Short-term memory effects on visual global/local processing in tufted capuchin monkeys (*Sapajus* spp.)

Valentina Truppa[a], Diego A. De Simone[a, b], Carlo De Lillo[c]

[a]Institute of Cognitive Sciences and Technologies, National Research Council of Italy (CNR), Via Ulisse Aldrovandi 16/B, 00197 Rome, Italy

[b]Department of Philosophy, Sapienza University of Rome, Via Carlo Fea 2, 00161 Rome, Italy

[c]School of Psychology, University of Leicester, Lancaster Road, Leicester, LE1 9HN, UK

All authors contributed equally to the paper**.**

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Correspondence concerning this article should be addressed to Valentina Truppa, Institute of Cognitive Sciences and Technologies, National Research Council of Italy (CNR), Via Ulisse Aldrovandi 16/B, 00197 Rome, Italy. E-mail address: valentina.truppa@istc.cnr.it

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Abstract

Non-human primates, differently from humans, are less proficient at processing global properties of visual compound stimuli. It has been suggested that humans preferentially process stimuli globally because this enables a more economical encoding of the stimuli. In this study we assessed the role of short-term memory in global/local processing by presenting tufted capuchin monkeys with Navon-type hierarchical figures in both simultaneous and delayed matching-to-sample tasks. Capuchins' ability to discriminate hierarchical stimuli was evaluated as a function of increasing delay intervals (0.0, 0.5, 1.0, 2.0 and 3.0 sec) between the disappearance of the sample and the presentation of the comparison stimuli. The results showed that recognition accuracy for local features was above chance level with delays of up to 3.0 sec, as previously reported when capuchins were faced with non-hierarchical stimuli. By contrast, the recognition of global configurations was above chance level in simultaneous, 0.0 and 0.5 sec delay conditions but not at delay intervals of 1.0 sec or longer. These findings indicate that capuchins' propensity to process the local properties of visual stimuli can be observed when a delay is interposed between the presentation of sample and comparison stimuli and was not reversed by increasing the delay. Moreover, our results show that capuchins' local propensity was not reversed by increasing stimulus size. Overall, our study confirms crucial differences between human and non-human primates and adds new insights into the comparative research on visual grouping functions of these species.

Keywords: visual perception, global/local processing, hierarchical stimuli, short-term memory, New-World monkeys

Introduction

In order to visually identify objects and segregate them from the background, we must be able to group their component elements into a coherent perceptual whole (Kimchi, Beherman & Olson, 2003). Many studies on visual grouping are focused on the ability to process hierarchical stimuli, i.e. small (local) shapes arranged to form large (global) shapes. By using these stimuli, Navon (1977) found that adult humans were faster at identifying global shapes than local features and proposed that the global properties of a visual object are processed first, followed by an analysis of local constituents (Navon, 1977, 1981). This hypothesis, called the 'global precedence hypothesis', has been widely confirmed in the human literature (e.g., Kimchi, 1992, 1998; Lamb, Robertson, & Knight,1990). Nevertheless, global preference seems to decrease with the increase of either stimulus size (Kinchla & Wolfe, 1979; Lamb & Robertson, 1988) or the distance between the elements composing the global configuration (Martin, 1979).

Comparative research on global/local processing of hierarchical stimuli has been conducted on a number of non-human species including fish (Truppa, Sovrano, Spinozzi, & Bisazza, 2010), birds (pigeons: Cavoto & Cook, 2001; Fremouw, Herbranson, & Shimp, 1998, 2002; Goto, Wills, & Lea, 2004; domestic chicks: Chiandetti, Pecchia, Patt, & Vallortigara, 2014), mammals (domestic dogs: Pitteri, Mongillo, Carnier, & Marinelli, 2014; primates: Deruelle & Fagot, 1998; Fagot & Deruelle, 1997; Fagot & Tomonaga, 1999; Hopkins & Washburn, 2002; Neiworth, Gleichman, Olinick, & Lamp, 2006; Spinozzi, De Lillo, & Truppa, 2003; Tanaka & Fujita, 2000; Tanaka, Onoe, Tsukada, & Fujita, 2001). Notably, differences found in global/local processing between

53 human and non-human primates raised intriguing questions because of similarities in
54 neuroanatomical correlates of visual functions in these species.

55 An unresolved problem in visual cognition is the reason why the well-established
56 advantage shown by humans in the processing of global properties of visual patterns is
57 not present in other primates species which nevertheless share very similar visual
58 systems (e.g., Fobes & King, 1982; Kremers, 2005; Ungerleider & Mishkin, 1982).
59 Whereas humans are faster at identifying the global configuration compared to the local
60 elements, monkey species, in most cases, process the local components of hierarchical
61 patterns more proficiently than their global structure (capuchins: De Lillo, Spinozzi,
62 Palumbo, & Giustino, 2011; De Lillo, Palumbo, Spinozzi, & Giustino, 2012; Spinozzi et
63 al., 2003; Spinozzi, De Lillo, & Salvi, 2006; baboons: Deruelle & Fagot, 1998; Fagot &
64 Deruelle, 1997; macaques: Hopkins & Washburn, 2002; for different results see
65 Neiworth et al., 2006; Tanaka & Fujita, 2000; Tanaka et al., 2001). On the other hand,
66 chimpanzees, in contrast with monkeys, do not always process the local features of the
67 compound patterns better than their global shape (Fagot & Tomonaga, 1999; Hopkins &
68 Washburn, 2002). This possible relationship between phylogenetic distance from humans
69 and the emergence of a clear global advantage could be of significant interest for the
70 explanation of human cognitive evolution. According to some authors, these results can
71 reflect a greater difficulty of monkeys compared with humans in grouping the local
72 elements into a coherent whole rather than a local advantage *per se* (Fagot & Barbet,
73 2006). Nevertheless, in contrast with humans, capuchin monkeys process at a higher
74 level of accuracy the local levels of hierarchical visual stimuli that are specifically
75 designed to require grouping at both levels of stimulus structure (De Lillo et al., 2012).

76 Also, results showing that monkeys can be resistant to visual illusions requiring the
77 processing the relationship between parts of a visual image have been put in relation to

78 their local mode of processing. Conversely, a global mode of processing makes humans
79 sensitive to these illusions (Parron & Fagot, 2007).
80 It has been claimed that the tendency of humans to process the global level of
81 stimulus structure first, supports the efficient and economic storage of information
82 (Navon, 1977). This notion would be consistent with the proposal that human cognition
83 strives to achieve the simplest form of stimulus coding (Chater, 1996; 1997). The fact
84 that monkeys, with whom humans share several homologous brain areas, do not seem to
85 show the same tendency raises important theoretical issues regarding when and why
86 data-reducing cognitive mechanisms started to emerge in primate cognitive evolution.
87 The sensitivity of monkeys to properties of visual stimuli that can potentially be
88 exploited by data-reducing cognitive mechanisms, such as the degree of redundancy of
89 their structure, is debatable. Early studies have failed to show an ability to detect
90 redundancy in visual stimuli in macaques (Schrier, Povar, & Schrier, 1979). More recent
91 studies, however, show that capuchin monkeys can be sensitive to the redundancy of
92 visual patterns (De Lillo et al., 2012).
93 It seems that higher processes in monkeys' visual cognition are involved in
94 determining their preference for processing the local details of visual stimuli. In fact, it is
95 possible to reverse the local advantage of capuchin monkey by inducing subjects to
96 attend the global level of visual stimuli (De Lillo et al., 2011). The inversion of the local
97 advantage determined by directing the attention of capuchin monkeys to global
98 properties of the stimuli, however, is due to changes that negatively affect the quality of
99 processing of local details of stimuli, whereas the quality of processing of their global
100 shape remains unaffected by manipulations of attention bias. Thus, it has proved difficult
101 to find the conditions that may ameliorate the ability of monkeys to efficiently process
102 global properties of hierarchical visual stimuli.

Yet, in order to determine if genuine differences exist in data-reducing cognitive devices of different primate species it is important to be able to rule-out that under appropriate circumstances monkeys can show the same degree of data reduction abilities shown by humans, and possibly chimpanzees. In fact, it is possible that monkeys would deploy data reducing strategies in visual cognition when provided with enough incentive to do so.

