach the criterion.

Delayed Non-Matching to Sample (DNMS)

This task assessed the development of the recognition memory using a DNMS procedure with young and adult subjects. The same 5 young subjects used in the CDL experiment and 6 different adult subjects (3 females and 3 males) with estimated age ranges from 4

to 8 years were tested. All animals of the adult group had previous experience in Delayed Matching to Sample (DMS) task. However, a recent study showed that performance in DNMS test by subjects that had experience in DMS task did not differ from naïve animals.³¹

Test procedures were as follows. At the start of each trial, an object was placed over the central food well in the tray. The screen was then raised, and the subject was able to see the object (sample trial). After an observing response was made towards the object, the wooden screen was lowered to prevent the subject's view of the food wells. Eight seconds later, the screen was raised once again and the animal was faced with two objects, one was the same presented before and the other a new one (test trial). The subject had to displace the new object in order to obtain the reward. Fifteen to twenty seconds later (intertrial interval) a new trial begun with a new pair of stimuli. Left or right position of the correct object varied pseudorandomly in order to avoid position bias. New pairs of objects were used on every trial. The experimental session lasted about one hour and testing occurred three days a week. A session could be interrupted before one hour if the subject had failed to respond for about 10-min. Training at 8 s delay condition continued until the animal reached the learning criterion of 9 correct responses out of 10 consecutive trials. After reaching the criterion, subjects' memory performance was assessed at delays of 15 s, 60 s e 120 s (100 trials to each delay) and 600 s (50 trials). Performance was scored in terms of number of trials to reach the learning criterion (8 s interval) and the mean percentage of correct responses across delays of 15 s to 600s (10 min).

Statistical Analysis

Wilcoxon Signed Ranks Test was used for intra-group comparisons and Mann-Whitney *U* -Test for inter-group comparisons in the CDL task.

To determine whether subjects' performance differed across delays, one-way ANOVA was used. A binomial test was employed to establish the 95% confidence limits around chance performance based on the number of test trials. Thus, the upper limit was calculated as 60% for 100 trials and 64% for 50 trials. The mean percentage of correct responses was compared to these confidence limits, and any performance above the upper limit was considered significant. A paired *t*-test was used to analyze if the number of trials to criterion that group required had attained significant differences.

RESULTS

The results indicated that both young and adult groups were able to perform the CDL task (Figure 1 a, b, c). However, the statistic analyses showed that only the young group had a significant decrease from Set A to Set B in terms of mean of sessions, trials and errors (Wilcoxon, all p s < .05).

Although the number of sessions, trials and errors had reduced from Set A to Set B in the adult group, these numbers were not significantly different (Wilcoxon; $Z = -1.483, p = .094$ for sessions; $Z = -1.214, p = .156$ for trials; $Z = -1.483, p = .094$ for errors).

Comparison between young and adult performances on Set A and on Set B indicated no significant differences (Set A: Mann-Whitney test; $U = 10.5, p = .369$; $U = 11, p = .421$; $U = 10, p = .325$, for sessions, errors and trials, respectively, Set B: Mann-Whitney test; $U = 5, p = .075$ for sessions; $U = 6, p = .111$ for errors; $U = 4.5, p = .056$ for trials).

