

Manuscript Number: BBR-D-13-01139R2

Title: Effects of brief time delays on matching-to-sample abilities in capuchin monkeys (*Sapajus* spp.)

Article Type: Research Reports

Keywords: Visual perception; Sensory memory; Short-term memory; Matching-to-sample; Capuchin monkeys

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**Abstract:** Traditionally, studies of delayed matching-to-sample (DMTS) tasks in nonhuman species have focused on the assessment of the limits of the retrieval of information stored in short- and long-term memory systems. However, it is still unclear if visual recognition in these tasks is affected by very brief delay intervals, which are typically used to study rapidly decaying types of visual memory. This study aimed at evaluating if tufted capuchin monkeys' ability to recognise visual stimuli in a DMTS task is affected by (i) the disappearance of the sample stimulus and (ii) the introduction of delay intervals (0.5, 1.0, 2.0 and 3.0 seconds) between the disappearance of the sample and the presentation of the comparison stimuli. The results demonstrated that the simple disappearance of the sample and the introduction of a delay of 0.5 seconds did not affect capuchins' performance either in terms of accuracy or response time. A delay interval of 1.0 second produced a significant increase in response time but still did not affect recognition accuracy. By contrast, delays of 2.0 and 3.0 seconds determined a significant increase in response time and a reduction in recognition accuracy. These findings indicate the existence in capuchin monkeys of processes enabling a very accurate retention of stimulus features within time frames comparable to those reported for humans' sensory memory (0.5-1.0 seconds). The extent to which such processes can be considered analogous to the sensory memory processes observed in human visual cognition is discussed.

## Research Highlights

- We examine capuchin monkeys' ability to match visual stimuli after brief delays.
- 0.5 sec intervals do not affect either response accuracy or response time.
- 1.0 sec intervals do not affect response accuracy but increase response time.
- 2.0 and 3.0 sec intervals decrease response accuracy and increase response time.
- Effects consistent with those ascribed to iconic memory in humans.

## Responses to the Reviewer

We were extremely pleased that the reviewer was satisfied with the vast majority of our revisions and that s/he felt that we had been very responsive and addressed most of her/his concerns. We are also pleased to read that the reviewer felt that all her/his specific comments have been addressed.

We have now further revised the article in several places (P 4 lines 46-48; P 6 lines 53-59; P 7 lines 1-3; P 13 lines 44-49; P 14 lines 1-7; P 18 lines 48-54; P 18 line 56 – P 19 line 1) in order to make it absolutely clear that we make no claims regarding the high-capacity of the memory system that we have observed in capuchin monkeys so that, in that respect it could be considered analogous to human iconic memory. All our claims are based on analyses of the effects of time delay which, because they suggest a discontinuous function of the delays, can be considered indicative of separate memory processes at early stages of the encoding of visual information in monkeys.

As suggested by the reviewer we now present effect sizes for paired  $t$  tests and 95% confidence intervals for all effect size values (i.e., CIs for partial Eta squared values in  $F$  tests and CIs for Cohen's  $d$  values in  $t$  tests) concerning both significant and non-significant differences to help readers interpret the range of effect sizes for each test (P 13 lines 12 and 27; P 16 line 7; P 17 lines 1, 27, 46 and 51).

As far as we understand from the reviewer comments, these were the only two concerns still outstanding and we hope to have addressed them and that the article could now be accepted for publication in BBR.

**Effects of brief time delays on matching-to-sample abilities in capuchin monkeys (*Sapajus* spp.)**

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Number of text pages: 30

Number of figures: 5

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## Abstract

Traditionally, studies of delayed matching-to-sample (DMTS) tasks in nonhuman species have focused on the assessment of the limits of the retrieval of information stored in short- and long-term memory systems. However, it is still unclear if visual recognition in these tasks is affected by very brief delay intervals, which are typically used to study rapidly decaying types of visual memory. This study aimed at evaluating if tufted capuchin monkeys' ability to recognise visual stimuli in a DMTS task is affected by (i) the disappearance of the sample stimulus and (ii) the introduction of delay intervals (0.5, 1.0, 2.0 and 3.0 seconds) between the disappearance of the sample and the presentation of the comparison stimuli. The results demonstrated that the simple disappearance of the sample and the introduction of a delay of 0.5 seconds did not affect capuchins' performance either in terms of accuracy or response time. A delay interval of 1.0 second produced a significant increase in response time but still did not affect recognition accuracy. By contrast, delays of 2.0 and 3.0 seconds determined a significant increase in response time and a reduction in recognition accuracy. These findings indicate the existence in capuchin monkeys of processes enabling a very accurate retention of stimulus features within time frames comparable to those reported for humans' sensory memory (0.5-1.0 seconds). The extent to which such processes can be considered analogous to the sensory memory processes observed in human visual cognition is discussed.

*Keywords:* Visual perception; Sensory memory; Short-term memory; Matching-to-sample; Capuchin monkeys

## 1. Introduction

Nonhuman primates are widely used as animal models of human memory in cognitive neuroscience (e.g., [1]). To assess the plausibility of such models it is important to gather as much information as possible concerning similarities and difference among memory processes in nonhuman primates in relation to the vast literature on human memory. Moreover, the assessment of the similarity of memory processes in a variety of species at different taxonomic distance from humans can provide important information concerning the evolution of human memory.

Atkinson and Shiffrin [2] proposed a Multistore Model of Memory including three separate memory stores: the Sensory Memory, the Short Term Memory (STM) and the Long Term Memory (LTM). In this model, each store has a different duration, capacity and mode of encoding. For example, the visual system possesses sensory memory for stimuli features such as size, shape, colour and location. It has been argued that the temporary permanence of information that enters the sensory store allows the visual system to select which aspects of the input should be elaborated by further memory processing before it is eliminated from this preliminary store [3]. Despite the ubiquity of this sensory store in models of visual processing, the relationship between sensory memory processes and the subsequent short-term elaboration of visual information is still to be fully understood. For example, it is not clear which visual memory tasks are supported by long-lasting sensory memory processes or by early short-term memory processes [4]. Moreover, little is known about how these very early stages of memory processing work in other species.

Two main questions led the study of memory processes and contributed to the formulation of the Multistore Model of Memory: (1) how long information can be retained by each store?, and (2) how much information can be retained by each store? Most research, especially on nonhuman species, has traditionally been directed to the former issue and has

1 focused on the duration of the memory traces with particular attention to short-term memory  
2 processes. Methodological differences between the memory tests used with human and  
3 animals contribute to the difficulty of direct comparisons of memory processes across species.  
4 Memory decay processes in humans are assessed by both recall and recognition tasks, whereas  
5 several tasks used with nonhuman species are based on recognition. In fact, nonhuman  
6 subjects' visual memory is usually assessed training animals to recognise familiar stimuli  
7 after delay intervals. As a consequence, in these tasks the stimulus which has to be identified  
8 is always available to the subject during the memory test. Notwithstanding this, both in  
9 human and nonhuman subjects, short-term memory processes have been shown to maintain  
10 memory traces for time intervals which may vary from few seconds to several minutes  
11 according to the type of tasks and stimuli presented (humans [5]; capuchins [6,7]; macaques  
12 [8]; baboons [9]; chicks [10]; crows [11]; pigeons [12]).

13  
14 Systematic studies using comparable procedures to evaluate short-term memory in  
15 human and nonhuman subjects are rare (e.g., [13-18]). For example, Weinstein [17] using an  
16 identical DMTS task found similar performance in rhesus monkeys and three years old  
17 children with delay intervals of 5, 10 and 15 seconds. Similarly, in a recent study by Chelonis  
18 and colleagues [15] it has been found that the forgetting rates of rhesus monkeys and children  
19 up to 7 years old are similar.

20  
21 It is reasonable to expect that species with visual systems similar to that of humans, such  
22 as nonhuman primate species, should be sensitive to manipulations affecting memory within  
23 the time frame typical of human sensory memory. Previous studies regarding persistence of  
24 sensory processes in monkey species evaluated if by reducing ambient illumination to a very  
25 low level immediately after stimulus presentation can preserve after-images as cues for  
26 subsequent stimulus recognition [19-22]. However, conflicting results emerged when the level  
27 of illumination was manipulated during the delay-interval [19-22]. For example, D'Amato

and O'Neill [19] found that a delay-interval presented in darkness facilitated capuchin monkeys' matching performance. On the contrary, King and Clawson [20] found that squirrel monkeys tested on a delayed-response task performed better when the delay interval was lighted than when it was darkened. Finally, McDowell and Lynn Brown [22] reported that rhesus monkeys' performance in a delay-response task could improve either under darkness or regular room illumination during the delay interval depending on both training and test conditions.

Comparative studies on the ability to recognise previously observed visual patterns have often employed variations of the matching-to-sample (MTS) task (e.g., [23-33]). In this task, two or more comparison stimuli are presented and participants choose which of them resembles most closely a stimulus presented as sample. In the simultaneous MTS (SMTS) the sample stimulus remains visible when the comparison stimuli appear. In the delayed matching-to-sample (DMTS), the sample stimulus disappears at the same time as the presentation of the comparison stimuli (0-delay MTS) or a variable time delay can be imposed between the disappearance of the sample and the presentation of the comparison stimuli. When no delays are imposed between the presentation of the sample and the comparison stimuli (either SMTS or 0-delay MTS) participants are not required to code the stimuli in capacity bound memory stores since they would always be available perceptually either as physical stimuli (SMTS) or possibly as part of sensory memory (0-delay MTS). By contrast, when a longer delay is introduced between the disappearance of the sample and the presentation of the comparison stimuli (DMTS), the recognition of the matching stimulus is likely to rely on the memory representation of the sample and can prove more or less demanding as a function of the delay length.

Because DMTS tasks are suitable for testing a variety of species, they can provide important insight into the mechanisms of visual cognition by allowing meaningful

interspecies comparisons. Previous studies using DMTS tasks in nonhuman species have focused mainly on the assessment of the limits of the retrieval of information stored in short- and long-term memory systems. The results of these DMTS studies show that animals of different species (e.g., [6,7,34] capuchin monkeys; [8,35] macaques; [9] baboons; [11] crows; [12,27] pigeons; see also [35-37] for reviews on this topic) are able to perform correct stimulus matching even, in some cases, with delays of several minutes interposed between the offset of the sample and the presentation of the comparison stimuli. However, these works were especially aimed at identifying the length of time intervals which cause recognition accuracy to fall to chance level. More subtle effects of brief delay intervals, which do not completely disrupt response accuracy, have received less attention. Hence, the rapid deterioration of performance that often characterise the decline of accuracy at very short delays, still deserves a thorough analysis. An effect of the manipulation of the length of very brief intervals would highlight the role of a rapidly decaying type of visual memory in pattern recognition and, as such, it would be important to assess.

The present study aimed at evaluating if visual stimuli discrimination in matching-to-sample tasks involves processes facilitating recognition in time frames comparable to those ascribed to sensory memory in humans. In particular, we carried out two experiments to evaluate the effect of (i) the disappearance of the sample stimulus (Experiment 1: SMTS *vs.* 0-delay MTS), and (ii) the introduction of delay intervals between the disappearance of the sample and the presentation of the comparison stimuli (Experiment 2: 0-delay *vs.* 0.5, 1.0, 2.0 and 3.0 seconds of delay). On the basis of the above considerations, we predicted that the sample stimulus disappearance should impair the matching performance only at delays above 0.5sec. In fact, if memory mechanisms with timing similar to those reported for sensory memory in humans also pertain to monkeys, the introduction of delays beyond 0.5-1.0 sec should result in a decrease of response accuracy and/or response time, since at these intervals

memory processes should be beyond the time frame of operation of these early storage systems that in humans retain a detailed image of the stimuli. A further suggestion that capuchin monkeys may be equipped with separate storage systems roughly equivalent to human sensory and short-term stores would be provided by the observation that the consequences of increasing delays within time windows corresponding to different hypothesised subsystems are qualitatively different. By contrast, results suggesting a continuous function of the effects of delays on MTS performance would be indicative of a single type of processing which operates at a wide range of delay timings. We also aimed to assess whether or not this was the case by considering together the effects of the range of delays featured across the two experiments.

## **2. Experiment 1. Effect of the disappearance of the sample stimulus**

In Experiment 1, we assessed the effect of the presence/absence of the sample stimulus during the discrimination between the two comparison stimuli by comparing a Simultaneous MTS with a 0-delay MTS condition. Thus, we compared a condition that required perception only, without any need to retain a trace of the stimulus, with a condition that required a longer lasting internal retention of the stimulus to produce accurate responses, albeit within the timeframe of perceptual after effects and sensory memory, as reported in humans.

## 2.1 Methods

### 2.1.1 Subjects

The subjects were five tufted capuchins (*Sapajus* spp.<sup>1</sup>), two males (Sandokan and Robot) and three females (Pippi, Roberta and Rucola). All subjects were adults (age range: 11-30 years) born in captivity and hosted at the Primate Center of the Institute of Cognitive Sciences and Technologies, CNR, Rome, Italy. They lived in three groups, each housed in an indoor-outdoor enclosure (indoor: 5 m<sup>2</sup> x 2.5 m high; outdoor: 40-130 m<sup>2</sup> x 3 m high). Capuchins were individually tested in an adjacent experimental cage (0.76 m long x 1.70 m wide x 0.73 m high), that they could access through a sliding door. Each subject was separated from the group just before the daily testing session solely for the purpose of testing. No physical constraints or attachments were imposed on subjects while viewing the stimulus presentation. The testing occurred between 10:30 a.m. and 4:00 p.m. Water was freely available at all times. Fresh fruit, vegetables and monkey chow were provided in the afternoon after testing.

All monkeys were already familiar with the Simultaneous MTS procedure because they had been tested with a touchscreen based apparatus in tasks involving categorisation of visual stimuli and abstract concept acquisition [30,40]. Moreover, one monkey, Pippi, had been previously trained on tasks involving visual pattern discrimination (e.g., [41,42]). However, subjects had never been tested with a Delayed MTS procedure before.

### 2.1.2 Ethical note

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<sup>1</sup> Recent data has revealed that capuchin monkeys, traditionally identified as the single genus *Cebus*, are two genera: (i) the robust (tufted) forms are now classified as the genus *Sapajus*, and (ii) the gracile (untufted) forms retained as the genus *Cebus* [38,39]. Tufted capuchin monkeys host at the Primate Center of the CNR derived from animals of different provenience and are considered as unknown combinations of species of the genus *Sapajus*.

