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ORIGINAL PAPER

Global/local processing of hierarchical visual stimuli in a conflict–choice task by capuchin monkeys (*Sapajus* spp.)

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Abstract In the last two decades, comparative research has addressed the issue of how the global and local levels of structure of visual stimuli are processed by different species, using Navon-type hierarchical figures, i.e. smaller local elements that form larger global configurations. Determining whether or not the variety of procedures adopted to test different species with hierarchical figures are equivalent is of crucial importance to ensure comparability of results. Among non-human species, global/local processing has been extensively studied in tufted capuchin monkeys using matching-to-sample tasks with hierarchical patterns. Local dominance has emerged consistently in these New World primates. In the present study, we assessed capuchins' processing of hierarchical stimuli with a method frequently adopted in studies of global/local processing in non-primate species: the conflict–choice task. Different from the matching-to-sample procedure, this task involved processing local and global information retained in long-term memory. Capuchins were trained to discriminate between consistent hierarchical stimuli (similar global and local shape) and then tested with inconsistent hierarchical stimuli (different global and local shapes). We found that capuchins preferred the hierarchical stimuli featuring the correct local elements rather than those with the correct global configuration. This finding confirms that capuchins' local dominance, typically observed using matching-to-sample procedures, is also expressed as a local preference in the conflict–choice task. Our study adds to the growing body of comparative studies on visual grouping functions by demonstrating that the methods most frequently used in the literature on global/local processing produce analogous results irrespective of extent of the involvement of memory processes.

Keywords Visual perception · Global/local processing · Hierarchical stimuli · Long-term memory · New World monkeys

Introduction

An important issue in visual cognition is the extent to which visual processing identifies local elements first and only subsequently integrates them into whole objects, or vice versa, detects the global properties of objects before an analysis of its component parts. The extent to which different species use one or the other of these perceptual strategies is a long-standing question in comparative cognition. A relative bias towards the processing of the local features of objects or their global configuration, in terms of accuracy or speed of processing, has often been regarded as indicative of the perceptual strategy used by a given species.

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Comparative studies in this area are inspired by a seminal article by Navon (1977). Navon (1977, 1981) demonstrated that human adults tested with hierarchical visual patterns, i.e. local elements spatially arranged to form global configurations, process the global configuration more accurately and faster than the local elements. Evidence confirming this global advantage in humans has been provided in several other studies (e.g. Kimchi 1998; Kimchi and Palmer 1982; Kinchla and Wolfe 1979; Lamb et al. 1990; for reviews, see Kimchi 1992; Navon 2003).

In the last two decades, comparative research has made extensive use of Navon-type hierarchical stimuli to assess global/local processing in an increasing number of species belonging to different taxa. Several studies have been conducted on pigeons (Cavoto and Cook 2001; Fremouw et al. 1998, 2002) and non-human primates (De Lillo et al. 2011; Deruelle and Fagot 1998; Fagot and Deruelle 1997; Fagot and Tomonaga 1999; Hopkins and Washburn 2002; Neiworth et al. 2006; Spinozzi et al. 2003, 2006; Tanaka and Fujita 2000; Tanaka et al. 2001; Truppa et al. 2016). Moreover, hierarchical stimuli have recently been used to study global/local preference also in honeybees (Avarguès-Weber et al. 2015), fish (redtail splitfins: Truppa et al. 2010b), domestic chicks (Chiandetti et al. 2014) and domestic dogs (Pitteri et al. 2014). Among studies that have used hierarchical patterns, local dominance has usually been found in monkeys (De Lillo et al. 2011, 2012; Deruelle and Fagot 1998; Fagot and Deruelle 1997; Hopkins and Washburn 2002; Spinozzi et al. 2003, 2006; Tanaka and Fujita 2000; Tanaka et al. 2001; Truppa et al. 2016; for different results, see Neiworth et al. 2006). More mixed results have been reported for bird species. One study that used large local elements and a very small separation between them reported a global dominance in pigeons (Goto et al. 2004). By contrast, other studies have reported local dominance in both pigeons (Cavoto and Cook 2001) and domestic chicks (Chiandetti et al. 2014). No clear dominance has been found in domestic dogs (Pitteri et al. 2014), whereas a global dominance emerged in fish (Truppa et al. 2010b) and honeybees (Avarguès-Weber et al. 2015). However, there is some variability in the procedures used to test animals in different studies, which may confound interspecies differences in global/local processing inferred from the comparison of results reported in different research articles.