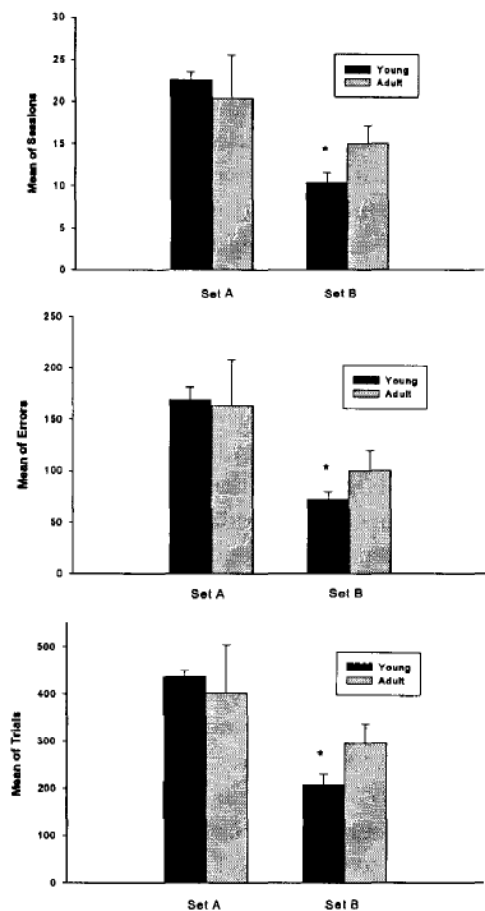


Figure 1. Mean of sessions required by young and adult capuchin monkeys in the Concurrent Discrimination Learning task to criterion. Mean of errors took by young and adult capuchin monkeys in the Concurrent Discrimination Learning task to criterion. Mean of trials required by young and adult capuchin monkeys in the Concurrent Discrimination Learning task to criterion.

The data indicated that all subjects in both groups reached criterion at the DNMS training. Although the young needed more trials ($X = 207.8 \pm SD = 41.56$) to learn the criterion than the adult group ($X = 173.67 \pm SD = 28.94$ trials), paired comparisons did not reach statistical significance ($t = .436, p = .673$).

Figure 2 summarized the mean of correct responses in the DNMS test in all different delays (8, 15, 60, 120 and 600 s) for the young and adult groups. In the memory task, the percentage of response choosing the new object did not differ across delays in young ($F = .142, p = .933$) and adults ($F = .417, p = .743$).

Also, in all intervals the adult group, but not young subjects, performed above the upper confidence limits (above 60% for 15 s, 60 s and 120 s; above 64% for 600 s).

DISCUSSION

The present study shows that young and adult capuchin monkeys are able to learn a concurrent discrimination learning task with a 24-hr delay interval.

The significant improvement from Set A to Set B in young capuchin monkeys indicate that these subjects were capable to learn a specific rule and transfer it to a task that requires the same cognitive process. This phenomena known as learning set, is considered a

DNMS

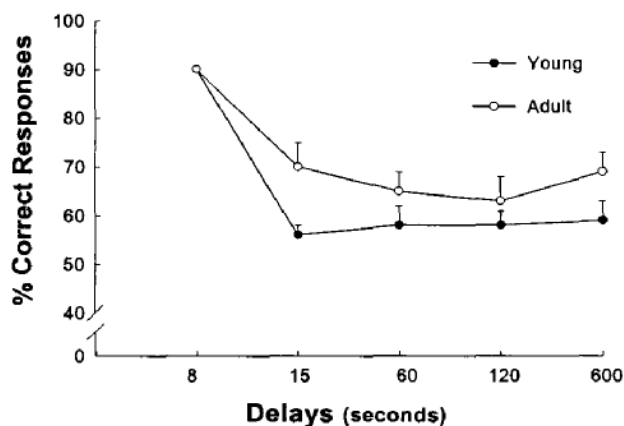


Figure 2. Percentage of correct responses in DNMS test by young and adult groups across delays of 8s, 15s, 60s, 120s, 600s (10 min)

characteristic of habit memory system evolved in problem solve skills. Our findings are similar to that observed for infant rhesus monkeys in a previous study.³² At 3 months of age they required an average of 18 sessions to attained the criterion on Set A and 6 sessions at the Set B, contrasting with our young capuchin monkeys that took in average 22 sessions on Set A and 13 sessions on Set B.

In addition, our adult capuchin monkeys needed an average of 20 sessions to attain the criterion on Set A and 15 sessions on Set B, while adult rhesus monkeys needed 10 sessions to learn the CDL task in both Sets.⁹ Controversially, the adult monkeys did not significantly reduced the number of sessions, errors or trials to attained the criterion from Set A to Set B as the young group did.

However, although only the young capuchins learned Set B faster than Set A, we did not find differences between young and adults' scores in both sets. Other study using rhesus monkeys found only a initial delay in learning of infant group compared with adults on Set A, but no differences in the infant' and adult' scores on Set B either.⁸ One possible explanation suggested by Bachevalier and co-workers^{8,10} is that the habit and the cognitive systems are both mature in adult subjects, which could be promoting a competition in the resolution of problems. Consequently, the adults could be applying a more complex strategy to solve CDL than necessary and it could causes no improvement from Set A to Set B. In young subjects, no competition between the memory systems could be established since only the habit memory is operating early in life. As a result, young monkeys would be more efficient in performing Set B than adults.