1 The research protocol for this study was approved by the Italian Health Ministry (Central  
2 Direction for the Veterinary Service, approval n. 11/2011-C). Housing conditions and  
3  
4 experimental procedures were performed in full accordance with the European law on  
5  
6 humane care and use of laboratory animals and complied with the recommendations of the  
7  
8 Weatherall report (The use of non-human primates in research). To increase three-  
9  
10 dimensional space available to the animals, indoor enclosures were furnished with perches  
11  
12 and ropes and outdoor enclosures were furnished with logs, branches and ropes. Moreover,  
13  
14 the presence of natural substrates, including woodchips on the ground, served to promote  
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16 monkeys' exploratory behaviours. All subjects were familiar with the experimental cage, the  
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18 experimental routine and the experimenters.  
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### 26 *2.1.3 Apparatus*

27  
28 The computerised testing station consisted of a PC (Model AMD Athlon 1200) connected  
29  
30 to a 19" touchscreen (Model E96f+SB, CRT, ViewSonic) and an automatic food dispenser  
31  
32 (Model ENV-203-45, MED Associates, Inc. Georgia, VT) (Figure 1). E-Prime software  
33  
34 (Psychology Software Tools, Inc.) was used for the presentation of the stimuli and the  
35  
36 recording of the subject's response. When the monkey provided the correct response, the  
37  
38 food dispenser delivered a 45-mg banana-flavoured pellet (TestDiet, Richmond, IN, USA)  
39  
40 into a Plexiglas feeding cup (10 cm wide x 5 cm deep x 3.5 cm high) located 16 cm below the  
41  
42 touchscreen in the centre.  
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48 A wooden frame (48 cm wide x 64 cm high x 30 cm deep) with a central aperture (36 cm  
49  
50 wide x 26 cm high) surrounded the touchscreen. The food dispenser was placed behind the  
51  
52 wooden frame, out of sight of the subject. Moreover, an additional LCD monitor was placed  
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54 at the back of the touchscreen to allow the experimenter to see the progress of the session so  
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56 as to remove the apparatus at the end of the session. The touchscreen, food dispenser and  
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additional LCD monitor were mounted on the top shelf of a trolley (81 cm long x 45 cm wide x 80 cm high), whereas the PC was on the bottom shelf.

The apparatus was placed 15 cm from the grid of the experimental cage within the arm's reach of the subject. The grid was made of horizontal metal bars (0.5 cm thick) that were separated by 4.5 cm.

A camcorder (Sony Handycam DCR-SR37) was positioned approximately 70 cm from the touchscreen monitor in order to record video images which included both the screen display and a back view of the monkey. This allowed us to monitor the subject's behaviour during testing.

#### *2.1.4 Stimuli*

The stimulus set comprised 192 stimuli (examples of the stimuli are shown in Figure 2). Each stimulus consisted of a white pattern (3 cm x 3 cm, i.e. 11.3° of visual angle) presented on a black background (6.5 cm x 6.5 cm, i.e. 23.4° of visual angle). All stimuli were constructed using cliparts and were converted into bitmaps before presentation on the computer screen.

#### *2.1.5 Procedure*

A matching-to-sample (MTS) task was adopted, in which three stimuli, the sample (SS) and the two comparison stimuli, the matching stimulus (S+), which was rewarded if selected, and the non-matching stimulus (S-), were presented on the computer screen. At the beginning of each trial, the sample stimulus appeared on the upper half of the screen, in the centre. Then, after the subject touched the sample stimulus, the two comparison stimuli were displayed simultaneously 4 cm below the sample, to the right and left, at a distance of 5 cm apart (Figure 1). In order to ensure that the monkeys attended the sample stimulus, the subject was required to touch the sample at the beginning of each trial. Then, according to the experimental condition,

the sample remained on the screen during the presentation of the comparison stimuli (simultaneous MTS, see Figure 1) or disappeared immediately after the subject had touched it (0-delay MTS). In both conditions, the comparison stimuli were produced without any delay when the subject touched the sample. The right/left positions of S+ and S- were randomly determined in each trial. The subject had to indicate its choice by touching one of the comparison stimuli on the screen; the computer automatically recorded the choice and the Response Time (RT). If the comparison stimulus was chosen correctly (S+), a food pellet was dispensed. If the incorrect stimulus (S-) was selected, no pellet was dispensed. A blank screen replaces the display immediately after the response of the subject. A correct response was followed by a 5-s inter-trial interval (ITI), whereas an incorrect response was followed by both a 10-s time-out (TO) and a 5-s ITI. During the experimental trials and the ITI, the screen was light grey; during the TO, the screen was green.

#### *2.1.6 Experimental design*

Experiment 1 included 16 48-trial sessions. In each session, half of the trials were of the simultaneous MTS condition and half of the trials were of the 0-delay MTS condition. Trials of the two conditions were randomly intermixed within each session. Within a session the same 24 pairs of stimuli were presented in both simultaneous and 0-delay conditions.

#### *2.1.7 Data analyses*

Both accuracy and the RT were used for the analyses. Accuracy was measured as the percentage of correct responses. RT was measured as the time between the appearance of the comparison stimuli and the subject's choice (i.e., the touch of a comparison stimulus). Only RT for correct choices were included in the analyses. All the experimental sessions were videotaped. The videos were used to detect instances where the subject turned away from the

1 screen/task during a trial, thus spuriously affecting the length of the delay interval between the  
2 appearance of the comparison stimuli and the subjects' response. All instances detected were  
3 removed from data analyses. One observer (VT) scored all videos and another observer (RS)  
4 scored independently a random selection of 20% of the videos (total 768 trials) to calculate  
5 inter-observer reliability. There was a perfect agreement between the two observers (Cohen's  
6 Kappa = 1.0).

7  
8 Because the Kolmogorov-Smirnov test showed that the distribution of data did not deviate  
9 from normality, we used parametric statistics to compare the accuracy scores and response times  
10 between different conditions. Statistical significance was set at  $p \leq 0.05$ .

## 2.2 Results

21  
22 The analyses of the videos of Experiment 1 revealed that there were no trials in which  
23 subjects turned away from the screen/task during the presentation of the stimuli.

24  
25 *Accuracy.* All subjects achieved 70% or a higher percentage of correct responses in both the  
26 simultaneous and the 0-delay condition [binomial  $z$  scores: Sandokan, sim = 87.3%, 0-del =  
27 91.4%; Roberta, sim = 85.7%, 0-del = 87.3%; Rucola, sim = 91.4%, 0-del = 91.7%; Pippi, sim =  
28 81.5%, 0-del = 78.1%; Robot, sim = 75.0%, 0-del = 72.4%, all  $P_s < .000003$ ]. Moreover, all  
29 subjects showed a performance that was significantly above the 50% level of chance  
30 performance in both the Simultaneous and the 0-delay MTS conditions from the very first  
31 testing session [binomial  $z$  scores: Sandokan, sim = 79.2% ( $p < .0008$ ), 0-del = 83.3% ( $p <$   
32 .0008); Roberta, sim = 95.8% ( $p < .0008$ ), 0-del = 87.5% ( $p < .0008$ ); Rucola, sim = 91.7% ( $p <$   
33 .0008), 0-del = 83.3% ( $p < .0008$ ); Pippi, sim = 83.33% ( $p < .0008$ ), 0-del = 75.0% ( $p = .0008$ );  
34 Robot, sim = 87.5% ( $p < .0008$ ), 0-del = 79.17% ( $p < .0008$ )].

Overall, across all testing sessions, capuchins' percentage of correct responses was significantly above the level of chance both in the Simultaneous [ $mean = 84.17\%$ ,  $SE = 2.79$ , one-sample  $t$ -test:  $t(4) = 12.26$ ,  $p = 0.0002$ ] and the 0-delay MTS [ $mean = 84.17\%$ ,  $SE = 3.83$ , one-sample  $t$ -test:  $t(4) = 8.93$ ,  $p = 0.0009$ ] conditions. Moreover, the mean percentage of correct responses did not vary significantly between the Simultaneous MTS and the 0-delay MTS [paired  $t$ -test:  $t(4) = .001$ ,  $p = 0.999$ , (Cohen's  $d = 0.0$ ; 95% CI for  $d$ : -1.24, 1.24)], (see Figure 3a).

*Response time.* The mean percentage of response time, as reported for accuracy measure, did not vary between the Simultaneous MTS ( $mean = 1157.37$  msec,  $SE = 87.56$ ) and the 0-delay MTS ( $mean = 1123.61$  msec,  $SE = 97.81$ ), [paired samples  $t$ -test:  $t(4) = 1.55$ ,  $p = 0.197$  (Cohen's  $d = 0.69$ ; 95% CI for  $d$ : -0.64, 1.89)], (see Figure 3b).

### 3. Experiment 2. Effect of short delay intervals

Experiment 2 aimed at evaluating the effect of the introduction of delay intervals between the disappearance of the sample and the presentation of the comparison stimuli. We compared the 0-delay condition with conditions with 0.5, 1.0, 2.0 and 3.0 seconds of delay, that is, to conditions in which the memory requirement of the task is minimal. In this experiment, we tested the following hypotheses. The first is that capuchin monkeys may possess memory processes operating within a timescale of human sensory memory and that preserve an accurate representation of incoming visual information. If that was the case we should have observed a selective impairment of matching performance at delays beyond 0.5-1.0, which is the time resolution of human sensory memory. The second is that, if separate memory mechanisms, with a different time resolution, operate within the range of intervals tested in this study, we should expect a pattern of significant effects of the increase of the delay indicative of a step function.

For example we should be able to detect the point in time where accurate memory processes operating at very short time frames and possibly akin to human sensory memory give way to a less detailed representation of the stimulus in short-term memory reflected in a significant decrease of performance at that point. Conversely, a more continuous pattern of deterioration of the memory trace reflected in a significant decrease in performance at different delay points would be more consistent with the gradual decay of the memory trace within a single storage systems encompassing the range of delays tested in this study.

### *3.1 Methods*

#### *3.1.1 Subjects, apparatus and stimuli*

Subjects, apparatus and stimuli were the same as those used in Experiment 1.

#### *3.1.2 Procedure*

The general procedure was the same as that used in the 0-delay condition of Experiment 1. However, in Experiment 2, four further different delay intervals were interposed between the disappearance of the sample and the appearance of the comparison stimuli: 0.5, 1.0, 2.0, 3.0 sec.

### 3.1.3 Experimental design

Experiment 2 included five 90-trial sessions of the delayed MTS condition. In each session there were five 18-trial blocks with different delays (0.0, 0.5, 1.0, 2.0, 3.0 sec). Trials of the five conditions were randomly intermixed within each session. To avoid the frequent repetition of the same stimuli, different stimuli were presented in different blocks of trials with a given delay. However, each stimulus was systematically presented in a different delay across sessions.

### 3.1.4 Data analyses

As in Experiment 1, both the accuracy and RT for correct responses were used for the analyses. All the experimental sessions were videotaped to assess if the subject turned away from the screen/task during the trials. One observer (VT) scored all videos and another observer (RS) scored independently a random selection of 20% of the videos (total 450 trials) to calculate inter-observer reliability. There was an excellent agreement between the two observers (Cohen's Kappa = 0.88).

As in Experiment 1, the Kolmogorov-Smirnov test showed that the group data did not differ from a normal distribution. Thus, we used parametric statistics to compare the accuracy and RT observed in the different conditions. Statistical significance was set at  $p \leq 0.05$ .

## 3.2 Results

The analyses of the videos of Experiment 2 revealed that in 136 trials (6.0 % of all trials) subjects were not looking at the screen when the comparison stimuli appeared (Rucola = 44, Sandokan = 34, Robot = 34, Pippi = 22, Roberta = 2). In the 0-delay condition this was an extremely rare event, which occurred in two subjects for only one time (Pippi, N = 1 and

Rucola,  $N = 1$ ). However, this happened more frequently with the increasing of the length of the delay, (Pearson correlation,  $r = .99$ ,  $N = 5$ ,  $p = 0.0003$ ). Moreover, the mean number of trials in which monkeys looked away or moved away from the screen differed significantly across delay intervals [ $F(4,16) = 7.83$ ,  $p = 0.0011$ ,  $\eta^2_p = .662$ , 95% CI for  $\eta^2_p$ : 0.01, 0.76]. Post hoc analyses (Tukey, HSD test) showed that subjects failed to maintain their attention on the task significantly more often in the 3-sec delay condition than in the 0-sec ( $p = 0.001$ ) and 0.5-sec ( $p = 0.006$ ) conditions, and that they failed more often in the 2-sec than in the 0-sec condition ( $p = 0.029$ ).

Because these trials featured an uncontrolled increase of the scheduled interval, which made them impossible to interpret, they were not subjected to any further analysis.

*Accuracy.* Each individual showed a level of performance which was significantly above the 50% chance level, in all five delay conditions (binomial  $z$  scores: all  $P_s < 0.05$ ), with the only exception of the oldest subject, Pippi, who showed a chance level of performance in the 2 and 3 sec delay conditions.

Overall, the percentage of correct responses for the group of monkeys was significantly above the level of chance in all the five conditions [one-sample  $t$ -tests: 0.0 sec,  $mean = 79.44\%$ ,  $SE = 3.47$ ,  $t(4) = 8.47$ ,  $p = 0.001$ ; 0.5 sec,  $mean = 73.15\%$ ,  $SE = 5.78$ ,  $t(4) = 4.00$ ,  $p = 0.016$ ; 1.0 sec,  $mean = 68.39\%$ ,  $SE = 4.98$ ,  $t(4) = 3.69$ ,  $p = 0.021$ ; 2.0 sec,  $mean = 63.63\%$ ,  $SE = 3.66$ ,  $t(4) = 3.72$ ,  $p = 0.020$ ; 3.0 sec,  $mean = 67.59\%$ ,  $SE = 5.47$ ,  $t(4) = 3.22$ ,  $p = 0.032$ ], (see Figure 4).