Comparative studies so far have used forms of matching-to-sample (MTS) in which participants are required to choose which of two comparison stimuli resembles most closely a stimulus presented as sample without any delays interposed between the presentation of the sample and the comparison stimuli (either simultaneous MTS or 0-delay MTS) (e.g., De Lillo et al., 2011, 2012; Fagot & Deruelle, 1997; Hopkins & Washburn, 2002; Spinozzi et al 2003, 2006). In simultaneous matching-to-sample (SMTS), the sample stimulus remains on the screen when the comparison stimuli are presented. In 0-delay matching-to-sample (DMTS), the sample stimulus disappears simultaneously with the presentation of the comparison stimuli. With these types of MTS, participants may not need to encode the stimuli in capacity bound memory stores (i.e., short- and long-term memory stores) because the stimuli can be available either perceptually or as part of large capacity sensory (iconic) memory (Averbach & Coriell, 1961; Sperling, 1960; Neisser, 1967). Therefore, the incentive for an economic encoding of global configurations, rather than disconnected features, would be minimal. There is also a second reason for predicting that global processing could be facilitated in delayed MTS. Influential approaches to visual perception (Milner & Goodale, 2006) suggest that the dorsal cortical visual system has the function of connecting sensory and motor information in order to allow rapid and efficient actions towards perceived objects. Such system would rely on egocentric co-ordinates that provide accurate information

regarding the position of the observer and the object that needs to be acted upon but would not encode relationships between parts of a visual scene. Processing within the dorsal visual stream operates on a rapid timescale supporting actions performed within 2.0 sec of the appearance of visual objects. Experiments that have compared fast actions directed to objects in the visual field and pantomimed action performed after visual objects have disappeared for 2.0 sec have shown striking differences in patterns of results. Only pantomimed actions, such as grasping for visual objects, are sensitive to visual illusions that require the processing of the relationships between different parts of the visual scene. Thus grip aperture, when attempting to grasp visual objects presented within contexts known to illusorily affect their perceived size, is only distorted when a delay of 2.0 sec is imposed between object presentation and motor response (Goodale, Jakobson, & Keillor, 1994; Aglioti, DeSouza, & Goodale, 1995; Milner & Goodale, 2008). These results are interpreted as indicating an involvement of the ventral visual system that allows the perception of the relations of stimulus parts, only for arbitrary and/or delayed responses to visual stimuli (Aglioti et al., 1995; Milner & Goodale, 2008).

Most experiments of global/local processing in capuchin monkeys so far have involved immediate responses to visual stimuli, often consisting in displacing three panels depicting the stimuli in a Wisconsin General Test Apparatus - WGTA (see Spinozzi et al., 2003; De Lillo et al., 2011). It is therefore possible that this method for presenting stimuli and collecting responses induced the subjects to rely mostly on the dorsal visual system that is not best suited to process the relationship between parts of a visual image. Imposing a delay between stimulus presentation and response may, by contrast, force the subjects to recruit ventral visual functions more sensitive to relational processing. In fact, the dorsal system, that is likely to be less sensitive to relational

properties of visual input given its reliance on egocentric co-ordinates, support actions performed towards visual objects within fractions of seconds. Hence, delayed responses (typically of 2 seconds, see Milner and Goodale, 2006) towards objects that are no longer visually available are used to ensure that the response is informed by a visual representation of the stimulus created by ventral stream processing. As the ventral stream relies on allocentric co-ordinates it is better suited to compute the relationship between different parts of a visual image.

Thus, it is possible that delayed MTS could provide an incentive to integrate parts in wholes and tap the visual system most suitable for doing so. Testing capuchin monkeys with delayed MTS is therefore important to determine the constraints under which the local advantage in monkeys could be reversed.

Recently, Truppa, De Simone, Piano Mortari, and De Lillo (2014) using a computerised procedure demonstrated that, although the introduction of very brief time intervals (up to 3.0 sec) in delayed matching-to-sample tasks did not prevent capuchin monkeys' ability to solve the task with non-hierarchical visual stimuli, it can affect recognition performance. Specifically (1) the simple disappearance of the sample and the introduction of a delay of 0.5 sec did not affect capuchins' recognition of the stimuli, (2) a delay interval of 1.0 sec produced a significant increase in response time but still did not affect recognition accuracy, and (3) delays of 2.0 and 3.0 sec determined a significant increase in response time and a reduction in recognition accuracy. These results indicate that shorter or longer delays around 2 sec produce non-linear effects on MTS performance in capuchin monkeys, which could be an expression of different types of processing. To evaluate how delays affect global/local processing in capuchin monkeys, in the present study we tested their ability to match hierarchical stimuli on the basis of global shapes or local features when: (i) the sample stimulus was always available on the

screen until subjects made a choice (SMTS); (ii) the sample disappeared with no delay in the presentation of the comparison stimuli (0-delay MTS); or (iii) different delays (0.5, 1.0, 2.0 and 3.0 sec) between the disappearance of the sample and the availability of the comparison stimuli were introduced (DMTS). If local elements are better preserved than global configuration independently of delay length, this could suggest a substantially different mode of encoding visual information in monkeys and humans. By contrast, if the local preference of capuchins could be reversed by increasing the need for efficient memory storage and/or by requiring the engagement of a different visual processing system this would suggest a more similar mode of processing in humans and monkeys than suggested by previous studies.

Taking advantage of a computerised procedure, which allowed a highly controlled presentation of the stimuli, we also assessed whether or not the local advantage of capuchins could be affected by stimulus size and order of presentation of global and local trials. Stimulus size was manipulated because early studies with humans suggested that it can affect the global precedence effect in humans (Kinchla & Wolfe, 1979). The role stimulus size has been considered confounded with effects related to the eccentricity of the stimuli in humans (Navon & Norman, 1983) and previously proved to be unable to reverse the local advantage typically shown by capuchin monkeys (Spinozzi et al., 2006), as well as the global advantage shown by fish (Truppa et al., 2010). Nevertheless, it was considered important to assess its role in a paradigm that involved delayed MTS. The order of presentation of global and local trials was manipulated because effects of the context of trials in which MTS occurs sometimes can affect performance (Truppa et al., 2014) and, to our knowledge, the effect of context provided by the order of presentation has not been assessed on capuchin monkeys before. Thus, it was considered important to assess the effects of this additional variable here.

Method

Subjects

Subjects were four tufted capuchin monkeys (*Sapajus*[1] spp.), two males (Robot and Sandokan) and two females (Roberta and Rucola). All subjects were adults (age: 11-25 years old) 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^2 x 2.5 m high; outdoor: 40-130 m^2 x 3 m high). The monkeys 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. 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 matching-to-sample procedure because they had been tested with a touchscreen based apparatus in tasks involving abstract concept acquisition and short-term memory effects (Truppa et al., 2014; Truppa, Garofoli et al., 2010; Truppa, Piano Mortari, Garofoli, Privitera, & Visalberghi, 2011). However, subjects had never been tested with Navon-type hierarchical figures before.

[1] On the basis of recent data, it has been proposed that capuchin monkey species, traditionally identified as belonging to a single genus (*Cebus*), can be grouped instead in two distinct genera: (i) the robust (tufted) forms have been referred to the genus *Sapajus*, and (ii) the gracile (untufted) forms have been retained in the genus *Cebus* (Lynch Alfaro, Boubli et al., 2012; Lynch Alfaro, De Souza Silva, & Rylands, 2012). Tufted capuchin monkeys hosted at the Primate Center of the CNR are derived from individuals of different provenience and are considered to be unknown combinations of species of the genus *Sapajus*.

Ethical note

The research protocol used in this study was approved by the Italian Health Ministry (Central Direction for the Veterinary Service, approvals n. 11/2011-C to V. Truppa). Housing conditions and experimental procedures were in full accordance with European law on humane care and use of laboratory animals and complied with the recommendations of the Weatherall Report (2006). To increase three-dimensional space available to the animals, indoor enclosures were furnished with perches and ropes and outdoor enclosures were furnished with logs, branches and ropes. Moreover, the presence of natural substrates, including woodchips on the ground, served to promote the monkeys' exploratory behaviours. All subjects were habituated to the experimental cage, the experimental routine and the experimenters.

Apparatus

The computerised workstation consisted of a PC (Model AMD Athlon 1200) connected to a 19" touchscreen (Model E96f+SB, CRT, ViewSonic) and an automatic food dispenser (Model ENV-203-45, MED Associates, Inc. Georgia, VT) (Figure 1A). When the monkey provided the correct response, the food dispenser delivered a 45-mg banana-flavoured pellet (TestDiet, Richmond, IN, USA) into a Plexiglas feeding cup (10 cm wide x 5 cm deep x 3.5 cm high) located 16 cm below the touchscreen, in the centre. E-Prime software (Psychology Software Tools, Inc.) was used for the presentation of the stimuli, the recording of the subject's response and the activation of the food dispenser.

A wooden frame (48 cm wide x 64 cm high x 30 cm deep) with a central aperture (36 cm wide x 26 cm high) surrounded the touchscreen. The food dispenser was placed behind the wooden frame, out of sight of the subject. Moreover, an additional LCD monitor was placed at the back of the touchscreen to allow the experimenter to see the

progress of the session so as to remove the apparatus at the end of the session. The touchscreen, food dispenser and 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 the experimenters to videotape the subject's behaviour during testing.