Furthermore, our results show a difference in performance between young and adult subjects in the DNMS task. While the adult' scores were above of the upper limit of confidence across all tested delays, the young subjects performed the DNMS memory test by chance level.

Similar results are found with Old World monkeys. Bachevalier and Mishkin (1984) demonstrated that 4 month-old rhesus monkeys were unable to perform DNMS differently from chance. Only with 2 years of age, the subjects obtained adult-like results.

Besides, data with humans showed the same developmental progression of the performance on the DNMS task. Overman and colleagues (1992) found that the youngest group (12-15 month-old) only attained the

learning criterion by the time they were 19 months-old, while the 26-month-old group reached criterion in an average of 11 days after the beginning of the test.

Nevertheless, our data pointed to some differences in the DNMS task performed by humans, *C. apella* and rhesus monkeys. Young capuchin monkeys attained the learning criterion at 8 s delay faster than children and infant rhesus monkeys. While our young monkeys took in an average of 208 trials, 12-15 month old children only attained the criterion in 1845 trials and monkeys with 3 months of age needed 720 trials. However, in the adulthood, humans were faster than monkeys. Capuchins and rhesus monkeys needed a similar number of trials (174 and 160 trials, respectively) to reach the criterion, while humans required only 90 trials to criterion.^{8,15}

Usually in DNMS tasks, performance is influenced by the length of the delay interval,^{33,34,35} where choice accuracy declines as a function of the time between sample and choice trials. Surprisingly, however, the subjects in the present study did not show a decrease in scores across the delays. Two possible explanations may account for capuchins' performance. First, a stable performance across delays may have been observed in our study due to the fact that subjects were free moving tested in their own home cages, without stress caused by removing the animals from their cages. On the other hand, Zola and colleagues (2000) found a drop in the performance of the control group at 10 min and 40 min delays. However, differently from our experimental procedures, during the long delays the animals were removed from the test apparatus and placed back in their home cage. It is possible that these methodological aspects may contribute for the decrease in performance observed in the previous study.⁷ A second possibility for the capuchins' performance is related to possible differences between species. Although it was already demonstrated that capuchin monkeys are able to process same/different concept in delays ranging from 0 to 32 s,^{27,28,29} there are few studies investigating DNMS with unique-trial.^{8,31}

Since it was found that human infants and infant monkeys have a good performance in the CDL task, their poor scores on DNMS test cannot be attributed to deficits in attention, motivation, stimulus-reward association or perceptual abilities.^{10,14} An explanation for the differences in performing CDL and DNMS by young subjects is the fact that these two tasks require distinct cognitive processes and these processes are mediated by two independent neural systems that mature at different times.^{8,12,36}

The CDL task requires that the subject retain a representation of stimuli, compare their features and associate objects' qualities with reward. However, in the DNMS test in our study we used a unique trial discriminanda, i.e. new pairs of stimuli are utilized on each trial. This procedure implies that, the subject has to use abstract relations in order to solve the problem, and not that the non-matching correct response occurs as an association between particular discriminanda.^{37,38} Thus, DNMS implies in a more demanded cognitive task than the object discrimination learning task.

It has been proposed that different brain areas are involved in the DNMS task. Several studies in macaques demonstrated a sustained neuronal activity within the dorsolateral prefrontal cortex during the delay period of DNMS memory task.^{39,40,41} In addition, selective lesions to the perirhinal and entorhinal cortex⁴² and hippocampus and parahippocampal area impair performance in DNMS.⁴³ However, several studies have demonstrated that some areas in this cortico-limbic circuit are not functionally mature early in the life.^{6,12,14,36} As a result, as showed later, the ability to perform the DNMS task improves with age according to the development of these cerebral areas.^{13,14,36}

Although no lesion data are available for *Cebus* genus, the outcomes from this behavioral study are similar to those obtained with rhesus monkeys. It is known that the genus *Cebus* is the only New World monkey whose cerebral cortex citoarchitecture pattern resembles that of Old World monkeys, particularly the genus *Macaca*.⁴⁴ The most apparent similarity between *Cebus* and *Macaca* is in the temporal and frontal lobes' cortices.⁴⁴ Thus, it seems reasonable to suggest that in *Cebus*, CDL and DNMS are mediated by neuroanatomical substrates similar to those found in *Macaca*, however neurophysiological studies are necessary to test this possibility.