To assess if capuchins' matching accuracy was affected by the length of delay intervals and/or by practice effects across sessions, an ANOVA was carried out on the percentage of correct responses with MTS conditions (0.0, 0.5, 1.0, 2.0, 3.0 sec delayed) and different sessions (s1, s2, s3, s4, s5) as repeated measures. A significant main effect of delay condition [ $F(4,16) =$

4.93,  $p = 0.009$ ,  $\eta p^2 = .552$ , 95% CI for  $\eta^2 p$ : 0.06, 0.68] was found. Post hoc comparisons revealed that the mean percentage of correct responses observed in the 0-delay condition was significantly higher than that of the 2 ( $p = 0.006$ ) and 3 ( $p = 0.049$ ) sec delay conditions but did not differ from the level of response accuracy of the 0.5 ( $p = 0.501$ ) and 1.0 ( $p = 0.073$ ) sec delay conditions. No other significant main effect or interaction was found.

*Response time.* An ANOVA for repeated measures was carried out to assess if RT for correct responses differed between delay conditions (0.0, 0.5, 1.0, 2.0, 3.0 sec delay) and testing sessions (s1, s2, s3, s4, s5). A significant main effect of MTS condition was found [0.0 sec *mean* = 1201.38 msec, *SE* = 131.29; 0.5 sec *mean* = 1346.11 msec, *SE* = 123.80; 1.0 sec *mean* = 1354.37 msec, *SE* = 113.12; 2.0 sec *mean* = 1428.23 msec, *SE* = 81.04; 3.0 sec *mean* = 1480.02 msec, *SE* = 99.03;  $F_{(4,16)} = 9.45$ ,  $p = 0.0004$ ,  $\eta p^2 = .702$ , 95% CI for  $\eta^2 p$ : 0.27, 0.79, see Figure 5]. Post-hoc comparisons revealed that the mean response time is significantly lower in the 0-delay condition than in the 1.0 ( $p = 0.042$ ), 2.0 ( $p = 0.002$ ) and 3.0 ( $p = 0.0003$ ) sec of delay, whereas it did not differ from the 0.5 sec condition, even though  $p$  value approaches the significance ( $p = 0.058$ ). No other significant main effect or interaction was found.

*Experiment 1 versus Experiment 2.* A comparison between 0-delay conditions of Experiment 1 and 2 revealed a degree of accuracy significantly higher in Experiment 1 than Experiment 2 [ $t(4) = 4.29$ ,  $p = 0.013$ , (Cohen's  $d = 1.91$ ; 95% CI for  $d$ : 0.28, 3.18) ], whereas no difference was found in response time between the two experiments [ $t(4) = 1.54$ ,  $p = 0.199$ , (Cohen's  $d = 0.69$ ; 95% CI for  $d$ : -0.65, 1.89)].

#### 4. Discussion

1 The present study demonstrated that capuchins had the same response accuracy in both  
2 Simultaneous (84.17%) and 0-delay (84.17%) conditions (Experiment 1). This performance is  
3 well above chance level and is consistent with the accuracy levels observed in other studies that  
4 have used comparable computerised matching-to-sample tasks with two comparison stimuli and  
5 no delay intervals (e.g., capuchins: 81.94% [43] and 78.2% [30]; gorillas and orangutans:  
6 79.98% [44]). Thus, our findings indicate that capuchins solved these two matching conditions  
7 in an undifferentiated way. The mere disappearance of the sample stimulus from the screen,  
8 without the introduction of any delay interval before the presentation of the comparison stimuli,  
9 did not affect their response accuracy. Similarly, sample stimulus disappearance did not affect  
10 subjects' response time.

11 This finding is also consistent with previous studies indicating that monkeys seem to have  
12 a spontaneous tendency to visually inspect the sample stimulus for very short time intervals  
13 and increasing the time of permanence of a stimulus on the screen does not improve subjects'  
14 discrimination performance [45] unless that they are required to actively manipulate the  
15 stimulus, for example by repeatedly touching it before making a choice [46].

16 When we introduced short delay intervals in the MTS task we found that: (i) a delay of 0.5  
17 sec between the sample offset and the choice stimuli onset did not affect capuchins' ability to  
18 match visual patterns, (ii) a delay interval of 1.0 sec produced a significant increase in response  
19 time but did not affect recognition accuracy, and (iii) delays of 2 and 3 sec determined a  
20 significant increase in response time and a reduction in recognition accuracy (Experiment 2: 0-  
21 delay *versus* 0.5, 1.0, 2.0, 3.0 sec. delay). However, no further deterioration of performance was  
22 observed when the interval was increased from 2 to 3 seconds, even if this difference in the  
23 length of the delay was the same as that produced an effect at shorter delays.

24 Overall, these findings suggest the existence in nonhuman primates of separate memory  
25 mechanisms which facilitate visual recognition in time frames of less than one second and

1 which are similar to those of human sensory memory [4,47-49]. The MTS paradigm as featured  
2 in this study does not enable us to assess whether the characteristic of this type of memory in  
3 capuchins resembles that of humans in terms of capacity but our results would not be  
4 inconsistent with such a possibility. This specific issue could be addressed in further studies  
5 using partial recall in monkeys. This is however beyond the scope of this paper and its  
6 implementation with monkeys housed in the semi-natural setting conditions as those in our  
7 centre may prove challenging. Nevertheless, our results provide important information  
8 regarding the visual cognition of nonhuman primates.  
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There are still controversies surrounding the characterisation of the physiological bases of  
very early stages of visual memory processing in nonhuman primates. Recent  
neurophysiological data on nonhuman primates suggest that specific cortical areas support  
activities which occur in concomitance with the stimulus removal. Findings on cynomolgus  
macaques revealed that lesions of inferotemporal cortical area - TE - severely impair  
performance on recognition memory tasks even at delays as short as 0.5 sec and 1.0 sec [23,50].  
The impairment of recognition at short delays suggests that the monkeys in the TE lesion group  
could not perceive, attend to, or process the visual stimuli adequately. Moreover, this difficulty  
seems to be specific to the visual modality, because the same monkeys had a normal  
performance on a recognition memory task in the tactual modality [50]. Furthermore, recent  
bio-imaging studies in human adults suggest that tasks involving iconic memory in our species  
are associated with persistent activation in higher-order visual areas such as the occipito-  
temporal cortex, particularly the lateral-occipital complex - LOC – [51,52].

Moreover, our findings suggest a recognition system that allows a high degree of accuracy  
for delays up to 1.0 second, albeit with increased response times. At 0.5 sec of delay capuchins'  
response time did not differ from 0.0 sec of delay (i.e., any delay), whereas at 1.0 sec of delay,  
as well as at 2.0 and 3.0 sec, their response time is significantly longer than at 0.0 sec. This

1 finding is consistent with data obtained with baboons, which demonstrates that these Old World  
2 monkeys are able to solve a DMTS task with the same accuracy at 0.0 and 1.0 sec delay,  
3  
4 although at 1.0 sec delay baboons showed longer response time [9]. This suggests that the  
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6 increase in RT in DMTS can be indicative of an increased difficulty of retrieval processes when  
7  
8 the memory trace starts to decay but has not deteriorated to a degree that would affect accuracy.  
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11 We cannot exclude that increasing the familiarity with the task may improve the response  
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13 accuracy and/or the reduction of the response time in the delayed conditions. However, the lack  
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15 of differences in performance across the five sessions of Experiment 2 indicates that learning  
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17 effects did not intervene for any condition during the entire data collection. Moreover, the  
18  
19 absence of difference between Simultaneous and 0-delay MTS conditions in Experiment 1,  
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21 suggests that the simple introduction of a non-familiar condition does not necessarily lead to a  
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23 performance decline. Moreover, an alleged novelty effect of the delayed conditions would not  
24  
25 explain why different delay intervals should affect subjects' performance to a different degree.  
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27 For all these reasons, we believe that the variation in MTS behaviour observed in the different  
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29 delay conditions should rather be attributed specifically to underlying variations in the visual  
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31 processing of the stimuli.  
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39 Another observation regarding the behaviour of our subjects that deserves a comment is  
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41 the tendency of capuchins to turn away from the screen/task during a trial when the delay  
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43 interval increased. This was probably due to the fact that individuals were dealing with delayed  
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45 MTS conditions for the first time and, thus, had not previously learnt to tolerate a delay before  
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47 the appearance of the choice stimuli. In this case, this effect should disappear with increased  
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49 familiarity with the task. Alternatively, considering that we use very short delay intervals, this  
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51 finding could suggest that capuchins' attention to the task is relatively vulnerable. This  
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53 possibility would be consistent with the observation that capuchin monkeys frequently direct  
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1 their visual attention to the surroundings even while they are engaging in a problem solving  
2 task, and even when they are tested singly in a familiar and safe context [53].  
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4 A counterintuitive finding, in relation to possible learning effects in DMTS, is the higher  
5 percentage of correct responses observed in the 0-delay condition of Experiment 1 compared to  
6 the same condition of Experiment 2. It could be due to an effect of the type of trials intermixed  
7 with the 0-delay trials in the two experiments. In Experiment 1, 0-delay trials were intermixed  
8 with trials of a less demanding, condition (i.e. SMTS), with which the monkeys were already  
9 familiar from their experience in previous studies [30,40]. By contrast, 0-delay trials were  
10 intermixed with unfamiliar, more demanding, conditions (i.e. DMTS with 0.5, 1.0, 2.0 and 3.0  
11 sec delay) in Experiment 2. This finding suggests that the context in which a particular  
12 condition is presented could affect subjects' performance. The sensitivity of capuchin monkeys  
13 to the context provided by different type of trials presented within a testing session has been  
14 documented in experiments featuring MTS of hierarchical visual patterns [54]. In the present  
15 study, such sensitivity could be explained by a deleterious effect, on the motivation of the  
16 subjects, induced by frustration caused by the higher error rate in the trials interspersed with the  
17 0-delay trials in Experiment 2. It is also possible that the decrease in accuracy in the 0-delay  
18 trials in Experiment 2 is due to the need to allocate more cognitive resources to the more  
19 demanding trials with which they were interspersed. This would have had a detrimental effect  
20 on the amount of attentional resources left for the processing of the 0-delay trials in Experiment  
21 2.  
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23 Finally, the observation that our oldest subject, Pippi, a 30 years old female, exhibited the  
24 lowest level of response accuracy in all conditions, with particular difficulties emerging in 2.0  
25 and 3.0 sec delay conditions also deserves a comment. This finding is consistent with data on  
26 both humans and nonhuman primates in relation to ageing (e.g., [55,56]). For example, studies  
27 carried out on rhesus monkeys indicate a selective impairment in older subjects in delayed-  
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1 response tasks requiring short-term memory [55,57]. Moreover, the difference observed  
2 between old and young monkeys could not be reduced by providing the monkeys with  
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4 extensive training on the task [57]. In elderly humans, and most severely in those affected by  
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6 Alzheimer's disease, DMTS tasks revealed a similar delay-dependent impairment [56,58]. In  
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8 some cases, patients with dementia failed to solve even 0-dealy DMTS tasks [59]. Thus, our  
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10 findings indicate that nonhuman primate models could be informative in relation to age-related  
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12 cognitive deficits in both healthy and pathological human ageing.  
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16 Overall, these results confirm that delayed matching-to-sample procedures afford reliable  
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18 measures that provide important information regarding cognitive processing in memory and  
19  
20 perception. Furthermore, our findings highlight that capuchin monkeys show a certain degree of  
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22 similarity with humans at the level of visual coding addressed in this study. The comparison of  
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24 primate species with a different degree of phylogenetic distance from humans can potentially  
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26 provide information about the evolution of human visual cognition. In particular, our findings  
27  
28 provide information about the evolution of human visual cognition. In particular, our findings  
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30 on capuchin monkeys, which shared a common ancestor with humans until 35 million years  
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32 ago, suggest that mechanisms supporting the brief storage of detailed visual information in aid  
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34 of recognition may have emerged relatively early during the evolutionary history of primate  
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36 species. This evidence only represents a starting point for our understanding of the early visual  
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38 memory storage mechanisms in monkeys. Nevertheless we hope that it will encourage further  
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40 detailed investigations on this topic. Future studies in nonhuman species would need to refine  
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42 experimental procedures to characterise the visual memory decay not only as a function of  
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44 amount of time the information can be retained, but also as a function of quantity of  
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46 information that can be stored in different stages of the memory process.  
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## Acknowledgements

We wish to thank Massimiliano Bianchi and Simone Cartarinacci for help with animal management. We acknowledge Sara Privitera, Luca Santini and Leonardo Ancilotto for help with data collection and Raffaele Sardella for help with video scoring. We thank the anonymous reviewer for her/his thoughtful and constructive comments. We also thank the Comune di Roma-Museo Civico Zoologia and the Fondazione Bioparco for hosting the Unit of Cognitive Primatology and Primate Centre. This research was supported by the PNR-CNR Aging Program 2012-2014. The authors declare that they have no conflict of interest.

## References

- [1] Goldman-Rakic PS. Working memory and the mind. *Sci Am* 1992; 267:111-17.
- [2] Atkinson RC, Shiffrin RM. Human memory: A proposed system and its control processes. In Spence KW, Spence JT, editors. *Psychology of learning and motivation: Advances in research and theory* (Vol. 2), New York: Academic Press; 1968, p. 90-191.
- [3] Coltheart M, Lea CD, Thompson K. In defence of iconic memory. *Q J Exp Psychol* 1974; 26:633-41.
- [4] Sligte IG, Scholte HS, Lamme VAF. Are there multiple visual short-term memory stores? *PloS One* 2008; 3, e1699.
- [5] Baddeley A. *Human memory. Theory and practice*. Hove, Lawrence Erlbaum Associates Ltd; 1990.
- [6] Colombo M, D'Amato MR. A comparison of visual and auditory short-term memory in monkeys (*Cebus apella*). *Q J Exp Psychol* 1986; 4:425-48.
- [7] Etkin M, D'Amato MR. Delayed matching-to sample and short-term memory in the capuchin monkey. *J Comp Physiol Psychol* 1969; 69:544-49.
- [8] Overman WH, Doty RW. Prolonged visual memory in macaques and man. *Neurosci* 1980; 5:1825-31.
- [9] Rodriguez JS, Zvrcher NR, Bartlett TQ, Nathanielsza PW, Nijlanda MJ. CANTAB delayed matching to sample task performance in juvenile baboons. *J Neurosci Methods* 2011; 196:258-63.
- [10] Gibbs ME, Ng KT. Behavioural stages in memory formation. *Neurosci Lett* 1979; 13:279-83.
- [11] Goto K, Watanabe S. Visual working memory in jungle crows (*Corvus macrorhynchos*) in operant delayed matching-to-sample. *Japanese Psychol Res* 2009; 3:122–31.