Stimuli

Two stimulus sets, each of 16 compound forms were used (Figure 1B). Each set included large circles, squares, rhombi, or letter Xs made up of smaller circles, squares, rhombi, or letter Xs. We label these stimuli as Cc, Cs, Cr, Cx, Ss, Sc, Sr, Sx, Rr, Rc, Rs, Rx, Xx, Xc, Xs, and Xr, indicating with the first letter the global shape and with the second one the local shape (e.g., Cs refers to a large circle made of small squares). Moreover, each set included four consistent figures (Cc, Ss, Rr, and Xx), where global and local shapes were the same and 12 inconsistent figures (Cs, Cr, Cx, Sc, Sr, Sx, Rc, Rs, Rx, Xc, Xs, and Xr), in which global and local shapes were different. Each stimulus consisted of 12 white elements, however the size of both local elements and global configurations varied between the two stimulus sets. The Set A, included 0.50 cm x 0.50 cm (i.e., 1.91° of visual angle) local elements spatially arranged to form 4 cm x 4 cm (i.e., 14.93° of visual angle) global shapes. The distance between two adjacent elements

was 0.66 cm (i.e., 2.52° of visual angle). The Set B, included 0.25 cm x 0.25 cm (i.e., 0.95° of visual angle) local elements spatially arranged to form 2 cm x 2 cm (i.e., 7.59° of visual angle) global shapes. The distance between two adjacent elements was 0.33 cm (i.e., 1.26° of visual angle). The sizes of the stimuli included in Set A and B mimicked conditions used with capuchin monkeys by Spinozzi et al. (2003). These authors used 4 cm x 4 cm hierarchical stimuli (same size of our Set A), which at the beginning of the trials were presented at a distance of 30 cm (i.e., 7.59° of visual angle, a condition we replicated by using Set B) and then moved within the monkey's reach at a distance of 15 cm (i.e., 14.9° of visual angle, a condition we replicated by using Set A).

Stimuli were all presented within a black background (6.5 cm x 6.5 cm, i.e. 23.4° of visual angle). They were created using Microsoft PowerPoint and were transformed into bitmap images for stimulus presentation on the computer screen.

Procedure

An MTS task was used, in which three stimuli, the sample stimulus (SS), the matching - rewarded - stimulus (S+), and the non-matching stimulus (S-), were presented on the computer screen. At the beginning of each trial, SS was automatically generated on the upper half of the screen, in the centre. Then, after the subject touched the sample stimulus one time, S+ and S- were displayed simultaneously 4 cm below the sample, to the right and left, at a distance of 5 cm apart (Figure 1A). The initial touch to the sample ensured that the monkey was paying attention to the sample stimulus at the beginning of each trial. Depending on the experimental condition, the sample could either remain present when the comparison stimuli appeared (SMTS) or disappear immediately after that the subject touched it (DMTS). In the DMTS different delay intervals were interposed between the disappearance of the sample and the appearance of the

comparison stimuli (0.0, 0.5, 1.0, 2.0, 3.0 sec). The right/left position of S+ and S- was randomly determined for each trial. The subject had to indicate its choice by touching one of the comparison stimuli on the screen (see supplemental videos: S1, S2, S3 and S4); the computer automatically recorded the choice and the Response Time (RT) to make the choice. If S+ was chosen, a food pellet was dispensed. If S- was selected, no pellet was dispensed. The display disappeared immediately after a response was recorded. 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.

Experimental design

All monkeys were tested with stimuli of Set A (larger stimuli) first and then with stimuli of Set B (smaller stimuli). For each stimulus set, the monkeys were faced with two different matching conditions. In the Global condition, S+ was identical to the sample and S- differed from the sample only at its global level. For example, a trial of the global condition featuring stimulus Rr (see Figure 1B) as the sample would have stimulus Rr presented as S+ and could have stimulus Cr presented as S-. In the Local condition, S+ was identical to the sample and S- differed from the sample only for the shape of its local elements. In this case, a trial featuring stimulus Rr as the sample would have stimulus Rr presented as S+ and could have stimulus Rs presented as S-. Each subject received 24 48-trial sessions (12 for each stimulus set), one session a day for a total of 1152 trials. Overall, each type of stimulus (n = 16) was presented as sample for a total of 6 trials for each level of processing (n = 2: global, local) in each matching condition (n = 6: simultaneous, 0.0, 0.5, 1.0, 2.0, 3.0 sec). For each stimulus set: (1) six

sessions (intermixed global/local session) included 24 Global trials and 24 Local trials presented in a pseudo-random order, with the only constraint that trials of the same condition (global or local) were presented no more than two times consecutively; (2) three sessions (blocked global sessions) included 48 Global trials; and (3) three sessions (blocked local sessions) included 48 Local trials. All sessions included five 8-trial blocks with different delays (0.0, 0.5, 1.0, 2.0, 3.0 sec) and one 8-trial block of simultaneous MTS. Trials of the six conditions were randomly intermixed within each session. The three types of session (intermixed global and local, blocked global, blocked local) were alternated according to an order of presentation which was different for each subject.

Data analyses

The percentage of correct responses and the mean RT were used for the analyses. 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 RTs for correct choices were included in the analyses. The videos of the experimental sessions were used to detect instances where the subject turned away from the screen during a trial, thus spuriously affecting the length of the delay interval between the appearance of the comparison stimuli and the subjects' response. All trials were such instances were detected were removed from those analyses.

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. For each test variable, a one-sample *t*-test was used to compare the observed percentage of correct responses of capuchins with the percentage expected by chance (i.e., 50%). Repeated measures ANOVAs were used to compare different conditions both in terms of percentage of correct responses and mean

RTs. Finally, post-hoc tests (Tukey, HSD test) for multiple comparisons were used to further analyse significant effects revealed by the ANOVAs. Statistical significance was set at $p \leq .05$.

Results

The analyses of the videos revealed that in 249 trials (5.4% of all trials) subjects were not looking at the screen when the comparison stimuli appeared (Rucola = 100, Sandokan = 37, Robot = 41, Roberta = 71). In the simultaneous and 0-delay conditions this was a very rare event, which occurred only 8 and 10 times, respectively. However, this happened more frequently with the increasing of the length of the delay (Spearman correlation, $r = .94$, $N = 6$, $p = .005$). Moreover, this happened with a similar frequency in the local [$M = 18.2$, 95% CI (9.12, 27.38)], and global trials [$M = 15.5$, 95% CI (4.44, 26.56)], [paired t-test: $t(3) = 1.36$, $p = .266$] of the blocked sessions. This latter analysis was only carried out for the blocked sessions. In fact, it would have been meaningless in the intermixed sessions. This is because in the intermixed sessions, the subjects did not have any information regarding whether the trial pertained to the local or global condition in the interval between the presentation of the sample and the comparison stimuli.

The trials in which subjects were not looking at the screen when the comparison stimuli appeared featured an uncontrolled increase of the scheduled interval, therefore they were not subjected to any further analysis.

Accuracy. Table 1 reports the results of one-sample *t*-tests for the local and global trials in each matching condition (SMTS, 0.0, 0.5, 1.0, 2.0, 3.0 sec delayed). In the local

trials, capuchins' percentage of correct responses was significantly above the level of chance (50%) in all different conditions. By contrast, in the global trials the percentage of responses was above chance level only in the SMTS condition, the 0-delay MTS condition and when the delay was 0.5 sec. Longer delays induced chance-level performance (see Figure 2).

An ANOVA was carried out on the percentage of correct responses with delay condition (simultaneous, 0.0, 0.5, 1.0, 2.0, 3.0 sec delayed), level of processing (global, local), stimulus size (larger, smaller), stimulus consistency (consistent, inconsistent), and trial order (global and local intermixed, global and local blocked) as repeated measures. The analysis revealed a significant main effect of the delay condition [$F_{(5, 15)} = 6.1$, $p = .003$, $\eta p^2 = .670$] and significant interactions between: (1) delay condition and trial order [$F_{(5, 15)} = 4.4$, $p = .011$, $\eta p^2 = .595$], (2) level of processing and trial order [$F_{(1, 3)} = 50.5$, $p = .006$, $\eta p^2 = .944$], and (3) level of processing and stimulus size [$F_{(1, 3)} = 26.5$, $p = .014$, $\eta p^2 = .898$]. No other significant main effects or interactions were found (all *ps* > .058).