According to previous evidence at literature^{8,15,36} our results suggest the existence of two distinct memory systems with different ontogenetic development, a non-cognitive learning system and a cognitive system. The first one seems to be present in young *Cebus apella*, at least, as early as one year old, and the later seems to be not functionally mature until the age of 3 ½ years.

Finally, the results in this present study, taken together with those reporting other cognitive abilities in capuchin monkeys,^{27,28,29,31} suggest that this specie can be a useful model in investigations of neurobiological basis of memory and its dysfunction .

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REFERENCES

1. Gibson KR. Evolution of human intelligence: the roles of brain size and mental construction. *Brain Behav Evol* 2002;59:10-20
2. Miller EK, Freedman DJ, Wallis JD. The prefrontal cortex: categories, concepts and cognition. *Olhar referencia*
3. Kety SS. The evolution of concepts of memory. In: Beckman AL, ed. *The Neural Basis of Behavior*. Spectrum Publications, 1982: 95-101
4. Baddeley A. Cognitive psychology and human memory. *Trends Neurosci* 1988; 11: 176-181
5. Tulving E. Multiple memory systems and consciousness. *Hum Neurobiol* 1987; 6: 67-80
6. Mishkin M, Malamut BL, Bachevalier J. Memories and habits: Two neural systems. In: Lynch G, McGaugh L, Weinberger NM, eds. *Neurobiology of learning and memory*. New York: Guilford Press, 1984: 65-77
7. Zola SM, Squire LR, Teng E, Stefanacci L, Buffalo EA, Clark RE. Impairment recognition memory in monkeys after damage limited to the hippocampal region. *J Neurosci* 2000; 20: 451-463
8. Bachevalier J, Mishkin M. An early and a late developing system for learning and retention in infant monkeys. *Behav Neurosci* 1984; 98: 770-778
9. Malamut BL, Saunders RC, Mishkin M. Monkeys with combined amygdalo-hippocampal lesions succeed in object discrimination learning despite 24-hour intertrial intervals. *Behav Neurosci* 1984; 98: 759-769
10. Bachevalier J, Brickson M, Hagger C, Mishkin M. Age and sex differences in the effects of selective temporal lobe lesion on the formation of visual discrimination habits in rhesus monkeys (*Macaca mulatta*). *Behav Neurosci* 1990; 104: 885-899
11. Gaffan D, Murray EA. Monkeys (*Macaca fascicularis*) with rhinal cortex ablations succeed in object discrimination learning despite 24-hr intertrial intervals and fail at matching to sample double sample presentations. *Behav Neurosci* 1992;106: 30-38
12. Alvarado MC, Bachevalier J. Revisiting the maturation of medial temporal lobe memory functions in primates. *Learn Mem* 2000; 7: 244-256