- [12] Roberts WA, Grant DS. Studies of short-term memory in the pigeons using the delayed matching-to-sample procedure. In: Medin DL, Roberts WA, Davis RT, editors. Processes of animal memory. Hillsdale, NJ: Erlbaum; 1976, p. 79-112.
- [13] Basile B, Hampton RR. Monkeys recall and reproduce simple shapes from memory. Curr Biol 2011; 21:774-78.
- [14] Elmore LC, Ma WJ, Magnotti JF, Leising KJ, Passaro AD, Katz JS, Wright AA. Visual short-term memory compared in rhesus monkeys and humans. Curr Biol 2011; 21:975-79.
- [15] Chelonis JJ, Cox AR, Karr MJ, Prunty PK, Baldwin RL, Paule MG. Comparison of delayed matching-to-sample performance in monkeys and children. Behav Process 2014; 103:261-68.
- [16] Fagot J, De Lillo C. A comparative study of working memory: Immediate serial spatial recall in baboons (*Papio papio*) and humans. Neuropsychologia 2011; 49:3870-80.
- [17] Weinstein B. Matching-from-sample by rhesus monkeys and by children. J Comp Psychol 1941 ; 31:195-213.
- [18] Wright AA, Santiago HC, Sands SF, Kendrick DF, Cook RG. Memory processing of serial lists by pigeons, monkeys, and people. Science 1985; 229 (4710):287-89.
- [19] D'Amato MR, O'Neill W. Effect of delay-interval illumination on matching behavior in the capuchin monkey. J Exp Anal Behav 1971; 15:327-33.
- [20] King JE, Clawson JR. Delayed response by squirrel monkeys under various delay lighting conditions. Psychon Sci 1966; 6:429-30.
- [21] King JE, Flaningam MR, Rees WW. Delayed response with different delay conditions by squirrel monkeys and fox squirrels. Anim Behav 1968; 16:271-75.
- [22] McDowell AA, Lynn Brown, W. Intervening darkness and delayed response performance by rhesus monkeys. J Genet Psychol 1960; 97:59-65.

- [23] Buffalo EA, Ramus SJ, Squire RL, Zola SM. Perception and recognition memory in monkeys following lesions of area TE and perirhinal cortex. *Learn & Mem* 2000; 7:375-82.
- [24] Fujita K. Metamemory in tufted capuchin monkeys (*Cebus apella*). *Anim Cogn* 2009; 12:575-85.
- [25] Galvão OF, Barros RS, Dos Santos JR, Brino ALF, Brandão S, Lavratti CM, et al. Extent and limits of the matching concept in *Cebus apella*: a matter of experimental control? *The Psychol Rec* 2005; 55:219-32.
- [26] Galvão OF, Soares-Filho PSD, Barros RS, Souza CBA. Matching-to-sample as a model of symbolic behaviour for bio-behavioral investigations. *Rev Neurosci* 2008; 19:149-56.
- [27] Nelson KR, Wasserman EA. Temporal factors influencing the pigeon's successive matching-to-sample performance: sample duration, intertrial interval, and retention interval. *J Exp Anal Behav* 1978; 30:153-62.
- [28] Mishkin M, Delacour J. An analysis of short-term visual memory in the monkey. *J Exp Psychol Anim Behav Process* 1975; 1:326-34.
- [29] Oden DL, Thompson RKR, Premack D. Spontaneous transfer of matching by infant chimpanzees (*Pan troglodytes*). *J Exp Psychol Anim Behav Process* 1988; 14:140-45.
- [30] Truppa V, Garofoli D, Castorina G, Piano Mortari E, Natale F et al. Identity concept learning in matching-to-sample tasks by tufted capuchin monkeys (*Cebus apella*). *Anim Cogn* 2010; 13:1-14.
- [31] Vauclair J, Fagot J, Hopkins WD. Rotations of mental images in baboons when the visual input is directed to the left cerebral hemisphere. *Psychol Sci* 1993; 2:99-103.
- [32] Washburn DA, Hopkins WD, Rumbaugh DM. Video-task assessment of learning and memory in macaques (*Macaca mulatta*): Effects of stimulus movement on performance. *J Exp Psychol Anim Behav Process* 1989; 15:393-400.

- [33] Wright AA, Delius JD. Learning processes in matching and oddity: the oddity preference effect and sample reinforcement. *J Exp Psychol Anim Behav Process* 2005; 31:425-32.
- [34] Tavares MCH, Tomaz C. Working memory in capuchin monkey (*Cebus apella*). *Behav Brain Res* 2002; 131:131-37.
- [35] Shettleworth S. *Cognition, Evolution and Behavior*. Oxford: Oxford University Press; 1998.
- [36] Tomasello M, Call J. *Primate Cognition*. Oxford: Oxford University Press; 1997.
- [37] Wright AA. Memory processing. In: Wasserman EA, Zentall TR, editors. *The Oxford Handbook of Comparative Cognition*. Oxford: Oxford University Press; 2012, p. 239-60.
- [38] Lynch Alfaro JW, Boubli JP, Olson LE, Di Fiore A, Wilson B, Gutiérrez-Espeleta GA et al. Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *J Biogeogr* 2012; 39:272-88.
- [39] Lynch Alfaro JW, Silva J de S Jr, Rylands AB. How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. *Am J Primatol* 2012; 74:273-86.
- [40] Truppa V, Piano Mortari E, Garofoli D, Privitera S, Visalberghi E. Same/different concept learning by capuchin monkeys in matching-to-sample tasks. *PloS ONE* 2011; 6(8):e23809. doi:10.1371/journal.pone.0023809.
- [41] De Lillo C, Spinozzi G, Truppa V. Pattern recognition in tufted capuchin monkeys (*Cebus apella*): the role of the spatial organization of stimulus parts. *Behav Brain Res* 2007; 181:96-109.
- [42] Spinozzi G, De Lillo C, Truppa V. Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). *J Comp Psychol* 2003; 117:15-23.
- [43] D'Amato MR, Salmon DP, Colombo M. Extent and limits of the matching concept in monkeys (*Cebus apella*). *J Exp Psychol Anim Behav Process* 1985, 11:35-51.

- [44] Vonk J. Gorilla (*Gorilla gorilla gorilla*) and orangutan (*Pongo abelii*) understanding of first- and second-order relations. *Anim Cogn* 2003; 6:77-86.
- [45] D'Amato MR, Worsham RW. Delayed matching in the capuchin monkey with brief sample durations. *Learn & Motiv* 1972; 3:304-12.
- [46] Katz JS, Wright AA, Bachevalier J. Mechanisms of same/different abstract-concept learning by rhesus monkeys (*Macaca mulatta*). *J Exp Psychol Anim Behav Process* 2002; 28:358-68.
- [47] Coltheart M. The persistence of vision. *Philos Trans R Soc Lond B Biol Sci* 1980; 290:57-69.
- [48] Sperling G. The information available in brief visual presentations. *Psychol Monogr Gen Appl* 1960; 74:1-29.
- [49] Averbach E, Coriell AS. Short-term memory in vision. *Bell Syst Tech J* 1961; 40:309-28.
- [50] Buffalo EA, Ramus SJ, Clark RE, Teng E, Squire LR, Zola SM. Dissociation between the effects of damage to perirhinal cortex and area TE. *Learn & Mem* 1999; 6:572-99.
- [51] Ruff CC, Kristjánsson Á, Driver J. Readout from iconic memory and selective spatial attention involve similar neural processes. *Psychol Sci* 2007; 18:901-9.
- [52] Wong YJ, Aldcroft AJ, Large ME, Culham JC, Vilis T. The role of temporal synchrony as a binding cue for visual persistence in early visual areas: An fMRI study. *J Neurophysiol* 2009; 102:3461-8.
- [53] Fragaszy DM, Visalberghi E, Fedigan LM. The complete capuchin. The biology of the genus *Cebus*. Cambridge University Press; 2004.
- [54] De Lillo C, Spinozzi G, Palumbo M, Giustino G. Attention allocation modulates the processing of hierarchical visual patterns: a comparative analysis of capuchin monkeys (*Cebus apella*) and humans. *J Exp Psychol Anim Behav Process* 2011; 37:341-52.

- [55] Bartus RT, Fleming DL, Johnson HR. Aging in the rhesus monkey: Debilitating effects on short-term memory. *J Gerontol* 1978; 33:858-71.
- [56] Flicker C, Ferris SF, Bartus RT, Crook T. Effects of aging and dementia upon recent visuo-spatial memory. *Neurobiol Aging* 1984; 5:75-83.
- [57] Marriott JG, Abelson JS. Age differences in short-term memory of test-sophisticated rhesus monkeys. *Age* 1980; 3:7-9.
- [58] Sahakian BJ, Morris RG, Evenden JL, Heald JL, Levy R, Philpot M et al. A comparative study of visuospatial memory and learning in Alzheimer-type dementia and Parkinson's disease. *Brain* 1988; 3:695-718.
- [59] Steinunn Steingrimsdottir H, Arntzen E. Identity Matching in a Patient With Alzheimer's Disease. *Am J Alzheimers Dis Other Demen* 2011; 26:247-53.

## Figure captions

**Figure 1.** Experimental apparatus and stimuli presentation in the Simultaneous matching-to-sample condition

**Figure 2.** Examples of the stimuli used in Experiments 1 and 2

**Figure 3.** Experiment 1: (a) Percentage of correct responses (mean±SE) performed by the monkeys the SMTS and 0-delay MTS conditions (One-sample t-test: \*\*\*  $p < 0.001$ ); (b) Response time of correct responses (mean±SE) recorded the SMTS and 0-delay MTS conditions

**Figure 4.** Experiment 2: Percentage of correct responses (mean±SE) performed by the monkeys in the five delay conditions (One-sample t-test: \*  $p < 0.05$ ; \*\*\*  $p < 0.001$ )

**Figure 5.** Experiment 2: Response time of correct responses (mean±SE) recorded in the five delay conditions

**Effects of brief time delays on matching-to-sample abilities in capuchin monkeys (*Sapajus* spp.)**

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Number of text pages: 30

Number of figures: 5

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## Abstract

Traditionally, studies of delayed matching-to-sample (DMTS) tasks in nonhuman species have focused on the assessment of the limits of the retrieval of information stored in short- and long-term memory systems. However, it is still unclear if visual recognition in these tasks is affected by very brief delay intervals, which are typically used to study rapidly decaying types of visual memory. This study aimed at evaluating if tufted capuchin monkeys' ability to recognise visual stimuli in a DMTS task is affected by (i) the disappearance of the sample stimulus and (ii) the introduction of delay intervals (0.5, 1.0, 2.0 and 3.0 seconds) between the disappearance of the sample and the presentation of the comparison stimuli. The results demonstrated that the simple disappearance of the sample and the introduction of a delay of 0.5 seconds did not affect capuchins' performance either in terms of accuracy or response time. A delay interval of 1.0 second produced a significant increase in response time but still did not affect recognition accuracy. By contrast, delays of 2.0 and 3.0 seconds determined a significant increase in response time and a reduction in recognition accuracy. These findings indicate the existence in capuchin monkeys of processes enabling a very accurate retention of stimulus features within time frames comparable to those reported for humans' sensory memory (0.5-1.0 seconds). The extent to which such processes can be considered analogous to the sensory memory processes observed in human visual cognition is discussed.

**Keywords:** Visual perception; Sensory memory; Short-term memory; Matching-to-sample; Capuchin monkeys

## 1. Introduction

Nonhuman primates are widely used as animal models of human memory in cognitive neuroscience (e.g., [1]). To assess the plausibility of such models it is important to gather as much information as possible concerning similarities and difference among memory processes in nonhuman primates in relation to the vast literature on human memory. Moreover, the assessment of the similarity of memory processes in a variety of species at different taxonomic distance from humans can provide important information concerning the evolution of human memory.

Atkinson and Shiffrin [2] proposed a Multistore Model of Memory including three separate memory stores: the Sensory Memory, the Short Term Memory (STM) and the Long Term Memory (LTM). In this model, each store has a different duration, capacity and mode of encoding. For example, the visual system possesses sensory memory for stimuli features such as size, shape, colour and location. It has been argued that the temporary permanence of information that enters the sensory store allows the visual system to select which aspects of the input should be elaborated by further memory processing before it is eliminated from this preliminary store [3]. Despite the ubiquity of this sensory store in models of visual processing, the relationship between sensory memory processes and the subsequent short-term elaboration of visual information is still to be fully understood. For example, it is not clear which visual memory tasks are supported by long-lasting sensory memory processes or by early short-term memory processes [4]. Moreover, little is known about how these very early stages of memory processing work in other species.