Post-hoc analyses (Tukey, HSD test) for the interaction between delay condition and trial order indicated that accuracy in different delay conditions varied according to the order of presentation of global and local trials (see Figure 3). When global and local trials were presented in blocked sessions the mean percentage of correct responses observed in simultaneous [$M = 67.53\%$, 95% *CI* (57.71, 77.36)], 0.0 sec [$M = 66.23\%$, 95% *CI* (45.55, 86.92)], 0.5 sec [$M = 65.71\%$, 95% *CI* (54.93, 76.49)], 1.0 sec [$M = 67.27\%$, 95% *CI* (55.21, 79.34)] and 2.0 sec [$M = 60.10\%$, 95% *CI* (40.37, 79.77)] delay conditions did not differ from each other. Capuchin' accuracy in simultaneous, 0.0, 0.5 and 1.0 sec delay conditions was significantly higher than that of the 3.0 [$M = 55.06\%$, 95% *CI* (38.72, 71.40)], (all *ps* < .028); moreover the percentage of correct responses

observed in the 2.0 and 3.0 sec delay conditions did not differ. When global and local trials were intermixed in the same session the mean percentage of correct responses observed in the simultaneous [*M* = 71.35%, 95% *CI* (62.13, 80.58)], 0.0 sec [*M* = 72.65%, 95% *CI* (60.37, 84.94)] and 0.5 sec [*M* = 70.31%, 95% *CI* (62.02, 78.60)] delay conditions did not differ from each other. By contrast, the percentage of correct responses recorded in all these conditions was significantly higher than that observed in the 1.0 sec [*M* = 58.59%, 95% *CI* (47.48, 69.70)], 2.0 sec [*M* = 61.20%, 95% *CI* (44.38, 78.01)] and 3.0 sec [*M* = 58.33%, 95% *CI* (49.88, 66.78)] delay conditions, (all *ps* < .040). Finally the level of response accuracy of the 1.0, 2.0 and 3.0 sec delay conditions did not differ from each other. The interaction is most likely explained by the fact that MTS performance in the blocked condition seems to deteriorate at 2 sec delay. By contrast, in the intermixed condition a deterioration of MTS performance starts to occur at 1 sec interval.

Post-hoc analyses for the interaction between level of processing and trial order indicated that the level of accuracy was significantly higher in local than global trials irrespectively of whether the two types of trials were intermixed [local: *M* = 74.22%, 95% *CI* (56.54, 91.89); global: *M* = 56.60%, 95% *CI* (51.39, 61.80); *p* = .0007] or blocked [local: *M* = 68.79%, 95% *CI* (48.26, 89.32); global: *M* = 58.51%, 95% *CI* (48.39, 68.62); *p* = .002] (see Figure 4). Moreover, whereas in local trials the percentage of correct responses was significantly higher when the two types of stimuli were intermixed than when they were blocked (*p* = .015), in global trials there was no difference between the two types of presentation order (*p* = .215).

Finally, post-hoc analyses for the interaction between level of processing and stimulus size indicated that, although the level of accuracy was always higher in local than global trials, this advantage was significant with larger stimuli [local: *M* = 75.35%,

95% *CI* (61.27, 89.43); global: *M* = 53.50%, 95% *CI* (46.25, 60.75); *p* = .006] but not with smaller stimuli [local: *M* = 67.66%, 95% *CI* (42.48, 92.84); global: *M* = 61.60%, 95% *CI* (52.63, 70.57); *p* = .188] (see Figure 5). Moreover, the mean percentage of correct responses in local trials with larger stimuli did not differ from that of local trials with smaller stimuli (*p* = .109). Likewise, the accuracy in global trials with larger stimuli did not differ with that observed in global trials with smaller stimuli (*p* = .096).

Response time. An ANOVA was carried out on the RT for correct responses with delay (simultaneous, 0.0, 0.5, 1.0, 2.0, 3.0 sec delay), level of processing (global, local), stimulus size (larger, smaller), stimulus consistency (consistent, inconsistent), and trial order (intermixed, blocked) as repeated measures factors. A significant main effect of delay was found [$F_{(5, 15)} = 7.6$, $p = .0009$, $\eta p^2 = .718$]. No other significant main effects or interactions were found (all *ps* > .076).

Post-hoc comparisons on the main effect of delay revealed that the mean RT of the Simultaneous condition [*M* = 1324.43 msec, 95% *CI* (830.26, 1818.60)] did not differ from the 0.0 [*M* = 1237.59 msec, 95% *CI* (703.93, 1771.24), *p* = .747], 0.5 [*M* = 1416.71 msec, 95% *CI* (885.90, 1947.52), *p* = .699], 1.0 [*M* = 1489.50 msec, 95% *CI* (1023.78, 1955.23), *p* = .160] and 2.0 [*M* = 1523.61 msec, 95% *CI* (1065.48, 1981.73), *p* = .063] sec conditions but it was significantly shorter than in the 3.0 sec delay condition [*M* = 1560.79 msec, 95% *CI* (1087.59, 2033.99), *p* = .021]. The mean RT in the 0.0 sec condition was significantly shorter than in the 1.0 (*p* = .013), 2.0 (*p* = .005) and 3.0 (*p* = .002) sec of delay. Finally, the RT for the 0.5, 1.0, 2.0 and 3.0 sec delay conditions did not significantly differ from each other (all *ps* > .268).

Discussion

This study demonstrated that capuchins monkeys are able to discriminate hierarchical figures in delayed matching-to-sample tasks when short delays are introduced, however, when they have to match the global configuration of the stimuli their MTS ability is compromised by delays of 1.0 sec or longer. In more detail, we used an MTS condition in which the sample was available on the screen during the entire trial (SMTS) and five conditions in which the sample disappeared and the comparison stimuli appeared after 0.0, 0.5, 1.0, 2.0 or 3.0 sec (DMTS). We found that capuchins' matching accuracy for local features was above chance level in conditions of up to 3.0 sec delay. Accuracy for global configurations was less robust. It was above chance level only in simultaneous, 0.0 and 0.5 sec delay conditions. These findings suggest that capuchin monkeys could have a more accurate short-term retention of the local features of visual patterns than their global configurations. The extent to which this is due to a less effective encoding of global information or to a more rapid decay of information pertaining to the global level of stimulus structure in this species would need to be determined with further investigations.

We did not find a significant Level of processing x Delay interaction. In fact, increasing the delay induced a decrement in accuracy level in both local and global trials. In particular, in the global trials it decreased to chance level when the delay was of 1.0 second or more. This happened contrary to the expectation that increasing delays could have provided an incentive to retain the global structure of the stimuli that allegedly supports a more economic storage of information (Navon, 1977). The local advantage in capuchin monkeys persists also for delay durations above 2.0 sec that have been shown to induce visual illusions and the processing of relationships between parts (Milner & Goodale, 2006). This suggests that the local advantage observed in simultaneous and

zero-delay conditions in capuchin monkeys cannot be explained by a selective engagement of the dorsal visual system induced by fast responding to stimuli that are perceptually available when acting upon them. Of particular relevance for this study are previous data by Truppa et al. (2014) showing that, when matching conditions identical to those of the present study were presented using non-hierarchical stimuli, capuchins were able to solve the task with up to 3 sec delay. Therefore, it seems that the encoding or the retention of the global properties of visual patterns is particularly vulnerable in capuchin monkeys. Capuchins can process the global aspects of stimuli, as shown here and in previous studies (De Lillo et al., 2011, 2012; Spinozzi et al., 2003, 2006). However, the results of this study show that global information is either encoded less accurately or deteriorates more rapidly in memory than local information. We cannot disambiguate these different scenarios in the present study. Nevertheless, it would be an interesting issue to address in further research.

The procedure we adopted in this study left the monkeys free to devote as much time as they wanted to the visual inspection of the sample. In fact, (i) in our SMTS condition the sample remained on the screen until the subject chose one of the comparison stimuli, and (ii) in our DMTS conditions, the sample remained on the screen until the subject touched it. It has been shown that increasing the duration of the sample presentation in MTS tasks does not improve monkeys' performance (D'Amato & Worsham, 1972) unless the subjects are required to repeatedly touch the sample stimulus before making a choice (Katz, Wright & Bachevalier, 2002). Therefore, it would be of interest to assess in future studies if by adopting the same procedure of Katz et al. (2002) it is possible to improve capuchins' MTS performance, especially when a more demanding condition, such as the processing of global properties, is required.

The order of presentation of the global and local trials differently affected capuchins' accuracy as a function of the delay condition (simultaneous, 0.0, 0.5, 1.0, 2.0 and 3.0 sec delay). When global and local trials were presented in blocked sessions the accuracy in simultaneous, 0.0, 0.5, 1.0 and 2.0 sec delay conditions did not differ from each other, whereas accuracy in 0.0, 0.5 and 1.0 sec delay conditions was significantly higher than those in the 3.0 sec delay condition; moreover level of response accuracy of the 2.0 and 3.0 sec delay conditions did not differ. Differently, when global and local trials were intermixed in the same session the mean percentage of correct responses observed in simultaneous, 0.0 and 0.5 sec delay conditions did not differ from each other, whereas the accuracy level in all these conditions was significantly above the accuracy level observed with 1.0, 2.0 and 3.0 sec delays; moreover, the level of response accuracy of the 1.0, 2.0 and 3.0 sec delay conditions did not differ from each other. Overall, our findings indicated that blocked sessions induced a similar trend to that observed by Truppa et al. (2014) in capuchins tested with non-hierarchical stimuli. In that study, the response accuracy did not decrease for intervals up to 1.0 sec and a deterioration of performance occurred at the 2.0 sec interval. By contrast, in intermixed sessions, the drop in accuracy occurred earlier. In fact, response accuracy in the intermixed sessions remained at similar level for intervals up to 0.5 sec and a drop in performance was observed at 1 sec interval. This may have been due to the potential requirement of having to repeatedly shift attention between the two levels of stimulus structure in the intermixed sessions.