13. Diamond A. Rate of maturation of the hippocampus and the developmental progression of children's performance on the delayed non-matching to sample and visual paired comparison tasks. In: Diamond A, ed. The development and neural basis of higher cognitive functions. New York: New York Academy of Sciences Press, 1990: 394-426
14. Overman WH. Performance on traditional match-to-sample, non-match-to-sample, and object discrimination task by 12 to 32 month-old children: A developmental progression. In: Diamond A, ed. The development and neural basis of higher cognitive functions. New York: New York Academy of Sciences Press, 1990: 365-383
15. Overman WH, Bachevalier J, Turner M, Peuster A. Object recognition versus object discrimination: comparison between human infants and infant monkeys. Behav Neurosci 1992; 106:15-29
16. King FA, Yarbrough CJ, Anderson DC, Gordon P, Gould KG. Primates. Science 1988; 240:1475-1482
17. Chevalier-Skolnikoff S. Spontaneous tool use and sensorymotor intelligence in *Cebus* compared with other monkeys and apes. Behav Brain Sci 1989; 12:561-627
18. Visalberghi E. Capuchin monkeys: a window into tool use in apes and humans. In: Gibson P, Ingold G, ed. Tools, Language and Cognition in Human Evolution. Cambridge: University Press, 1993:138-150.
19. Visalberghi E, Fragaszy DM, Savage-Runbaugh S. Performance in a tool-using task by common chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), an orangutan (*Pongo pygmaeus*), and capuchin monkeys (*Cebus apella*). J Comp Psychol 1995; 109:52-60
20. De Waal FB, Berger ML. Payment for labour in monkeys. Nature 2000; 404:563
21. Westergaard GC, Suomi SJ. Transfer of tools and food between groups of tufted capuchins (*Cebus apella*). Am J Primatol 1997; 43:33-41
22. De Lillo C, Aversano M, Tuci E, Visalberghi E. Spatial constraints and regulatory functions in monkeys' (*Cebus apella*) search. J Comp Psychol 1998; 112:353-362
23. De Lillo C, Visalberghi E, Aversano M. The organization of exhaustive searches in a patchy space by capuchin monkeys (*Cebus apella*). J Comp Psychol 1997; 111:82-90
24. Janson CH. Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. Anim Behav 1998; 55:1229-1243
25. Custance D, Whiten A, Fredman T. Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). J Comp Psychol 1999; 113:13-23
26. Visalberghi E, Limongelli L. Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). J Comp Psychol 1994; 108:15-22
27. D'Amato MR, Colombo M. Auditory matching to sample in monkeys (*Cebus apella*). Anim Learn Behav 1985; 13:375-382
28. D'Amato MR, Colombo M. On the limits of the matching concept in monkeys (*Cebus apella*). J Exp Anal Behav 1989; 52:225-236
29. D'Amato MR, Salmon DP, Colombo M. Extent and limits of the matching concept in monkeys (*Cebus apella*). J Exp Psychol (Anim Behav) 1985; 11: 35-51
30. Thomas RK, Boyd MG. A comparison of *Cebus albifrons* and *Saimiri sciureus* on oddity performance. Anim Learn Behav 1973; 5:151-3
31. Tavares MCH, Tomaz C. Working memory in capuchin monkeys (*Cebus apella*). Behav Brain Res 2002; 131: 131-137
32. Bachevalier J, Hagger C, Bercu BB. Gender differences in visual habit formation in 3-month-old rhesus monkeys. Dev Psychobiol 1989; 22: 585-599
33. Pontecorvo MJ, Sahgal A, Steckler T. Further developments in the measures of working memory in rodents. Cogn Brain Res 1996; 3:205-13
34. Squire LR, Zola SM. Structure and function of declarative and nondeclarative memory systems. Proc Natl Acad Sci USA 1996; 93:13515-13522
35. Squire LR, Zola-Morgan S, Chen, KS. Human amnesia and animal models of amnesia: performance of amnesic patients on tests designed for the monkey. Behav Neurosci 1988; 102: 210-221
36. Bachevalier J. Ontogenetic development of habit and memory formation in primates. In: Diamond A, ed. The development and neural basis of higher cognitive functions. New York: New York Academy of Sciences Press, 1990: 1-19
37. Thomas RK. Investigating cognitive abilities in animals: unrealized potential. Cogn Brain Res 1996; 3:157-66
38. Zayan R, Vauclair J. Categories as paradigms for comparative cognition. Behav Proc 1998; 42:87-99
39. Fuster JM. Executive frontal functions. Exp Brain Res 2000; 133:66-70
40. Goldman-Rakic PS. Cellular basis of working memory. Neuron 1995; 14:477-85
41. Petrides M. The role of the mid-dorsolateral prefrontal cortex in working memory. Exp Brain Res 2000; 133:44-54
42. Gaffan D, Murray EA. Monkeys (*Macaca fascicularis*) with rhinal cortex ablations succeed in object discrimination learning despite 24-hr intertrial intervals and fail at matching to sample double sample presentations. Behav Neurosci 1992; 106: 30-38

43. Zola-Morgan S, Squire LR, Amaral DG. Lesions of the hippocampal-formation but not lesions of the fornix or mammillary nuclei produce long-lasting memory impairment in monkeys. *J Neurosci* 1989; 9: 898-913
44. Falk D. Comparative study of the endocranial casts of New and Old World monkeys. In: Ciochon RL, Chiarelli, AB, editors. *Evolutionary Biology of the New World Monkeys and Continental Drift*. San Diego: Plenum Press, 1981:157-201