Two main questions led the study of memory processes and contributed to the formulation of the Multistore Model of Memory: (1) how long information can be retained by each store?, and (2) how much information can be retained by each store? Most research, especially on nonhuman species, has traditionally been directed to the former issue and has

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3 focused on the duration of the memory traces with particular attention to short-term memory  
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5 processes. Methodological differences between the memory tests used with human and  
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7 animals contribute to the difficulty of direct comparisons of memory processes across species.  
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9 Memory decay processes in humans are assessed by both recall and recognition tasks, whereas  
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11 several tasks used with nonhuman species are based on recognition. In fact, nonhuman  
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13 subjects' visual memory is usually assessed training animals to recognise familiar stimuli  
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15 after delay intervals. As a consequence, in these tasks the stimulus which has to be identified  
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17 is always available to the subject during the memory test. Notwithstanding this, both in  
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19 human and nonhuman subjects, short-term memory processes ~~are proved~~have been shown to  
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21 maintain memory traces for time intervals which may vary from few seconds to several  
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23 minutes according to the type of tasks and stimuli presented (humans [5]; capuchins [6,7];  
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25 macaques [8]; baboons [9]; chicks [10]; crows [11]; pigeons [12]).  
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27       Systematic studies using comparable procedures to evaluate short-term memory in  
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29 human and nonhuman subjects are rare (e.g., [13-18]). For example, Weinstein [17] using an  
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31 identical DMTS task found similar performance in rhesus monkeys and three years old  
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33 children with delay intervals of 5, 10 and 15 seconds. Similarly, in a recent study by Chelonis  
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35 and colleagues [15] it has been found that the forgetting rates of rhesus monkeys and children  
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37 up to 7 years old are similar.  
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39       It is reasonable to expect that species with visual systems similar to that of humans, such  
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41 as nonhuman primate species, should be sensitive to manipulations affecting ~~sensory~~  
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43 within the time frame typical of human sensory memory. Previous studies regarding  
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45 persistence of sensory processes in monkey species evaluated if by reducing ambient  
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47 illumination to a very low level immediately after stimulus presentation can preserve after-  
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49 images as cues for subsequent stimulus recognition [19-22]. However, conflicting results  
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51 emerged when the level of illumination was manipulated during the delay-interval [19-22].  
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3 For example, D'Amato and O'Neill [19] found that a delay-interval presented in darkness  
4 facilitated capuchin monkeys' matching performance. On the contrary, King and Clawson  
5 [20] found that squirrel monkeys tested on a delayed-response task performed better when the  
6 delay interval was lighted than when it was darkened. Finally, McDowell and Lynn Brown  
7 [22] reported that rhesus monkeys' performance in a delay-response task could improve either  
8 under darkness or regular room illumination during the delay interval depending on both  
9 training and test conditions.  
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11 Comparative studies on the ability to recognise previously observed visual patterns have  
12 often employed variations of the matching-to-sample (MTS) task (e.g., [23-33]). In this task,  
13 two or more comparison stimuli are presented and participants choose which of them  
14 resembles most closely a stimulus presented as sample. In the simultaneous MTS (SMTS) the  
15 sample stimulus remains visible when the comparison stimuli appear. In the delayed  
16 matching-to-sample (DMTS), the sample stimulus disappears at the same time as the  
17 presentation of the comparison stimuli (0-delay MTS) or a variable time delay can be imposed  
18 between the disappearance of the sample and the presentation of the comparison stimuli.  
19 When no delays are imposed between the presentation of the sample and the comparison  
20 stimuli (either SMTS or 0-delay MTS) participants are not required to code the stimuli in  
21 capacity bound memory stores since they would always be available perceptually either as  
22 physical stimuli (SMTS) or possibly as part of sensory memory (0-delay MTS). By contrast,  
23 when a longer delay is introduced between the disappearance of the sample and the  
24 presentation of the comparison stimuli (DMTS), the recognition of the matching stimulus is  
25 likely to rely on the memory representation of the sample and can prove more or less  
26 demanding as a function of the delay length.  
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28 Because DMTS tasks are suitable for testing a variety of species, they can provide  
29 important insight into the mechanisms of visual cognition by allowing meaningful  
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interspecies comparisons. Previous studies using DMTS tasks in nonhuman species have focused mainly on the assessment of the limits of the retrieval of information stored in short- and long-term memory systems. The results of these DMTS studies show that animals of different species (e.g., [6,7,34] capuchin monkeys; [8,35] macaques; [9] baboons; [11] crows; [12,27] pigeons; see also [35-37] for reviews on this topic) are able to perform correct stimulus matching even, in some cases, with delays of several minutes interposed between the offset of the sample and the presentation of the comparison stimuli. However, these works were especially aimed at identifying the length of time intervals which cause recognition accuracy to fall to chance level. More subtle effects of brief delay intervals, which do not completely disrupt response accuracy, have received less attention. Hence, the rapid deterioration of performance that often characterise the decline of accuracy at very short delays, still deserves a thorough analysis. An effect of the manipulation of the length of very brief intervals would highlight the role of a rapidly decaying type of visual memory in pattern recognition and, as such, it would be important to assess.

The present study aimed at evaluating if visual stimuli discrimination in matching-to-sample tasks involves processes facilitating recognition in time frames comparable to those ascribed to sensory memory in humans. In particular, we carried out two experiments to evaluate the effect of (i) the disappearance of the sample stimulus (Experiment 1: SMTS vs. 0-delay MTS), and (ii) the introduction of delay intervals between the disappearance of the sample and the presentation of the comparison stimuli (Experiment 2: 0-delay vs. 0.5, 1.0, 2.0 and 3.0 seconds of delay). On the basis of the above considerations, we predicted that the sample stimulus disappearance should impair the matching performance only at delays above 0.5sec. In fact, if ~~sensory~~ memory mechanisms with timing similar to those reported for sensory memory in humans also pertain to monkeys, the introduction of delays beyond 0.5-1.0 sec should result in a decrease of response accuracy and/or response time, since at these

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3 intervals ~~sensory~~ memory processes should be beyond the time frame of operation of these  
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5 early storage systems that in humans retain a detailed image of the stimuli. A further  
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7 suggestion that capuchin monkeys may be equipped with separate storage systems roughly  
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9 equivalent to human sensory and short-term stores would be provided by the observation that  
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11 the consequences of increasing delays within time windows corresponding to different  
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13 hypothesised subsystems are qualitatively different. By contrast, results suggesting a  
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15 continuous function of the effects of delays on MTS performance would be indicative of a  
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17 single type of processing which operates at a wide range of delay timings. We also aimed to  
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19 assess whether or not this was the case by considering together the effects of the range of  
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21 delays featured across the two experiments.  
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## 25 **2. Experiment 1. Effect of the disappearance of the sample stimulus**

26  
27 In Experiment 1, we assessed the effect of the presence/absence of the sample stimulus  
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29 during the discrimination between the two comparison stimuli by comparing a Simultaneous  
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31 MTS with a 0-delay MTS condition. Thus, we compared a condition that required perception  
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33 only, without any need to retain a trace of the stimulus, with a condition that required a  
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35 longer lasting internal retention of the stimulus to produce accurate responses, albeit within  
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37 the timeframe of perceptual after effects and sensory memory, as reported in humans.  
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## 2.1 Methods

### 2.1.1 Subjects

The subjects were five tufted capuchins (*Sapajus* spp.<sup>1</sup>), two males (Sandokan and Robot) and three females (Pippi, Roberta and Rucola). All subjects were adults (age range: 11-30 years) born in captivity and hosted at the Primate Center of the Institute of Cognitive Sciences and Technologies, CNR, Rome, Italy. They lived in three groups, each housed in an indoor-outdoor enclosure (indoor: 5 m<sup>2</sup> x 2.5 m high; outdoor: 40-130 m<sup>2</sup> x 3 m high). Capuchins were individually tested in an adjacent experimental cage (0.76 m long x 1.70 m wide x 0.73 m high), that they could access through a sliding door. Each subject was separated from the group just before the daily testing session solely for the purpose of testing. No physical constraints or attachments were imposed on subjects while viewing the stimulus presentation. The testing occurred between 10:30 a.m. and 4:00 p.m. Water was freely available at all times. Fresh fruit, vegetables and monkey chow were provided in the afternoon after testing.

All monkeys were already familiar with the Simultaneous MTS procedure because they had been tested with a touchscreen based apparatus in tasks involving categorisation of visual stimuli and abstract concept acquisition [30,40]. Moreover, one monkey, Pippi, had been previously trained on tasks involving visual pattern discrimination (e.g., [41,42]). However, subjects had never been tested with a Delayed MTS procedure before.

### 2.1.2 Ethical note

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<sup>1</sup> Recent data has revealed that capuchin monkeys, traditionally identified as the single genus *Cebus*, are two genera: (i) the robust (tufted) forms are now classified as the genus *Sapajus*, and (ii) the gracile (untufted) forms retained as the genus *Cebus* [38,39]. Tufted capuchin monkeys host at the Primate Center of the CNR derived from animals of different provenience and are considered as unknown combinations of species of the genus *Sapajus*.

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3 The research protocol for this study was approved by the Italian Health Ministry (Central  
4 Direction for the Veterinary Service, approval n. 11/2011-C). Housing conditions and  
5 experimental procedures were performed in full accordance with the European law on  
6 humane care and use of laboratory animals and complied with the recommendations of the  
7 Weatherall report (The use of non-human primates in research). To increase three-  
8 dimensional space available to the animals, indoor enclosures were furnished with perches  
9 and ropes and outdoor enclosures were furnished with logs, branches and ropes. Moreover,  
10 the presence of natural substrates, including woodchips on the ground, served to promote  
11 monkeys' exploratory behaviours. All subjects were familiar with the experimental cage, the  
12 experimental routine and the experimenters.  
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### 25 *2.1.3 Apparatus*

26 The computerised testing station consisted of a PC (Model AMD Athlon 1200) connected  
27 to a 19" touchscreen (Model E96f+SB, CRT, ViewSonic) and an automatic food dispenser  
28 (Model ENV-203-45, MED Associates, Inc. Georgia, VT) (Figure 1). E-Prime software  
29 (Psychology Software Tools, Inc.) was used for the presentation of the stimuli and the  
30 recording of the subject's response. When the monkey provided the correct response, the  
31 food dispenser delivered a 45-mg banana-flavoured pellet (TestDiet, Richmond, IN, USA)  
32 into a Plexiglas feeding cup (10 cm wide x 5 cm deep x 3.5 cm high) located 16 cm below the  
33 touchscreen in the centre.  
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43 A wooden frame (48 cm wide x 64 cm high x 30 cm deep) with a central aperture (36 cm  
44 wide x 26 cm high) surrounded the touchscreen. The food dispenser was placed behind the  
45 wooden frame, out of sight of the subject. Moreover, an additional LCD monitor was placed  
46 at the back of the touchscreen to allow the experimenter to see the progress of the session so  
47 as to remove the apparatus at the end of the session. The touchscreen, food dispenser and  
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additional LCD monitor were mounted on the top shelf of a trolley (81 cm long x 45 cm wide x 80 cm high), whereas the PC was on the bottom shelf.

The apparatus was placed 15 cm from the grid of the experimental cage within the arm's reach of the subject. The grid was made of horizontal metal bars (0.5 cm thick) that were separated by 4.5 cm.

A camcorder (Sony Handycam DCR-SR37) was positioned approximately 70 cm from the touchscreen monitor in order to record video images which included both the screen display and a back view of the monkey. This allowed us to monitor the subject's behaviour during testing.

#### *2.1.4 Stimuli*

The stimulus set comprised 192 stimuli (examples of the stimuli are shown in Figure 2). Each stimulus consisted of a white pattern (3 cm x 3 cm, i.e. 11.3° of visual angle) presented on a black background (6.5 cm x 6.5 cm, i.e. 23.4° of visual angle). All stimuli were constructed using cliparts and were converted into bitmaps before presentation on the computer screen.

#### *2.1.5 Procedure*

A matching-to-sample (MTS) task was adopted, in which three stimuli, the sample (SS) and the two comparison stimuli, the matching stimulus (S+), which was rewarded if selected, and the non-matching stimulus (S-), were presented on the computer screen. At the beginning of each trial, the sample stimulus appeared on the upper half of the screen, in the centre. Then, after the subject touched the sample stimulus, the two comparison stimuli were displayed simultaneously 4 cm below the sample, to the right and left, at a distance of 5 cm apart (Figure 1). In order to ensure that the monkeys attended the sample stimulus, the subject was required to touch the sample at the beginning of each trial. Then, according to the experimental condition,

the sample remained on the screen during the presentation of the comparison stimuli (simultaneous MTS, see Figure 1) or disappeared immediately after the subject had touched it (0-delay MTS). In both conditions, the comparison stimuli were produced without any delay when the subject touched the sample. The right/left positions of S+ and S- were randomly determined in each trial. The subject had to indicate its choice by touching one of the comparison stimuli on the screen; the computer automatically recorded the choice and the Response Time (RT). If the comparison stimulus was chosen correctly (S+), a food pellet was dispensed. If the incorrect stimulus (S-) was selected, no pellet was dispensed. A blank screen replaces the display immediately after the response of the subject. A correct response was followed by a 5-s inter-trial interval (ITI), whereas an incorrect response was followed by both a 10-s time-out (TO) and a 5-s ITI. During the experimental trials and the ITI, the screen was light grey; during the TO, the screen was green.

#### *2.1.6 Experimental design*

Experiment 1 included 16 48-trial sessions. In each session, half of the trials were of the simultaneous MTS condition and half of the trials were of the 0-delay MTS condition. Trials of the two conditions were randomly intermixed within each session. Within a session the same 24 pairs of stimuli were presented in both simultaneous and 0-delay conditions.

#### *2.1.7 Data analyses*

Both accuracy and the RT were used for the analyses. Accuracy was measured as the percentage of correct responses. RT was measured as the time between the appearance of the comparison stimuli and the subject's choice (i.e., the touch of a comparison stimulus). Only RT for correct choices were included in the analyses. All the experimental sessions were videotaped. The videos were used to detect instances where the subject turned away from the

screen/task during a trial, thus spuriously affecting the length of the delay interval between the appearance of the comparison stimuli and the subjects' response. All instances detected were removed from data analyses. One observer (VT) scored all videos and another observer (RS) scored independently a random selection of 20% of the videos (total 768 trials) to calculate inter-observer reliability. There was a perfect agreement between the two observers (Cohen's Kappa = 1.0).

Because the Kolmogorov-Smirnov test showed that the distribution of data did not deviate from normality, we used parametric statistics to compare the accuracy scores and response times between different conditions. Statistical significance was set at  $p \leq 0.05$ .

## 2.2 Results

The analyses of the videos of Experiment 1 revealed that there were no trials in which subjects turned away from the screen/task during the presentation of the stimuli.

*Accuracy.* All subjects achieved 70% or a higher percentage of correct responses in both the simultaneous and the 0-delay condition [binomial  $z$  scores: Sandokan, sim = 87.3%, 0-del = 91.4%; Roberta, sim = 85.7%, 0-del = 87.3%; Rucola, sim = 91.4%, 0-del = 91.7%; Pippi, sim = 81.5%, 0-del = 78.1%; Robot, sim = 75.0%, 0-del = 72.4%, all  $P_s < .000003$ ]. Moreover, all subjects showed a performance that was significantly above the 50% level of chance performance in both the Simultaneous and the 0-delay MTS conditions from the very first testing session [binomial  $z$  scores: Sandokan, sim = 79.2% ( $p < .0008$ ), 0-del = 83.3% ( $p < .0008$ ); Roberta, sim = 95.8% ( $p < .0008$ ), 0-del = 87.5% ( $p < .0008$ ); Rucola, sim = 91.7% ( $p < .0008$ ), 0-del = 83.3% ( $p < .0008$ ); Pippi, sim = 83.33% ( $p < .0008$ ), 0-del = 75.0% ( $p = .0008$ ); Robot, sim = 87.5% ( $p < .0008$ ), 0-del = 79.17% ( $p < .0008$ )].