A recent study specifically aimed at comparing different testing procedures for the assessment of global/local processing in children diagnosed with autistic spectrum disorder, a population known for their local processing tendency, showed that different patterns of results can be obtained with different testing procedures. Children with ASD showed a reduced preference to report global properties of a stimulus when given a choice, whereas their ability to process global properties, when instructed to do so, was unimpaired (Koldewyn et al. 2013).

Therefore, it is of crucial importance to determine whether or not the procedures adopted to test different species' global and local processing are comparable. In fact, variations across species may be ascribable to genuine differences in the way in which animals process global and local aspects of hierarchical patterns only when potential differences in the results that may stem from the use of different testing methods are ruled out. For example, paradigms may inadvertently differ in their memory requirements with possible consequences for the type of visual system and resources that need to be recruited for the analysis of the stimuli.

Many comparative studies carried out on primate species have used matching-to-sample (MTS) procedures (e.g. De Lillo et al. 2011, 2012; Fagot and Deruelle 1997; Hopkins and Washburn 2002; Spinozzi et al. 2003, 2006; Truppa et al. 2016). In MTS, individuals are required to choose which of two comparison stimuli (S+ and S−) more closely resembles a stimulus presented as a sample (SS). For example, to study global/local processing with an identity MTS procedure, monkeys are faced with two different matching conditions, the global condition and the local condition. In the global condition, S+ is identical to the sample and S− differs from the sample only at its global level. In the local condition, S+ is identical to the sample and S− differs from the sample only for the shape of its local elements. In this type of MTS-based studies, differences in accuracy and/or response time between the global and the local condition are informative with respect to the visual processing style of the species under investigation. Comparative studies so far have either used simultaneous MTS procedures which do not require memory for the stimulus structure (e.g. De Lillo et al. 2011, 2012; Fagot and Deruelle 1997; Hopkins and Washburn 2002; Spinozzi et al. 2003, 2006) or delayed MTS with brief delays which require the short-term retention of stimulus structure (Truppa et al. 2016).

MTS tasks are relatively difficult to use with non-human animals. Even animals of species that succeed in matching stimuli on the basis of an identity rule usually need a long training before they can transfer this ability to novel stimuli (e.g. Truppa et al. 2010a). Therefore, many comparative studies have adopted forced-choice procedures rather than MTS for the study of global/local processing in a variety of species (cotton-top tamarins: Neiworth et al. 2006; domestic dogs: Pitteri et al. 2014; pigeons: Cavoto and Cook 2001; Fremouw et al. 1998, 2002; domestic chicks: Chiandetti et al. 2014; redtail splitfins: Truppa et al. 2010b; honeybees: Avarguès-Weber et al. 2015). Typically, in studies based on forced-choice tasks individuals are initially trained to discriminate between consistent hierarchical stimuli (i.e. patterns where the same shape is presented as the local and global level of stimulus structure) and then tested with inconsistent hierarchical stimuli (i.e. patterns where a different shape is presented at the local and global level). Thus, individuals are tested with hierarchical patterns in which the global configuration and the shape of the local elements are in conflict. Moreover, this kind of task, different from the MTS procedures often adopted with non-human primates, requires the long-term coding and retention of the hierarchical stimuli. In fact, when tested with inconsistent stimuli individuals are being evaluated for their ability to retrieve and select global or local features of visual patterns reinforced during the preliminary training phase. The processing of visual information in long-term memory involves brain structures, such as the hippocampus, that are active in the encoding of the spatial organisation of visual patterns in humans and other animals (Kumaran et al. 2007; Sanderson et al. 2006). Therefore, it is possible that during the long-term encoding of compound stimuli the integration of the parts in global configurations is enhanced compared to conditions that only require the short-term retention of the stimuli.