Moreover, the order of presentation of the global and local trials in the experimental sessions (intermixed or blocked) affected capuchins' response accuracy in a different way depending on the level of processing (global or local). Whereas in global trials there was no difference between the two types of presentation, counterintuitively, in local trials

the percentage of correct responses was significantly higher when global and local trials were intermixed than when they were blocked. In the present study, six intermixed sessions including 50% global trials and 50% local trials were alternated with six blocked sessions, three involving 100% global trials and three involving 100% local trials. Thus, the percentages of the two different types of trials varied always in an unpredictable way across experimental sessions. The reason why these variations affected local but not global response accuracy remains an unexplained phenomenon. Different results emerged when the proportion of trials requiring global and local processing are varied systematically to induce attentional biases. Using a simultaneous matching-to-sample task with the same monkey species, De Lillo et al. (2011) demonstrated that systematic variations of the proportion of global and local trials could reverse capuchins' preference. These authors showed a local advantage in the local bias condition (i.e., 85.7% local trials, 14.3% global trials) but a global advantage in the global bias condition (i.e., 85.7% global trials, 14.3% local trials). In the study by De Lillo et al. (2011), in fact, capuchins received a total of 16 experimental sessions with global bias and local bias conditions that were regularly alternated every 4 sessions.

The larger version of the stimuli used in this study (i.e., Set A) subtended 14.9° of visual angle whereas the smaller version (i.e., Set B) subtended 7.59° of visual angle. Whereas the level of accuracy was significantly higher in local than global trials with larger stimuli, the opposite pattern was not found with smaller stimuli. Specifically, by halving the size of our larger stimuli, the local preference of capuchin monkeys decreased but was not reversed. Effects ascribable to stimulus size have been also found in the human visual cognition literature. Studies in humans demonstrated that manipulations of stimulus size can reverse the global advantage in humans (Kinchla & Wolfe, 1979; Lamb & Robertson, 1988). For example, Kinchla and Wolfe (1979)

548 varying the stimulus from 4.8° to 22.1° of visual angle, found that human subjects had a
549 global preference for patterns subtending less than 6° to 9° of visual angle, but a local
550 preference for larger patterns. Thus, whereas in humans there is evidence that the
551 stimulus size can produce a reversal of the global advantage, capuchins' strong local
552 advantage shown with larger stimuli was decreased but was not reversed by a reduction
553 of stimulus size. This result, indicates that variations of stimulus size do not seem to be
554 sufficiently powerful to produce a global advantage in this monkey species, at least
555 within the range of size variation considered in this study. Moreover, our results
556 corroborate findings from other studies in non-human species which did not find a
557 reversal of local (Spinozzi et al., 2006) or global (Truppa, Sovrano et al., 2010)
558 preference, albeit with methodological procedures that did not allow to precisely control
559 the visual angle subtended by the stimulus during the course of the trials. For example, in
560 the study by Spinozzi et al. (2006) capuchin monkeys at the beginning of each trial
561 viewed the stimuli mounted on a panel from approximately 30 cm, then the panel was
562 brought closer to the cage (about 15 cm), within reach of the monkey's arm. Similarly,
563 the experimental procedure adopted by Truppa, Sovrano et al. (2010) to test fish did not
564 allow a strict control of the distance between the subject and the stimuli to discriminate
565 since the fish was free to swim inside the experimental apparatus and to explore the
566 stimuli visually from different distances before making a choice.

567 Finally, when RTs were considered, a significant main effect of the delay condition
568 emerged indicating that, when the sample disappeared from the screen, the increase of
569 the delay intervals led to significantly longer RTs, especially when 1.0, 2.0 and 3.0 sec of
570 delay were introduced. This suggests that the increase in RT in DMTS can be indicative
571 of an increased difficulty of retrieval processes when the memory trace starts to decay.
572 Such a significant increase of the response time for delay intervals equal or longer than

1.0 sec has also been documented in capuchins (Truppa et al., 2014) and baboons (Rodriguez, Zvrcher, Bartlett, Nathanielsza, & Nijlanda, 2011) when brief delay intervals and non-hierarchical stimuli were used in DMTS tasks.

Overall, our findings indicate that the local advantage in capuchins is a very robust phenomenon and that it persists even when a delay is imposed between the presentation of the sample and the comparison stimuli. Thus, this study provides important additional information regarding the way in which monkeys encode global and local visual information in short-term visual memory. We hope that this evidence will encourage further detailed investigations on both attention and visual memory storage mechanisms in primate as well as other taxonomic groups. Future studies in human and non-human species would need to characterise the effect of memory load on the processing of global and local level of the hierarchical patterns, both when short- and long-memory systems are involved.

References

Aglioti, S., DeSouza, J. F. X., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*, 679-685. http://dx.doi.org/10.1016/S0960-9822(95)00133-3

Averbach, E., & Coriell, A. S. (1961). Short-term memory in vision. *Bell System Technical Journal*, *40*, 309-328. doi: 10.1002/j.1538-7305.1961.tb03987.x

Cavoto, K. K., & Cook, R. G. (2001). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *27*, 3-16. http://dx.doi.org/10.1037/0097-7403.27.1.3

Chater, N. (1996). Reconciling simplicity and likelihood principles in perceptual organisation. *Psychological Review*, *103*, 566-581. http://dx.doi.org/10.1037/0033-295X.103.3.566

Chater, N. (1997). Simplicity and the mind. *The Psychologist*, *November*, 495-498.

Chiandetti, C., Pecchia, T., Patt, F., & Vallortigara, G. (2014). Visual hierarchical processing and lateralization of cognitive functions through domestic chicks' eyes. *PLoS ONE*, 9(1): e84435. doi:10.1371/journal.pone.0084435.

D'Amato, M. R., & Worsham, R. W. (1972). Delayed matching in the capuchin monkey with brief sample durations. *Learning & Motivation*, *3*, 304-312.

De Lillo, C., Spinozzi, G., Palumbo, M., & Giustino, G. (2011). Attention allocation modulates the processing of hierarchical visual patterns: a comparative analysis of capuchin monkeys (*Cebus apella*) and humans. *Journal of Experimental Psychology: Animal Behavior Processes*, *37*, 341–352. doi:10.1037/a0022989.

De Lillo, C., Palumbo, M., Spinozzi, G., & Giustino, G. (2012). Effects of pattern redundancy and hierarchical grouping on global-local visual processing in monkeys

(*Cebus apella*) and humans (*Homo sapiens*). *Behavioural Brain Research*, *226*, 445-455. doi:10.1016/j.bbr.2011.09.040.

Deruelle, C., & Fagot, J. (1998). Visual search for global/local stimulus features in humans and baboons. *Psychonomic Bulletin & Review*, *5*, 476-481. doi: 10.3758/BF03208825

Fagot, J., & Barbet, I. (2006). Grouping and segmentation of visual objects by baboons (*Papio papio*) and humans (*Homo sapiens*). In: E. A. Wasserman & T. R. Zental (Eds.), *Comparative cognition*, (pp. 15-28). Oxford: University Press.

Fagot, J., & Deruelle, C. (1997). Processing of global and local visual information and hemispheric specialization in humans (*Homo sapiens*) and baboons (*Papio papio*). *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 429-442. http://dx.doi.org/10.1037/0096-1523.23.2.429

Fagot, J., & Tomonaga, M. (1999). Comparative assessment of global-local processing in humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*): Use of a visual search task with compound stimuli. *Journal of Comparative Psychology*, *113*, 3-12. http://dx.doi.org/10.1037/0735-7036.113.1.3

Fobes, J. L., & King, J. E. (1982). Vision: the dominant primate modality. In: J. L. Fobes & J. E. King (Eds.), *Primate behaviour*, (pp. 219-243). New York: Academic Press.