Overall, across all testing sessions, capuchins' percentage of correct responses was significantly above the level of chance both in the Simultaneous [ $mean = 84.17\%$ ,  $SE = 2.79$ , one-sample  $t$ -test:  $t(4) = 12.26$ ,  $p = 0.0002$ ] and the 0-delay MTS [ $mean = 84.17\%$ ,  $SE = 3.83$ , one-sample  $t$ -test:  $t(4) = 8.93$ ,  $p = 0.0009$ ] conditions. Moreover, the mean percentage of correct responses did not vary significantly between the Simultaneous MTS and the 0-delay MTS [paired  $t$ -test:  $t(4) = .001$ ,  $p = 0.999$ , (Cohen's  $d = 0.0$ ; 95% CI for  $d$ : -1.24, 1.24)], (see Figure 3a).

*Response time.* The mean percentage of response time, as reported for accuracy measure, did not vary between the Simultaneous MTS ( $mean = 1157.37$  msec,  $SE = 87.56$ ) and the 0-delay MTS ( $mean = 1123.61$  msec,  $SE = 97.81$ ), [paired samples  $t$ -test:  $t(4) = 1.55$ ,  $p = 0.197$  (Cohen's  $d = 0.69$ ; 95% CI for  $d$ : -0.64, 1.89)], (see Figure 3b).

### 3. Experiment 2. Effect of short delay intervals

Experiment 2 aimed at evaluating the effect of the introduction of delay intervals between the disappearance of the sample and the presentation of the comparison stimuli. We compared the 0-delay condition with conditions with 0.5, 1.0, 2.0 and 3.0 seconds of delay, that is, to conditions in which the memory requirement of the task is minimal. In this experiment, we tested the following hypotheses. The first is that capuchin monkeys may possess memory processes operating within a timescale of human sensory memory and that preserve an accurate representation of incoming visual information. If that was the case we should have observed a selective impairment of matching performance at delays beyond 0.5-1.0, which is the time resolution of human sensory memory. The second is that, if separate memory mechanisms, with a different time resolution, operate within the range of intervals tested in this study, we should expect a pattern of significant effects of the increase of the delay indicative of a step

function. For example we should be able to detect the point in time where accurate ~~sensory~~ memory processes operating at very short time frames and possibly akin to human sensory memory give way to a less detailed representation of the stimulus in short-term memory reflected in a significant decrease of performance at that point. Conversely, a more continuous pattern of deterioration of the memory trace reflected in a significant decrease in performance at different delay points would be more consistent with the gradual decay of the memory trace within a single storage systems encompassing the range of delays tested in this study.

### 3.1 Methods

#### 3.1.1 Subjects, apparatus and stimuli

Subjects, apparatus and stimuli were the same as those used in Experiment 1.

#### 3.1.2 Procedure

The general procedure was the same as that used in the 0-delay condition of Experiment 1. However, in Experiment 2, four further different delay intervals were interposed between the disappearance of the sample and the appearance of the comparison stimuli: 0.5, 1.0, 2.0, 3.0 sec.

### 3.1.3 Experimental design

Experiment 2 included five 90-trial sessions of the delayed MTS condition. In each session there were five 18-trial blocks with different delays (0.0, 0.5, 1.0, 2.0, 3.0 sec). Trials of the five conditions were randomly intermixed within each session. To avoid the frequent repetition of the same stimuli, different stimuli were presented in different blocks of trials with a given delay. However, each stimulus was systematically presented in a different delay across sessions.

### 3.1.4 Data analyses

As in Experiment 1, both the accuracy and RT for correct responses were used for the analyses. All the experimental sessions were videotaped to assess if the subject turned away from the screen/task during the trials. One observer (VT) scored all videos and another observer (RS) scored independently a random selection of 20% of the videos (total 450 trials) to calculate inter-observer reliability. There was an excellent agreement between the two observers (Cohen's Kappa = 0.88).

As in Experiment 1, the Kolmogorov-Smirnov test showed that the group data did not differ from a normal distribution. Thus, we used parametric statistics to compare the accuracy and RT observed in the different conditions. Statistical significance was set at  $p \leq 0.05$ .

## 3.2 Results

The analyses of the videos of Experiment 2 revealed that in 136 trials (6.0 % of all trials) subjects were not looking at the screen when the comparison stimuli appeared (Rucola = 44, Sandokan = 34, Robot = 34, Pippi = 22, Roberta = 2). In the 0-delay condition this was an extremely rare event, which occurred in two subjects for only one time (Pippi, N = 1 and

Rucola,  $N = 1$ ). However, this happened more frequently with the increasing of the length of the delay, (Pearson correlation,  $r = .99$ ,  $N = 5$ ,  $p = 0.0003$ ). Moreover, the mean number of trials in which monkeys looked away or moved away from the screen differed significantly across delay intervals [ $F(4,16) = 7.83$ ,  $p = 0.0011$ ,  $\eta^2_p = .662$ , 95% CI for  $\eta^2_p$ : 0.01, 0.76]. Post hoc analyses (Tukey, HSD test) showed that subjects failed to maintain their attention on the task significantly more often in the 3-sec delay condition than in the 0-sec ( $p = 0.001$ ) and 0.5-sec ( $p = 0.006$ ) conditions, and that they failed more often in the 2-sec than in the 0-sec condition ( $p = 0.029$ ).

Because these trials featured an uncontrolled increase of the scheduled interval, which made them impossible to interpret, they were not subjected to any further analysis.

*Accuracy.* Each individual showed a level of performance which was significantly above the 50% chance level, in all five delay conditions (binomial  $z$  scores: all  $P_s < 0.05$ ), with the only exception of the oldest subject, Pippi, who showed a chance level of performance in the 2 and 3 sec delay conditions.

Overall, the percentage of correct responses for the group of monkeys was significantly above the level of chance in all the five conditions [one-sample  $t$ -tests: 0.0 sec,  $mean = 79.44\%$ ,  $SE = 3.47$ ,  $t(4) = 8.47$ ,  $p = 0.001$ ; 0.5 sec,  $mean = 73.15\%$ ,  $SE = 5.78$ ,  $t(4) = 4.00$ ,  $p = 0.016$ ; 1.0 sec,  $mean = 68.39\%$ ,  $SE = 4.98$ ,  $t(4) = 3.69$ ,  $p = 0.021$ ; 2.0 sec,  $mean = 63.63\%$ ,  $SE = 3.66$ ,  $t(4) = 3.72$ ,  $p = 0.020$ ; 3.0 sec,  $mean = 67.59\%$ ,  $SE = 5.47$ ,  $t(4) = 3.22$ ,  $p = 0.032$ ], (see Figure 4).

To assess if capuchins' matching accuracy was affected by the length of delay intervals and/or by practice effects across sessions, an ANOVA was carried out on the percentage of correct responses with MTS conditions (0.0, 0.5, 1.0, 2.0, 3.0 sec delayed) and different sessions (s1, s2, s3, s4, s5) as repeated measures. A significant main effect of delay condition [ $F(4,16) =$

4.93,  $p = 0.009$ ,  $\eta^2 = .552$ , 95% CI for  $\eta^2_p$ : 0.06, 0.68] was found. Post hoc comparisons revealed that the mean percentage of correct responses observed in the 0-delay condition was significantly higher than that of the 2 ( $p = 0.006$ ) and 3 ( $p = 0.049$ ) sec delay conditions but did not differ from the level of response accuracy of the 0.5 ( $p = 0.501$ ) and 1.0 ( $p = 0.073$ ) sec delay conditions. No other significant main effect or interaction was found.

*Response time.* An ANOVA for repeated measures was carried out to assess if RT for correct responses differed between delay conditions (0.0, 0.5, 1.0, 2.0, 3.0 sec delay) and testing sessions (s1, s2, s3, s4, s5). A significant main effect of MTS condition was found [0.0 sec *mean* = 1201.38 msec, *SE* = 131.29; 0.5 sec *mean* = 1346.11 msec, *SE* = 123.80; 1.0 sec *mean* = 1354.37 msec, *SE* = 113.12; 2.0 sec *mean* = 1428.23 msec, *SE* = 81.04; 3.0 sec *mean* = 1480.02 msec, *SE* = 99.03;  $F_{(4,16)} = 9.45$ ,  $p = 0.0004$ ,  $\eta^2 = .702$ , 95% CI for  $\eta^2_p$ : 0.27, 0.79, see Figure 5]. Post-hoc comparisons revealed that the mean response time is significantly lower in the 0-delay condition than in the 1.0 ( $p = 0.042$ ), 2.0 ( $p = 0.002$ ) and 3.0 ( $p = 0.0003$ ) sec of delay, whereas it did not differ from the 0.5 sec condition, even though  $p$  value approaches the significance ( $p = 0.058$ ). No other significant main effect or interaction was found.

*Experiment 1 versus Experiment 2.* A comparison between 0-delay conditions of Experiment 1 and 2 revealed a degree of accuracy significantly higher in Experiment 1 than Experiment 2 [ $t(4) = 4.29$ ,  $p = 0.013$ , (Cohen's  $d = 1.91$ ; 95% CI for  $d$ : 0.28, 3.18)], whereas no difference was found in response time between the two experiments [ $t(4) = 1.54$ ,  $p = 0.199$ , (Cohen's  $d = 0.69$ ; 95% CI for  $d$ : -0.65, 1.89)].

#### 4. Discussion

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3 The present study demonstrated that capuchins had the same response accuracy in both  
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5 Simultaneous (84.17%) and 0-delay (84.17%) conditions (Experiment 1). This performance is  
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7 well above chance level and is consistent with the accuracy levels observed in other studies that  
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9 have used comparable computerised matching-to-sample tasks with two comparison stimuli and  
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11 no delay intervals (e.g., capuchins: 81.94% [43] and 78.2% [30]; gorillas and orangutans:  
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13 79.98% [44]). Thus, our findings indicate that capuchins solved these two matching conditions  
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15 in an undifferentiated way. The mere disappearance of the sample stimulus from the screen,  
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17 without the introduction of any delay interval before the presentation of the comparison stimuli,  
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19 did not affect their response accuracy. Similarly, sample stimulus disappearance did not affect  
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21 subjects' response time.

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23 This finding is also consistent with previous studies indicating that monkeys seem to have  
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25 a spontaneous tendency to visually inspect the sample stimulus for very short time intervals  
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27 and increasing the time of permanence of a stimulus on the screen does not improve subjects'  
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29 discrimination performance [45] unless that they are required to actively manipulate the  
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31 stimulus, for example by repeatedly touching it before making a choice [46].

32  
33 When we introduced short delay intervals in the MTS task we found that: (i) a delay of 0.5  
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35 sec between the sample offset and the choice stimuli onset did not affect capuchins' ability to  
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37 match visual patterns, (ii) a delay interval of 1.0 sec produced a significant increase in response  
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39 time but did not affect recognition accuracy, and (iii) delays of 2 and 3 sec determined a  
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41 significant increase in response time and a reduction in recognition accuracy (Experiment 2: 0-  
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43 delay *versus* 0.5, 1.0, 2.0, 3.0 sec. delay). ~~Conversely~~However, no further deterioration of  
44  
45 performance was observed when the interval was increased from 2 to 3 seconds~~further~~, even if  
46  
47 ~~when the~~ this difference in the length of the delay was the same as that produced an effect at  
48  
49 shorter delays. ~~Now we obtained additional information which could help the characterisation~~  
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~~of the potential contribution of sensory memory processes in visual pattern recognition in monkeys.~~

Overall, these findings suggest the existence in nonhuman primates of separate memory mechanisms which facilitate visual recognition in time frames ~~of less than one second and (0.5-1.0 seconds) and with a time frame which are~~ similar to ~~those of that reported for~~ human sensory memory [4,47-49]. The MTS paradigm as featured in this study does not enable us to assess whether the characteristic of this type of memory in capuchins resembles that of humans in terms of capacity but our results would not be inconsistent with such a possibility. This specific issues could be addressed in further studies using partial recall in monkeys. This is however beyond the scope of this paper and its implementation with monkeys housed in the semi-natural setting conditions as those in our centre may prove challenging. Nevertheless, our results provides important information regarding the visual cognition of nonhuman primates.

~~Despite the fact that iconic memory features in several models of visual processing (e.g., (2,47)), there~~ There are still controversies surrounding the characterisation of the physiological bases of very early stages of visual memory processing this type of memory in nonhuman primates. Recent neurophysiological data on nonhuman primates suggest that specific cortical areas support activities which occur in concomitance with the stimulus removal. Findings on cynomolgus macaques revealed that lesions of inferotemporal cortical area - TE - severely impair performance on recognition memory tasks even at delays as short as 0.5 sec and 1.0 sec [23,50]. The impairment of recognition at short delays suggests that the monkeys in the TE lesion group could not perceive, attend to, or process the visual stimuli adequately. Moreover, this difficulty seems to be specific to the visual modality, because the same monkeys had a normal performance on a recognition memory task in the tactual modality [50]. Furthermore, recent bio-imaging studies in human adults suggest that tasks involving iconic memory in our

species are associated with persistent activation in higher-order visual areas such as the occipito-temporal cortex, particularly the lateral-occipital complex - LOC – [51,52].

Moreover, our findings suggest a recognition system that allows a high degree of accuracy for delays up to 1.0 second, albeit with increased response times. At 0.5 sec of delay capuchins' response time did not differ from 0.0 sec of delay (i.e., any delay), whereas at 1.0 sec of delay, as well as at 2.0 and 3.0 sec, their response time is significantly longer than at 0.0 sec. This finding is consistent with data obtained with baboons, which demonstrates that these Old World monkeys are able to solve a DMTS task with the same accuracy at 0.0 and 1.0 sec delay, although at 1.0 sec delay baboons showed longer response time [9]. This suggests that the increase in RT in DMTS can be indicative of an increased difficulty of retrieval processes when the memory trace starts to decay but has not deteriorated to a degree that would affect accuracy.