Among non-human species, global/local processing has been extensively studied in tufted capuchin monkeys (De Lillo et al. 2011, 2012; Spinozzi et al. 2003, 2006; Truppa et al. 2016). Studies that adopted MTS procedures have consistently revealed a local advantage in these New World primates. This local advantage in capuchin monkeys has proved to be a very robust finding. It emerges irrespective of the size of the local elements, and their relative density and distance (Spinozzi et al. 2006). The presence of a strong local dominance in monkeys under a variety of manipulations of the separation of the local elements is consistent with seminal findings in baboons showing a local advantage in that species even when the local elements are connected by line segments (Fagot and Deruelle 1998). A local advantage in capuchin monkeys also emerged in a delayed-MTS task with brief time intervals between the presentation of the sample and the comparison stimuli (Truppa et al. 2016). However, capuchins have not been tested in tasks requiring long-term memory, such as the conflict–choice discrimination task, which has been used with several non-primate species (e.g. Chiandetti et al. 2014; Truppa et al. 2010b). Thus, we considered it important to assess if the encoding of visual information in long-term memory could potentially strengthen capuchins' ability to recognise the global configuration of hierarchical visual patterns.

The aim of this study was twofold. Firstly, we aimed to determine whether or not the local dominance previously observed in tufted capuchin monkeys also emerged when using a conflict–choice task. In this task, capuchins were first trained with pairs of consistent hierarchical stimuli (same shape featured at the local and global level of stimulus structure) and then tested with pairs of inconsistent stimuli (different shapes at local and global level of stimulus structure). We hypothesised that if the conflict–choice task was equivalent to the MTS for the assessment of global/local processing, then capuchins should have shown a preference for local properties of the stimuli in such task too. In addition, this study allowed us to evaluate whether or not capuchins' local dominance in short-term memory for hierarchical patterns, previously found by Truppa et al. (2016), also pertained to tasks involving the long-term retention of the stimuli.

Methods

Subjects

The subjects were six capuchin monkeys (see Table 1) considered to be unknown combinations of species of the genus *Sapajus* that, in accord with the current taxonomy, includes the "tufted/robust" species previously referred to the genus *Cebus* (Lynch Alfaro et al. 2012a, b, 2014). All subjects were adults born in captivity and housed at the Primate Center of the Institute of Cognitive Sciences and Technologies, CNR, Rome, Italy. They were kept in social groups, each housed in an indoor–outdoor enclosure (indoor: 5 m^2 × 2.5 m high; outdoor: 40–130 m^2 × 3 m high). To enrich the monkeys' living space, indoor enclosures were provided with perches and ropes and outdoor enclosures were provided with logs, branches and ropes. Moreover, outdoor enclosures were supplied with natural substrates, including woodchips on the ground, to promote the monkeys' exploratory behaviour.

Capuchins were individually tested in an experimental cubicle (180 cm × 75 cm × 75 cm; the cubicle floor is 80 cm higher than the floor of the rest of the room) to which they had access through a sliding door from an adjacent indoor cage. Each subject was separated from the group just before the daily experimental session solely for the purpose of testing (approximately 20 min). Testing took place between 9:30 a.m. and 3:15 p.m. Water was freely available at all times. Fresh fruit, vegetables and monkey chow were provided in the afternoon after testing. All subjects were familiar with the experimental cage/cubicle, the experimental routine and the experimenters. More details concerning the previous experience of our subjects with relevant testing procedures and experimental protocols are provided in Table 1. None of the subjects had been tested with the hierarchical figures used in this study before.

Table 1 Monkeys participating in this study: age, sex, previous experience with hierarchical stimuli and performance

Name	Age (years)	Sex	Previous experience	Training trials to criterion NHS	Training trials to criterion HS	Test % local choices	Retest % local choices
Roberta	29	F	a, b, c	480	2880	62.5	62.5
Robiola	17	F	a, b	300	1472	62.5	62.5
Rucola	15	F	a, b, c	100	440	87.5	75.0
Robot	20	M	a, b, c	124	448	87.5	93.7
Sandokan	15	M	a, b, c	172	360	56.2	43.7
Vispo	15	M	a	616	1608	81.2	62.5

NHS Non-hierarchical stimuli, *HS* hierarchical stimuli

a Computerised MTS tasks (e.g. Truppa et al. 2010a, 2011, 2014, 2016)

b Two-alternative forced-choice procedure (Truppa et al. 2015)

c Global/local processing of hierarchical stimuli using an MTS task (Truppa et al. 2016)