Fremouw, T., Herbranson, W. T., & Shimp, C. P. (2002). Dynamic shifts of pigeon local/global attention. *Animal Cognition*, *5*, 233–243. doi: 10.1007/s10071-002-0152-9

Fremouw, T., Herbranson, W. T., & Shimp, C. P. (1998). Priming of attention to global and local levels of visual analysis. *Journal of Experimental Psychology: Animal Behavior Processes*, *24*, 278–290. http://dx.doi.org/10.1037/0097-7403.24.3.278

636 Goodale, M. A., Jakobson, L. S., & Keillor, J.M. (1994). Differences in the visual control
637 of pantomimed and natural grasping movements. *Neuropsychologia, 32,* 1159-1178.
638 doi:10.1016/0028-3932(94)90100-7
639 Goto, K., Wills, A. J., & Lea, S. E. G. (2004). Global-feature classification can be
640 acquired more rapidly than local-feature classification in both humans and pigeons,
641 *Animal Cognition, 7,* 109-113. doi: 10.1007/s10071-003-0193-8
642 Hopkins, W. D., & Washburn, D. (2002). Matching visual stimuli on the basis of global
643 and local features by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca*
644 *mulatta*). *Animal Cognition, 5,* 27-31. doi: 10.1007/s10071-001-0121-8
645 Kimchi, R. (1992). Primacy of wholistic processing and global/local paradigm: a critical
646 review. *Psychological Bulletin, 112,* 24–38. http://dx.doi.org/10.1037/0033-
647 2909.112.1.24
648 Katz, J. S., Wright, A. A., & Bachevalier, J. (2002). Mechanisms of same/different
649 abstract-concept learning by rhesus monkeys (*Macaca mulatta*). *Journal of*
650 *Experimental Psychology: Animal Behavior Processes, 28,* 358–368.
651 http://dx.doi.org/10.1037/0097-7403.28.4.358
652 Kimchi, R. (1998). Uniform connectedness and grouping in the perceptual organization
653 of hierarchical pattern. *Journal of Experimental Psychology: Human Perception and*
654 *Performance, 24,* 1105-1118. http://dx.doi.org/10.1037/0096-1523.24.4.1105
655 Kimchi, R., Beherman, M., & Olson, C. (2003). *Perceptual organization in vision.*
656 *Behavioral and neural perspectives*. New Jersey: Lawrence Erlbaum Associates.
657 Kimchi, R., & Palmer, S. E. (1982). Form and texture in hierarchically constructed
658 patterns. *Journal of Experimental Psychology: Human Perception and Performance,*
659 *8,* 521-35. http://dx.doi.org/10.1037/0096-1523.8.4.521

660 Kinchla, R. A., & Wolfe, J. M. (1979). The order of visual processing: “top down”,
661 “bottom-up” or “middle out”. *Perception & Psychophysics, 25,* 225-331. doi:
662 10.3758/BF03202991
663 Kremers, J. (2005). *Structure, function and evolution of the primate visual system*. New
664 York: John Wiley & Sons.
665 Lamb, M. R., & Robertson, L. (1988). The processing of hierarchical stimuli: effects of
666 retinal locus, location uncertainty, and stimulus identity. *Perception &*
667 *Psychophysics*, *44*, 172-181. doi: 10.3758/BF03208710
668 Lamb, M. R., Robertson, L. C., & Knight, R. T. (1990). Component mechanisms
669 underlying the processing of hierarchically organized patterns: Interferences from
670 patients with unilateral cortical lesions. *Journal of Experimental Psychology:*
671 *Learning, Memory, and Cognition, 16,* 471-483. http://dx.doi.org/10.1037/0278-
672 7393.16.3.471
673 Lynch Alfaro, J. W., Boubli, J. P., Olson, L. E., Di Fiore, A., Wilson, B., Gutiérrez-
674 Espeleta, G. A., Chiou, K. L., Schulte, M., Neitzel, S., Ross, V., Schwochow, D.,
675 Nguyen, M. T. T., Farias, I., Janson, C., & Alfaro, M. E. (2012). Explosive
676 Pleistocene range expansion leads to widespread Amazonian sympatry between
677 robust and gracile capuchin monkeys. *Journal of Biogeography*, *39*, 272-88. doi:
678 10.1111/j.1365-2699.2011.02609.x
679 Lynch Alfaro, J. W., De Souza Silva, J., & Rylands, A. B. (2012). How different are
680 robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and
681 *Cebus*. *American Journal of Primatology, 74*, 273-86. doi: 10.1002/ajp.22007
682 Martin, M. (1979). Local and global processing: the role of sparsity. *Memory &*
683 *Cognition*, *7*, 476-484. doi: 10.3758/BF03198264

684 Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action* (2nd ed.). Oxford:
685 Oxford University Press.
686 Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed.
687 *Neuropsychologia*, *46*, 774-785. doi:10.1016/j.neuropsychologia.2007.10.005
688 Navon, D. (1977). Forest before the trees: The precedence of global features in visual
689 perception. *Cognitive Psychology*, *9*, 353-383. doi:10.1016/0010-0285(77)90012-3
690 Navon, D. (1981). The forest revisited: More on global precedence. *Psychological*
691 *Research*, *43*, 1-32. doi: 10.1007/BF00309635
692 Navon, D. & Norman, J. (1983). Does global precedence really depend on visual angle?
693 *Journal of Experimental Psychology: Human Perception and Performance*, *9*, 955-965.
694 http://dx.doi.org/10.1037/0096-1523.9.6.955
695 Neisser, U. (1967). *Cognitive Psychology*. New York: Appleton-Century-Crofts.
696 Neiworth, J. J., Gleichman, A. J., Olinick, A. S., & Lamp, K. E. (2006). Global and local
697 processing in adult humans (*Homo sapiens*), 5-year-old children (*Homo sapiens*),
698 and adult cotton-top tamarins (*Saguinus oedipus*). *Journal of Comparative*
699 *Psychology*, *120*, 323-330. http://dx.doi.org/10.1037/0735-7036.120.4.323
700 Parron, C., & Fagot, J. (2007). Comparison of Grouping Abilities in Humans (*Homo*
701 *sapiens*) and Baboons (*Papio papio*) with the Ebbinghaus Illusion. *Journal of*
702 *Comparative Psychology*, *4*, 405-411. http://dx.doi.org/10.1037/0735-
703 7036.121.4.405
704 Pitteri, E., Mongillo, P., Carnier, P., & Marinelli, L. (2014). Hierarchical stimulus
705 processing by dogs (*Canis familiaris*). *Animal Cognition*, *17*, 869-877. doi:
706 10.1007/s10071-013-0720-1
707 Rodriguez, J. S., Zvrcher, N. R., Bartlett, T. Q., Nathanielsza, P. W., & Nijlanda, M. J.
708 (2011). CANTAB delayed matching to sample task performance in juvenile

baboons. *Journal of Neuroscience Methods*, *196*, 258-263. doi:10.1016/j.jneumeth.2011.01.012

Schrier, A. M., Povar, M. L., & Schrier, J. E. (1979). Effects of goodness and other properties of patterns on discriminative performance of monkeys. *Perception & Psychophysics*, *25*, 215-220. doi: 10.3758/BF03202989

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, *74*, 1-29. http://dx.doi.org/10.1037/h0093759

Spinozzi, G., De Lillo, C., & Truppa, V. (2003). Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *117*, 15-23. doi:10.1037/0735-7036.117.1.15.

Spinozzi, G., De Lillo, C., & Salvi, V. (2006). Local advantage in the visual processing of hierarchical stimuli following manipulations of stimulus size and element numerosity in monkeys (*Cebus apella*). *Behavioural Brain Research*, *166*, 45–54. doi:10.1016/j.bbr.2005.06.043

Tanaka, H. K., & Fujita, I. (2000). Global and local processing of visual patterns in macaque monkeys. *Neuroreport*, *11*, 2881-2884.

Tanaka, H. K., Onoe, H., Tsukada, H., & Fujita, I. (2001). Attentional modulation of neural activity in the macaque inferior temporal cortex during global and local processing. *Neuroscience Research*, *39*, 469-472. doi:10.1016/S0168-0102(01)00202-4

Truppa, V., Garofoli, D., Castorina, G., Piano Mortari, E., Natale, F., & Visalberghi, E. (2010). Identity concept learning in matching-to-sample tasks by tufted capuchin monkeys (*Cebus apella*). *Animal Cognition*, *13*, 1-14. doi: 10.1007/s10071-010-0332-y

734 Truppa, V., Piano Mortari, E., Garofoli, D., Privitera, S., & Visalberghi, E. (2011).
735 Same/different concept learning by capuchin monkeys in matching-to-sample tasks.
736 *PloS ONE*, 6(8):e23809. doi:10.1371/journal.pone.0023809.
737 Truppa, V., De Simone, D., Piano Mortari, E., & De Lillo, C. (2014). Effects of brief
738 time delays on matching-to-sample abilities in capuchin monkeys (*Sapajus* spp.).
739 *Behavioural Brain Research, 271*, 240-248. doi:10.1016/j.bbr.2014.05.023
740 Truppa, V., Sovrano, V., Spinozzi, G., & Bisazza, A. (2010). Processing of visual
741 hierarchical stimuli by fish (*Xenotoca eiseni*). *Behavioural Brain Research*, *207*, 51-
742 60. doi:10.1016/j.bbr.2009.09.039
743 Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M.
744 A. Goodale, & R. J. W. Mansfield (Eds), *Analysis of visual behaviour* (pp. 549-586).
745 Cambridge, MA: MIT Press.
746 Weatherall, D. (2006). The use of non-human primates in research: A working group
747 report. Available: http://www.acmedsci.ac.uk/images/project/nhpdownl.pdf.