We cannot exclude that increasing the familiarity with the task may improve the response accuracy and/or the reduction of the response time in the delayed conditions. However, the lack of differences in performance across the five sessions of Experiment 2 indicates that learning effects did not intervene for any condition during the entire data collection. Moreover, the absence of difference between Simultaneous and 0-delay MTS conditions in Experiment 1, suggests that the simple introduction of a non-familiar condition does not necessarily lead to a performance decline. Moreover, an alleged novelty effect of the delayed conditions would not explain why different delay intervals should affect subjects' performance to a different degree. For all these reasons, we believe that the variation in MTS behaviour observed in the different delay conditions should rather be attributed specifically to underlying variations in the visual processing of the stimuli.

Another observation regarding the behaviour of our subjects that deserves a comment is the tendency of capuchins to turn away from the screen/task during a trial when the delay interval increased. This was probably due to the fact that individuals were dealing with delayed

MTS conditions for the first time and, thus, had not previously learnt to tolerate a delay before the appearance of the choice stimuli. In this case, this effect should disappear with increased familiarity with the task. Alternatively, considering that we use very short delay intervals, this finding could suggest that capuchins' attention to the task is relatively vulnerable. This possibility would be consistent with the observation that capuchin monkeys frequently direct their visual attention to the surroundings even while they are engaging in a problem solving task, and even when they are tested singly in a familiar and safe context [53].

A counterintuitive finding, in relation to possible learning effects in DMTS, is the higher percentage of correct responses observed in the 0-delay condition of Experiment 1 compared to the same condition of Experiment 2. It could be due to an effect of the type of trials intermixed with the 0-delay trials in the two experiments. In Experiment 1, 0-delay trials were intermixed with trials of a less demanding, condition (i.e. SMTS), with which the monkeys were already familiar from their experience in previous studies [30,40]. By contrast, 0-delay trials were intermixed with unfamiliar, more demanding, conditions (i.e. DMTS with 0.5, 1.0, 2.0 and 3.0 sec delay) in Experiment 2. This finding suggests that the context in which a particular condition is presented could affect subjects' performance. The sensitivity of capuchin monkeys to the context provided by different type of trials presented within a testing session has been documented in experiments featuring MTS of hierarchical visual patterns [54]. In the present study, such sensitivity could be explained by a deleterious effect, on the motivation of the subjects, induced by frustration caused by the higher error rate in the trials interspersed with the 0-delay trials in Experiment 2. It is also possible that the decrease in accuracy in the 0-delay trials in Experiment 2 is due to the need to allocate more cognitive resources to the more demanding trials with which they were interspersed. This would have had a detrimental effect on the amount of attentional resources left for the processing of the 0-delay trials in Experiment 2.

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3 Finally, the observation that our oldest subject, Pippi, a 30 years old female, exhibited the  
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5 lowest level of response accuracy in all conditions, with particular difficulties emerging in 2.0  
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7 and 3.0 sec delay conditions also deserves a comment. This finding is consistent with data on  
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9 both humans and nonhuman primates in relation to ageing (e.g., [55,56]). For example, studies  
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11 carried out on rhesus monkeys indicate a selective impairment in older subjects in delayed-  
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13 response tasks requiring short-term memory [55,57]. Moreover, the difference observed  
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15 between old and young monkeys could not be reduced by providing the monkeys with  
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17 extensive training on the task [57]. In elderly humans, and most severely in those affected by  
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19 Alzheimer's disease, DMTS tasks revealed a similar delay-dependent impairment [56,58]. In  
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21 some cases, patients with dementia failed to solve even 0-dealy DMTS tasks [59]. Thus, our  
22  
23 findings indicate that nonhuman primate models could be informative in relation to age-related  
24  
25 cognitive deficits in both healthy and pathological human ageing.  
26

27 Overall, these results confirm that delayed matching-to-sample procedures afford reliable  
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29 measures that provide important information regarding cognitive processing in memory and  
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31 perception. Furthermore, our findings highlight that capuchin monkeys show a certain degree of  
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33 similarity with humans at the level of visual coding addressed in this study. The comparison of  
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35 primate species with a different degree of phylogenetic distance from humans can potentially  
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37 provide information about the evolution of human visual cognition. In particular, our findings  
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39 on capuchin monkeys, which shared a common ancestor with humans until 35 million years  
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41 ago, suggest that mechanisms supporting the brief storage of detailed visual information in aid  
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43 of recognition may have emerged relatively early during the evolutionary history of primate  
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45 species. This evidence only represents a starting point for our understanding of the early visual  
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47 memory storage mechanisms in monkeys. Nevertheless we hope that it will encourage further  
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49 detailed investigations on this topic. Future studies in nonhuman species would need to refine  
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51 experimental procedures to characterise the visual memory decay not only as a function of  
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amount of time the information can be retained, but also as a function of quantity of information that can be stored in different stages of the memory process.

## Acknowledgements

We wish to thank Massimiliano Bianchi and Simone Cartarinacci for help with animal management. We acknowledge Sara Privitera, Luca Santini and Leonardo Ancilotto for help with data collection and Raffaele Sardella for help with video scoring. We thank the anonymous reviewer for her/his thoughtful and constructive comments. We also thank the Comune di Roma-Museo Civico Zoologia and the Fondazione Bioparco for hosting the Unit of Cognitive Primatology and Primate Centre. This research was supported by the PNR-CNR Aging Program 2012-2014. The authors declare that they have no conflict of interest.

## References

- [1] Goldman-Rakic PS. Working memory and the mind. *Sci Am* 1992; 267:111-17.
- [2] Atkinson RC, Shiffrin RM. Human memory: A proposed system and its control processes. In Spence KW, Spence JT, editors. *Psychology of learning and motivation: Advances in research and theory* (Vol. 2), New York: Academic Press; 1968, p. 90-191.
- [3] Coltheart M, Lea CD, Thompson K. In defence of iconic memory. *Q J Exp Psychol* 1974; 26:633-41.
- [4] Sligte IG, Scholte HS, Lamme VAF. Are there multiple visual short-term memory stores? *PloS One* 2008; 3, e1699.
- [5] Baddeley A. *Human memory. Theory and practice*. Hove, Lawrence Erlbaum Associates Ltd; 1990.
- [6] Colombo M, D'Amato MR. A comparison of visual and auditory short-term memory in monkeys (*Cebus apella*). *Q J Exp Psychol* 1986; 4:425-48.
- [7] Etkin M, D'Amato MR. Delayed matching-to sample and short-term memory in the capuchin monkey. *J Comp Physiol Psychol* 1969; 69:544-49.
- [8] Overman WH, Doty RW. Prolonged visual memory in macaques and man. *Neurosci* 1980; 5:1825-31.
- [9] Rodriguez JS, Zvrcher NR, Bartlett TQ, Nathanielsza PW, Nijlanda MJ. CANTAB delayed matching to sample task performance in juvenile baboons. *J Neurosci Methods* 2011; 196:258-63.
- [10] Gibbs ME, Ng KT. Behavioural stages in memory formation. *Neurosci Lett* 1979; 13:279-83.
- [11] Goto K, Watanabe S. Visual working memory in jungle crows (*Corvus macrorhynchos*) in operant delayed matching-to-sample. *Japanese Psychol Res* 2009; 3:122-31.

- 1  
2  
3 [12] Roberts WA, Grant DS. Studies of short-term memory in the pigeons using the delayed  
4 matching-to-sample procedure. In: Medin DL, Roberts WA, Davis RT, editors. Processes  
5 of animal memory. Hillsdale, NJ: Erlbaum; 1976, p. 79-112.  
6  
7  
8  
9 [13] Basile B, Hampton RR. Monkeys recall and reproduce simple shapes from memory. Curr  
10 Biol 2011; 21:774-78.  
11  
12  
13 [14] Elmore LC, Ma WJ, Magnotti JF, Leising KJ, Passaro AD, Katz JS, Wright AA. Visual  
14 short-term memory compared in rhesus monkeys and humans. Curr Biol 2011; 21:975-79.  
15  
16  
17 [15] Chelonis JJ, Cox AR, Karr MJ, Prunty PK, Baldwin RL, Paule MG. Comparison of delayed  
18 matching-to-sample performance in monkeys and children. Behav Process 2014; 103:261-  
19 68.  
20  
21  
22 [16] Fagot J, De Lillo C. A comparative study of working memory: Immediate serial spatial  
23 recall in baboons (*Papio papio*) and humans. Neuropsychologia 2011; 49:3870-80.  
24  
25  
26 [17] Weinstein B. Matching-from-sample by rhesus monkeys and by children. J Comp Psychol  
27 1941 ; 31:195-213.  
28  
29  
30 [18] Wright AA, Santiago HC, Sands SF, Kendrick DF, Cook RG. Memory processing of serial  
31 lists by pigeons, monkeys, and people. Science 1985; 229 (4710):287-89.  
32  
33  
34 [19] D'Amato MR, O'Neill W. Effect of delay-interval illumination on matching behavior in the  
35 capuchin monkey. J Exp Anal Behav 1971; 15:327-33.  
36  
37  
38 [20] King JE, Clawson JR. Delayed response by squirrel monkeys under various delay lighting  
39 conditions. Psychon Sci 1966; 6:429-30.  
40  
41  
42 [21] King JE, Flaningam MR, Rees WW. Delayed response with different delay conditions by  
43 squirrel monkeys and fox squirrels. Anim Behav 1968; 16:271-75.  
44  
45  
46 [22] McDowell AA, Lynn Brown, W. Intervening darkness and delayed response performance  
47 by rhesus monkeys. J Genet Psychol 1960; 97:59-65.  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
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61  
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63  
64  
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- [23] Buffalo EA, Ramus SJ, Squire RL, Zola SM. Perception and recognition memory in monkeys following lesions of area TE and perirhinal cortex. *Learn & Mem* 2000; 7:375-82.
- [24] Fujita K. Metamemory in tufted capuchin monkeys (*Cebus apella*). *Anim Cogn* 2009; 12:575-85.
- [25] Galvão OF, Barros RS, Dos Santos JR, Brino ALF, Brandão S, Lavratti CM, et al. Extent and limits of the matching concept in *Cebus apella*: a matter of experimental control? *The Psychol Rec* 2005; 55:219-32.
- [26] Galvão OF, Soares-Filho PSD, Barros RS, Souza CBA. Matching-to-sample as a model of symbolic behaviour for bio-behavioral investigations. *Rev Neurosci* 2008; 19:149-56.
- [27] Nelson KR, Wasserman EA. Temporal factors influencing the pigeon's successive matching-to-sample performance: sample duration, intertrial interval, and retention interval. *J Exp Anal Behav* 1978; 30:153-62.
- [28] Mishkin M, Delacour J. An analysis of short-term visual memory in the monkey. *J Exp Psychol Anim Behav Process* 1975; 1:326-34.
- [29] Oden DL, Thompson RKR, Premack D. Spontaneous transfer of matching by infant chimpanzees (*Pan troglodytes*). *J Exp Psychol Anim Behav Process* 1988; 14:140-45.
- [30] Truppa V, Garofoli D, Castorina G, Piano Mortari E, Natale F et al. Identity concept learning in matching-to-sample tasks by tufted capuchin monkeys (*Cebus apella*). *Anim Cogn* 2010; 13:1-14.
- [31] Vauclair J, Fagot J, Hopkins WD. Rotations of mental images in baboons when the visual input is directed to the left cerebral hemisphere. *Psychol Sci* 1993; 2:99-103.
- [32] Washburn DA, Hopkins WD, Rumbaugh DM. Video-task assessment of learning and memory in macaques (*Macaca mulatta*): Effects of stimulus movement on performance. *J Exp Psychol Anim Behav Process* 1989; 15:393-400.

- [33] Wright AA, Delius JD. Learning processes in matching and oddity: the oddity preference effect and sample reinforcement. *J Exp Psychol Anim Behav Process* 2005; 31:425-32.
- [34] Tavares MCH, Tomaz C. Working memory in capuchin monkey (*Cebus apella*). *Behav Brain Res* 2002; 131:131-37.
- [35] Shettleworth S. *Cognition, Evolution and Behavior*. Oxford: Oxford University Press; 1998.
- [36] Tomasello M, Call J. *Primate Cognition*. Oxford: Oxford University Press; 1997.
- [37] Wright AA. Memory processing. In: Wasserman EA, Zentall TR, editors. *The Oxford Handbook of Comparative Cognition*. Oxford: Oxford University Press; 2012, p. 239-60.
- [38] Lynch Alfaro JW, Boubli JP, Olson LE, Di Fiore A, Wilson B, Gutiérrez-Espeleta GA et al. Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *J Biogeo* 2012; 39:272-88.
- [39] Lynch Alfaro JW, Silva J de S Jr, Rylands AB. How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. *Am J Primatol* 2012; 74:273-86.
- [40] Truppa V, Piano Mortari E, Garofoli D, Privitera S, Visalberghi E. Same/different concept learning by capuchin monkeys in matching-to-sample tasks. *PloS ONE* 2011; 6(8):e23809. doi:10.1371/journal.pone.0023809.
- [41] De Lillo C, Spinozzi G, Truppa V. Pattern recognition in tufted capuchin monkeys (*Cebus apella*): the role of the spatial organization of stimulus parts. *Behav Brain Res* 2007; 181:96-109.
- [42] Spinozzi G, De Lillo C, Truppa V. Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). *J Comp Psychol* 2003; 117:15-23.
- [43] D'Amato MR, Salmon DP, Colombo M. Extent and limits of the matching concept in monkeys (*Cebus apella*). *J Exp Psychol Anim Behav Process* 1985, 11:35-51.