Figure captions

Figure 1. (A) Experimental apparatus and stimuli presentation in the Simultaneous matching-to-sample condition (redrawn from Truppa et al., 2014); (B) Set of stimuli used in the experiment.

Figure 2. Mean percentage of correct responses performed by the monkeys in the Local and Global trials as a function of the different matching conditions (Simultaneous, 0.0, 0.5, 1.0, 2.0, 3.0 sec delay), (One-sample t-test: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Error bars represent 95% confidence interval.

Figure 3. Mean percentage of correct responses performed by the monkeys in the simultaneous and the five delay (0.0, 0.5, 1.0, 2.0, 3.0 sec) conditions as a function of the order of trials. Error bars represent 95% confidence interval.

Figure 4. Mean percentage of correct responses performed by the monkeys in the Local and Global trials as a function of the order of trials. Error bars represent 95% confidence interval.

Figure 5. Mean percentage of correct responses performed by the monkeys in the Global and Local trials as a function of the stimulus size. Error bars represent 95% confidence interval.

748

Supporting information

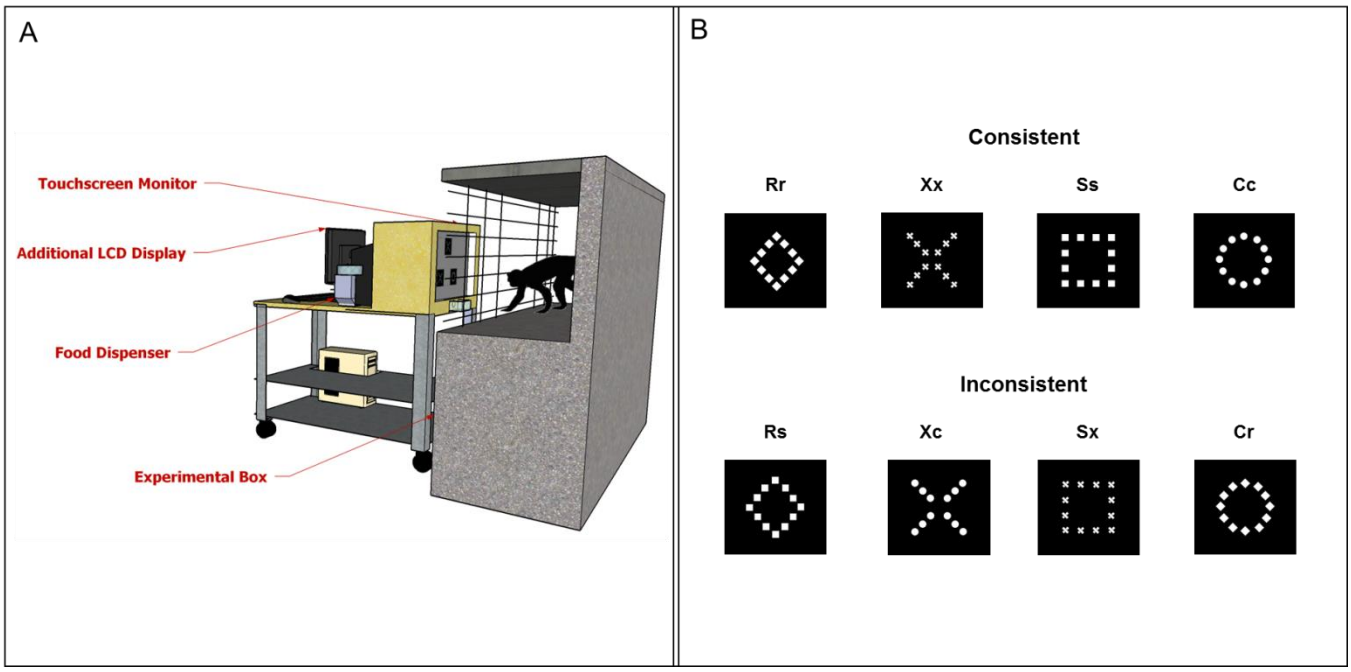
Video S1. Rucola, a female capuchin, carrying out a simultaneous matching-to-sample trial in the local condition.

Video S2. Rucola, a female capuchin, carrying out a 1-sec delayed matching-to-sample trial in the local condition.

Video S3. Rucola, a female capuchin, carrying out a simultaneous matching-to-sample trial in the global condition.

Video S4. Rucola, a female capuchin, carrying out a 0-sec delayed matching-to-sample trial in the global condition.

Figure 1


A
Touchscreen Monitor
Additional LCD Display
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B
Consistent
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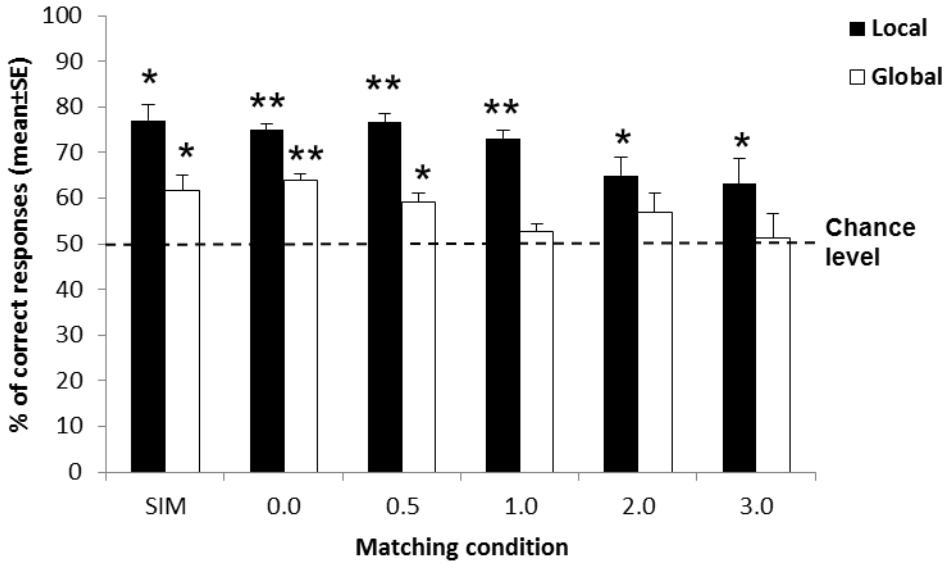
Figure 2


100
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0
% of correct responses (mean±SE)
Local
Global
Chance level
*
**
SIM
0.0
0.5
1.0
2.0
3.0
Matching condition

Figure 3

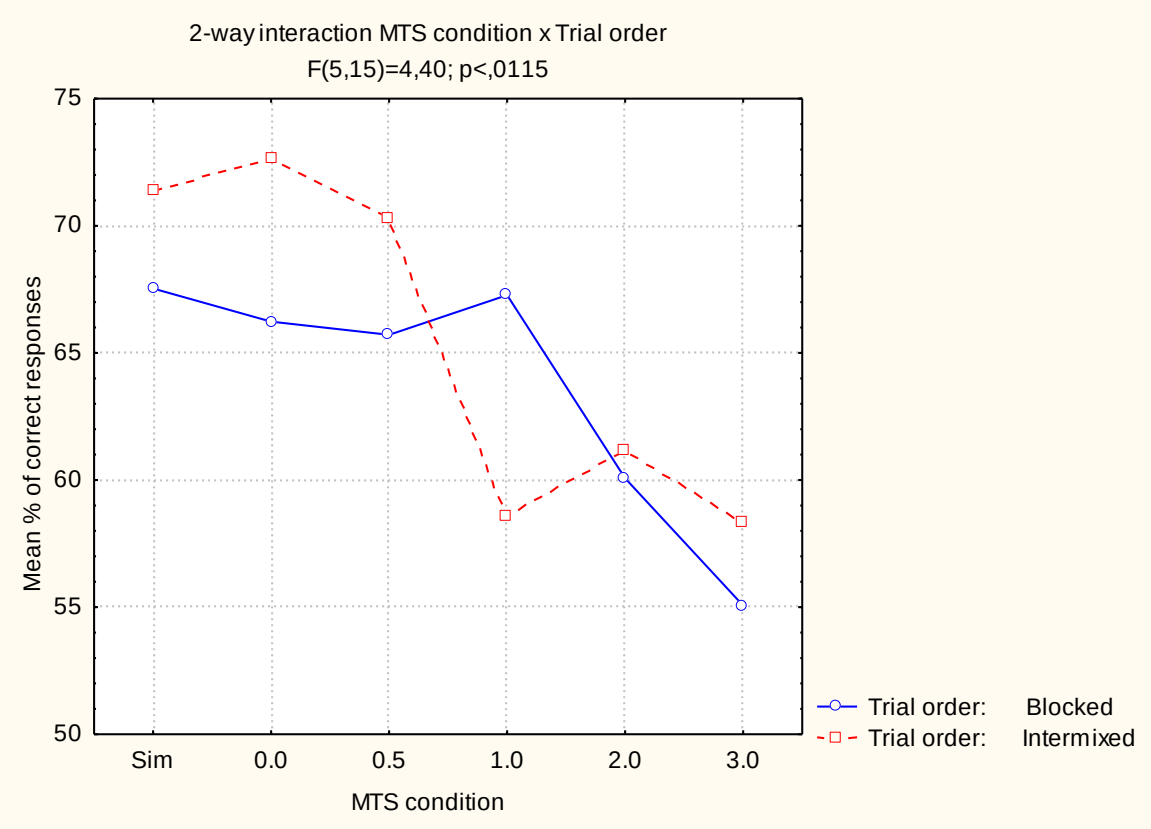

2-way interaction MTS condition x Trial order
F(5,15)=4,40; p<,0115
Mean % of correct responses
75
70
65
60
55
50
Sim
0.0
0.5
1.0
2.0
3.0
MTS condition
Trial order: Blocked
Trial order: Intermixed

Figure 4

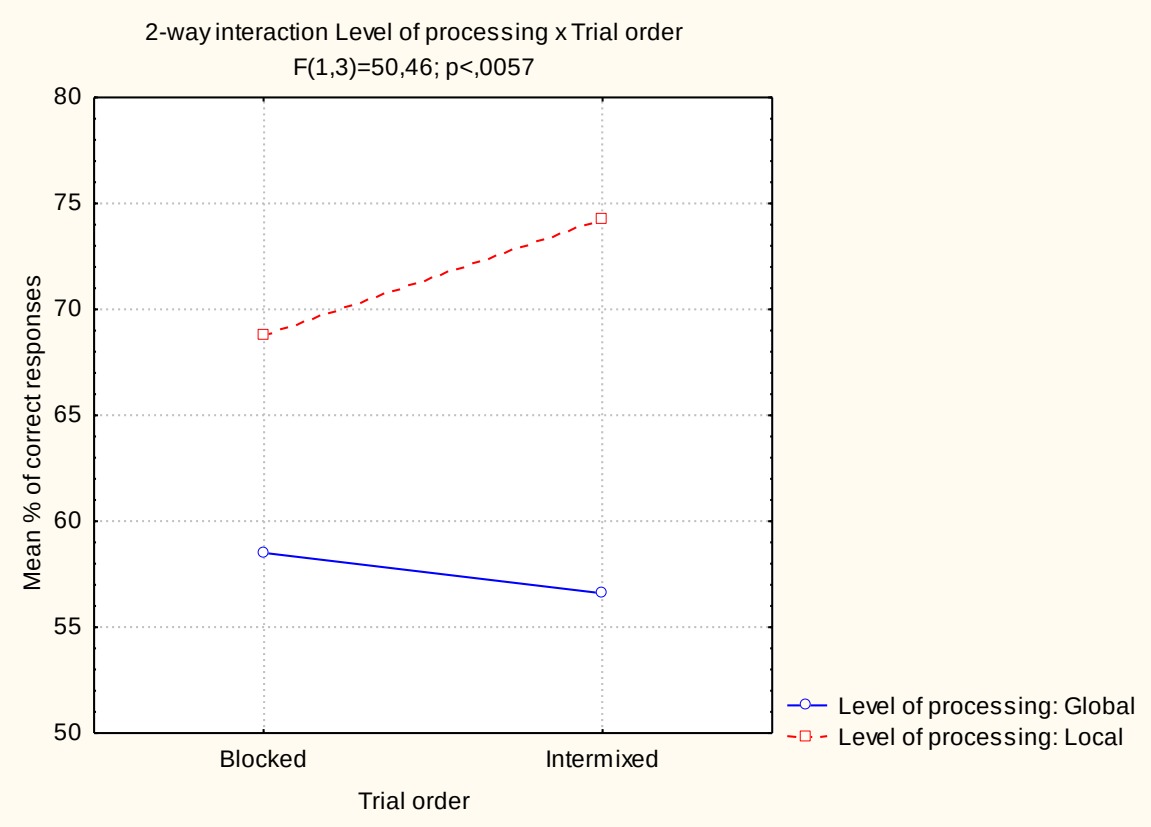
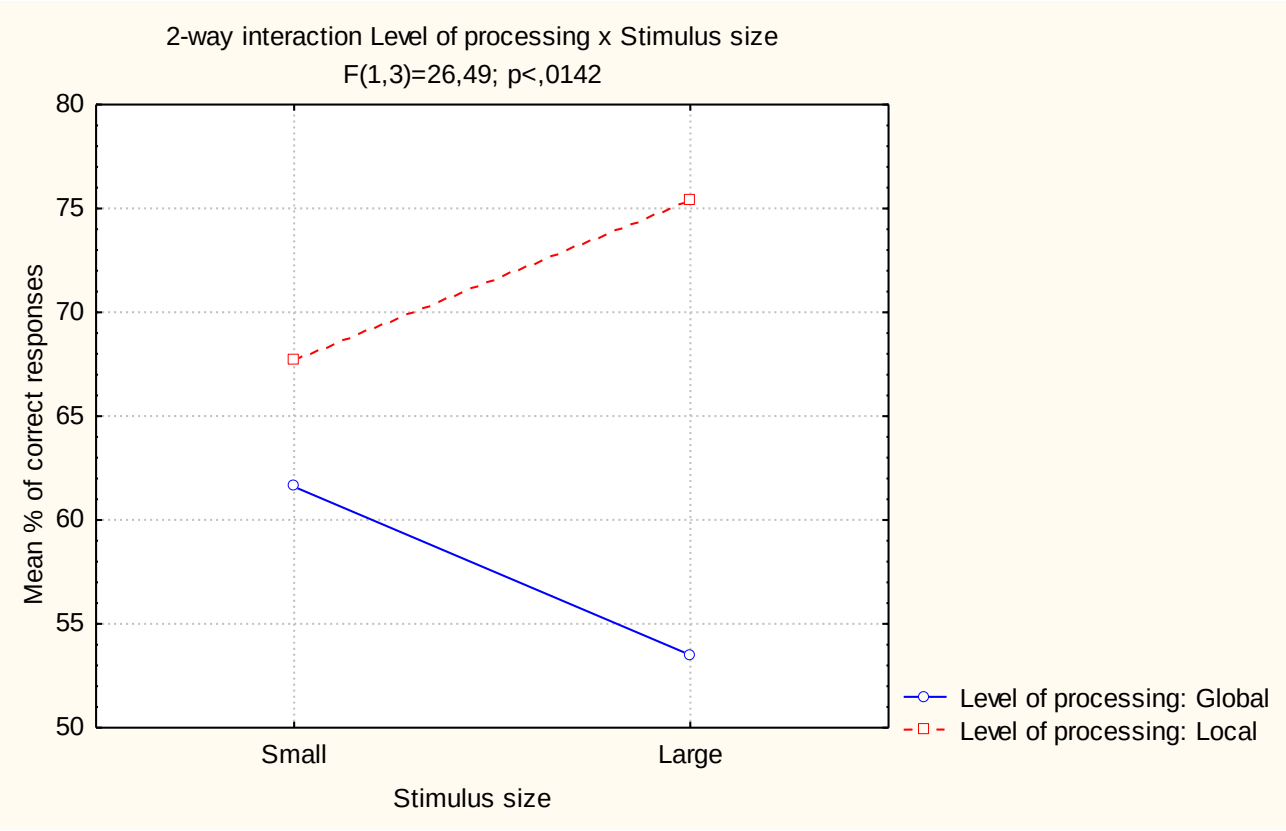

2-way interaction Level of processing x Trial order
F(1,3)=50,46; p<,0057
Mean % of correct responses
80
75
70
65
60
55
50
Blocked
Intermixed
Trial order
Level of processing: Global
Level of processing: Local

Figure 5


2-way interaction Level of processing x Stimulus size
F(1,3)=26,49; p<,0142
Mean % of correct responses
80
75
70
65
60
55
50
Small
Large
Stimulus size
Level of processing: Global
Level of processing: Local