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- [44] Vonk J. Gorilla (*Gorilla gorilla gorilla*) and orangutan (*Pongo abelii*) understanding of first- and second-order relations. *Anim Cogn* 2003; 6:77-86.
- [45] D'Amato MR, Worsham RW. Delayed matching in the capuchin monkey with brief sample durations. *Learn & Motiv* 1972; 3:304-12.
- [46] Katz JS, Wright AA, Bachevalier J. Mechanisms of same/different abstract-concept learning by rhesus monkeys (*Macaca mulatta*). *J Exp Psychol Anim Behav Process* 2002; 28:358-68.
- [47] Coltheart M. The persistence of vision. *Philos Trans R Soc Lond B Biol Sci* 1980; 290:57-69.
- [48] Sperling G. The information available in brief visual presentations. *Psychol Monogr Gen Appl* 1960; 74:1-29.
- [49] Averbach E, Coriell AS. Short-term memory in vision. *Bell Syst Tech J* 1961; 40:309-28.
- [50] Buffalo EA, Ramus SJ, Clark RE, Teng E, Squire LR, Zola SM. Dissociation between the effects of damage to perirhinal cortex and area TE. *Learn & Mem* 1999; 6:572-99.
- [51] Ruff CC, Kristjánsson Á, Driver J. Readout from iconic memory and selective spatial attention involve similar neural processes. *Psychol Sci* 2007; 18:901-9.
- [52] Wong YJ, Aldcroft AJ, Large ME, Culham JC, Vilis T. The role of temporal synchrony as a binding cue for visual persistence in early visual areas: An fMRI study. *J Neurophysiol* 2009; 102:3461-8.
- [53] Fragaszy DM, Visalberghi E, Fedigan LM. The complete capuchin. The biology of the genus *Cebus*. Cambridge University Press; 2004.
- [54] De Lillo C, Spinozzi G, Palumbo M, Giustino G. Attention allocation modulates the processing of hierarchical visual patterns: a comparative analysis of capuchin monkeys (*Cebus apella*) and humans. *J Exp Psychol Anim Behav Process* 2011; 37:341-52.

- 1  
2  
3 [55] Bartus RT, Fleming DL, Johnson HR. Aging in the rhesus monkey: Debilitating effects on  
4 short-term memory. J Gerontol 1978; 33:858-71.  
5  
6  
7 [56] Flicker C, Ferris SF, Bartus RT, Crook T. Effects of aging and dementia upon recent visuo-  
8 spatial memory. Neurobiol Aging 1984; 5:75-83.  
9  
10  
11 [57] Marriott JG, Abelson JS. Age differences in short-term memory of test-sophisticated rhesus  
12 monkeys. Age 1980; 3:7-9.  
13  
14  
15 [58] Sahakian BJ, Morris RG, Evenden JL, Heald JL, Levy R, Philpot M et al. A comparative  
16 study of visuospatial memory and learning in Alzheimer-type dementia and Parkinson's  
17 disease. Brain 1988; 3:695-718.  
18  
19  
20  
21 [59] Steinunn Steingrimsdottir H, Arntzen E. Identity Matching in a Patient With Alzheimer's  
22 Disease. Am J Alzheimers Dis Other Demen 2011; 26:247-53.  
23  
24  
25  
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**Figure captions**

**Figure 1.** Experimental apparatus and stimuli presentation in the Simultaneous matching-to-sample condition

**Figure 2.** Examples of the stimuli used in Experiments 1 and 2

**Figure 3.** Experiment 1: (a) Percentage of correct responses (mean±SE) performed by the monkeys the SMTS and 0-delay MTS conditions (One-sample t-test: \*\*\*  $p < 0.001$ ); (b) Response time of correct responses (mean±SE) recorded the SMTS and 0-delay MTS conditions

**Figure 4.** Experiment 2: Percentage of correct responses (mean±SE) performed by the monkeys in the five delay conditions (One-sample t-test: \*  $p < 0.05$ ; \*\*\*  $p < 0.001$ )

**Figure 5.** Experiment 2: Response time of correct responses (mean±SE) recorded in the five delay conditions

Figure 1

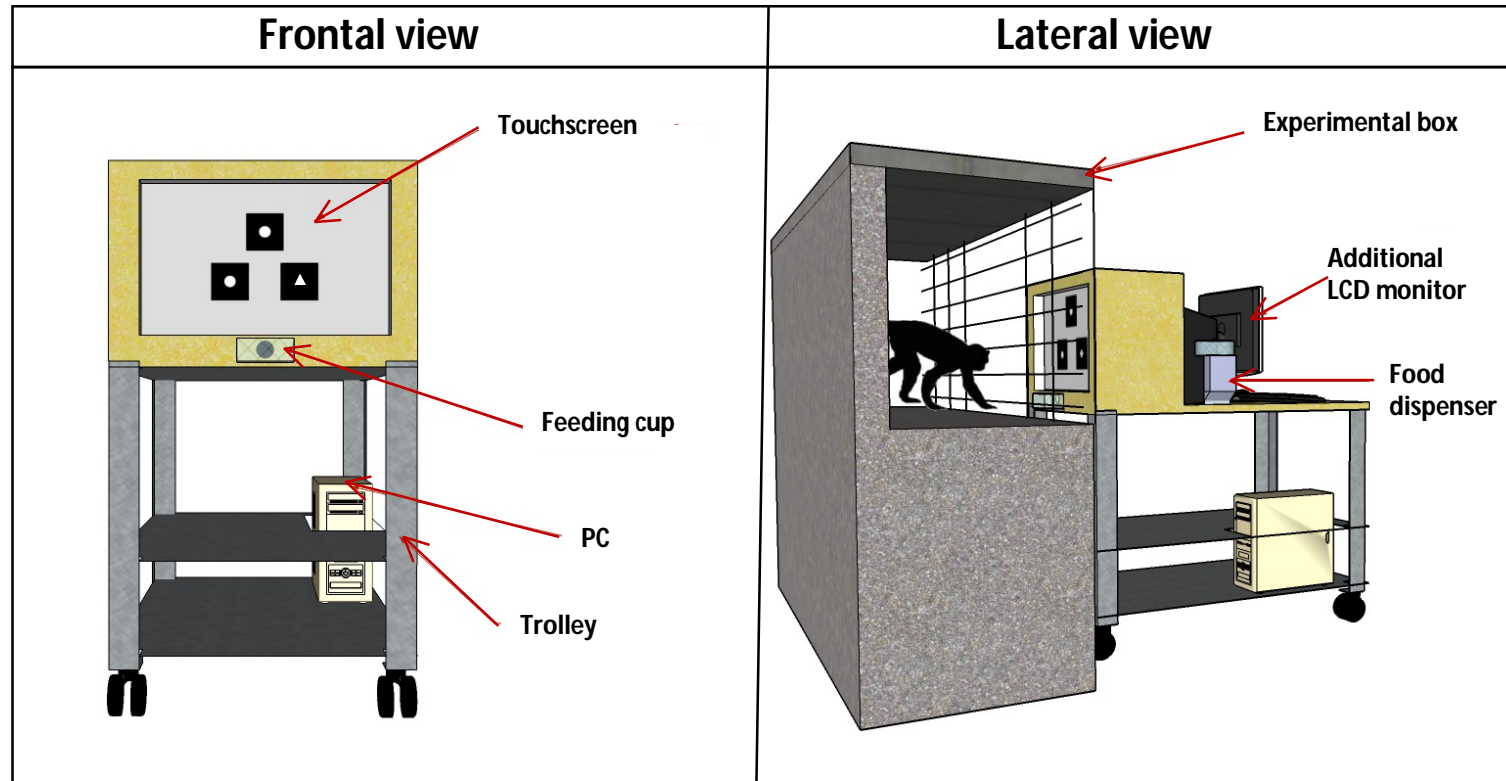


Figure 2

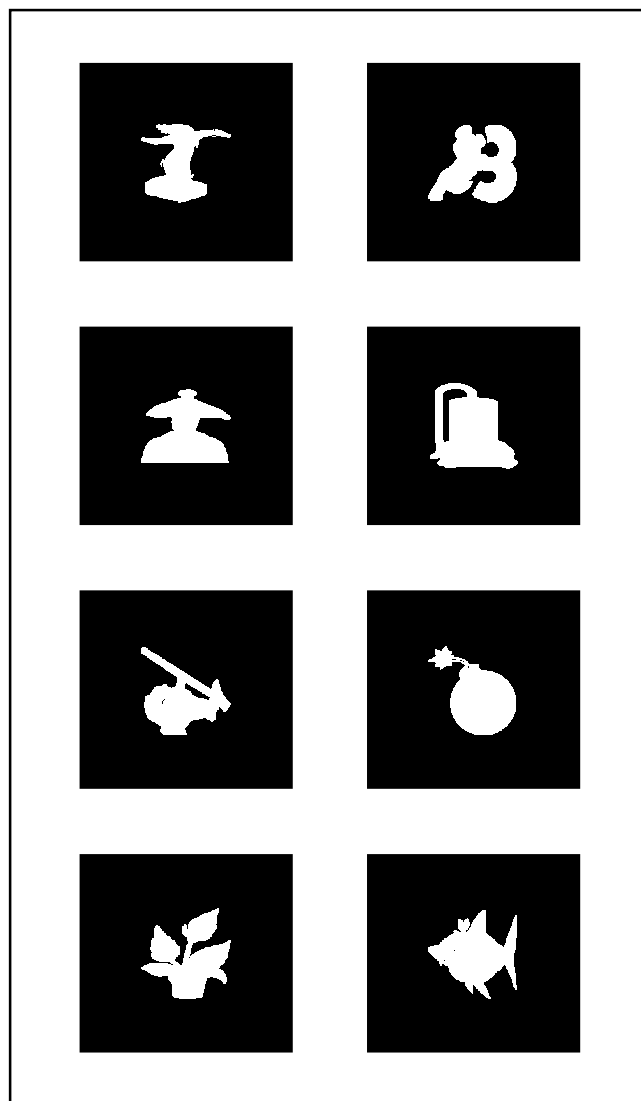
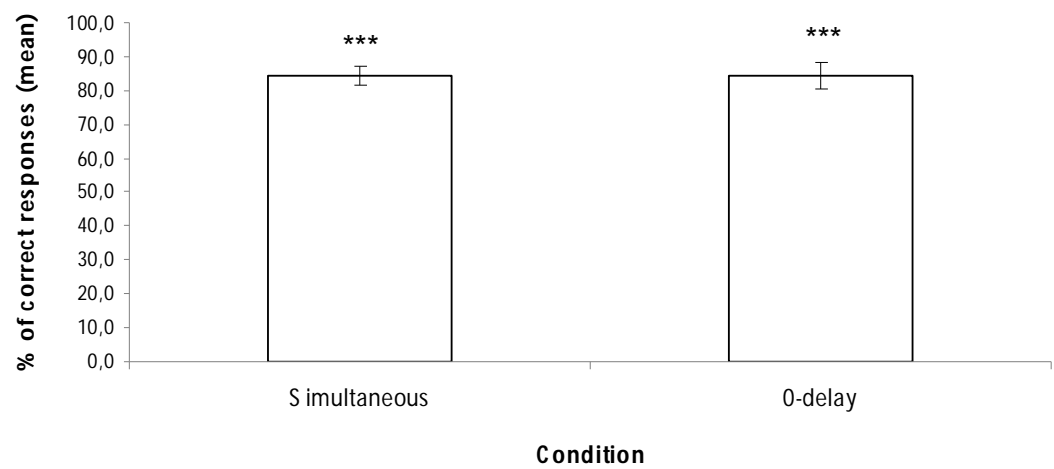


Figure 3

Experiment 1

(a) Accuracy



(b) Response time

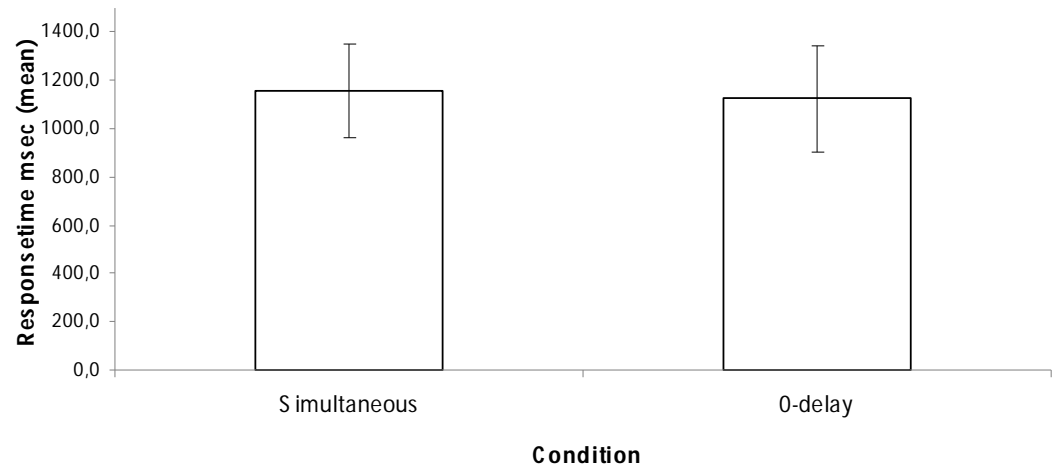


Figure 4

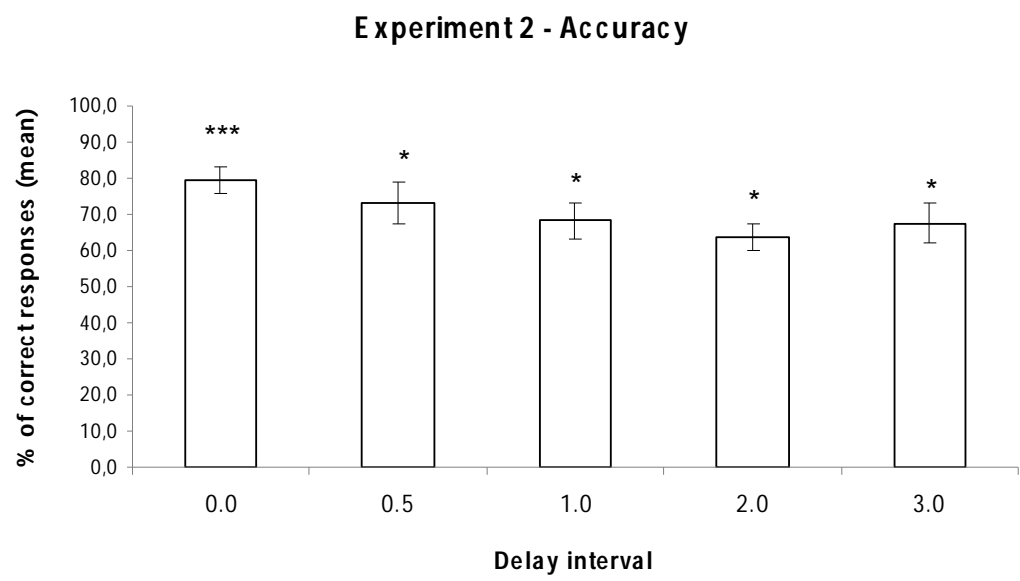


Figure 5