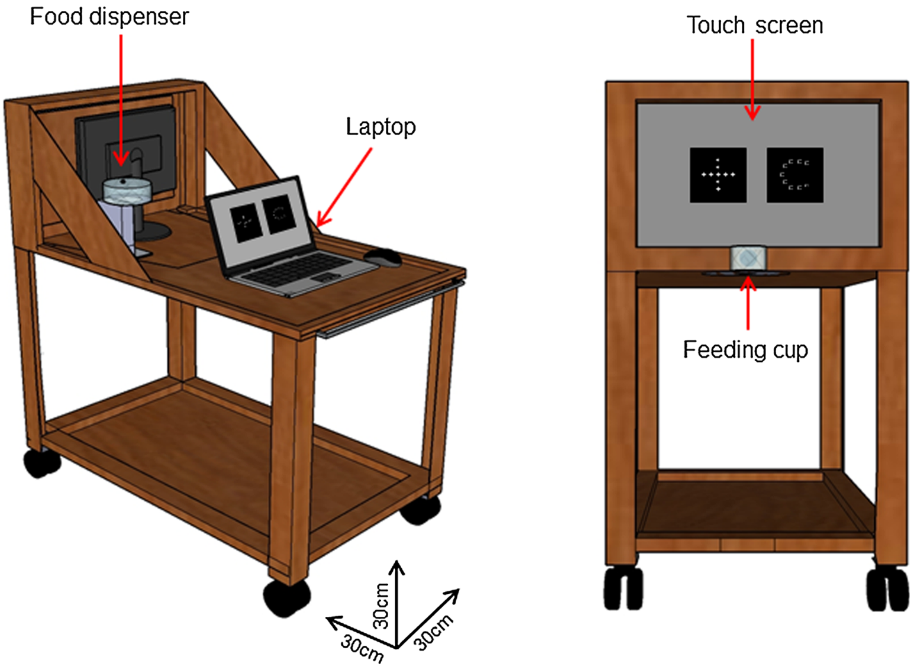
Apparatus

The apparatus consisted of a laptop (Acer Aspire 1400 Series) connected to a 17″ touch screen (Tyco Electronics, ET1729L-7UEA-1-D-GY-G) and an automatic food dispenser (ENV-203-45, MED Associates, Inc. Georgia, VT) (Fig. 1). E-Prime software (Psychology Software Tools, Inc.) was used to present the stimuli and to record the subjects' responses. The food dispenser was programmed to deliver one 45-mg banana-flavoured pellet (TestDiet, Richmond, IN, USA) when the monkey provided a correct response. The pellet was delivered into a PVC feeding cup (with a diameter of 4 cm) located 14.5 cm below the touch screen, in the centre. A wooden frame (58 cm wide × 54 cm high) with a central aperture (36 cm wide × 30 cm high) surrounded the touch screen. The food dispenser was placed behind the wooden frame, out of sight of the subject. The laptop was placed at the back of the touch screen. The touch screen, the food dispenser and the laptop were mounted on a trolley (90 cm long × 58 cm wide × 85 cm high). The apparatus was placed 15 cm from the horizontal metal bars (0.5 cm in diameter, separated by 4.5 cm) of the experimental cubicle, within the subject's arm reach.

Stimuli

The stimulus set included 16 pairs of non-hierarchical figures and 16 pairs of hierarchical figures. Non-hierarchical pairs included 32 digital icons (2.30 cm × 2.30 cm, i.e. 8.7° of visual angle, Fig. 2a). Hierarchical pairs included 32 compound images composed of identical local

Fig. 1 Experimental apparatus



elements (0.35 cm × 0.35 cm). The elements subtended 1.3° of visual angle at a distance of 15 cm. This was the distance of the touch screen from the horizontal bars of the cubicle that monkeys approached closely when responding, and it was taken as the viewing distance. The local elements (range 6–13) were spatially arranged to form global configurations (2.30 cm × 2.30 cm, i.e. 8.7° of visual angle). The distance between adjacent elements was kept approximately at 0.35 cm (i.e. 1.3° of visual angle). Global configurations of comparable density were obtained by varying the number of local elements. Each hierarchical figure was paired with another one, which had approximately the same number of local elements in it. If there was a difference, it was of two items maximum. Given that capuchins are unable to detect a difference in numerosity of two items for quantities like those featuring the stimuli in our study (see Addessi et al. 2008; vanMarle et al. 2006), it is unlikely that the monkeys could use the numerosity of the local elements in the hierarchical figures to guide their choices. In fact, our stimuli always contained at least six elements and any two stimuli could not differ by more than two elements. Depending on the experimental phase (see below), hierarchical stimuli could be either *consistent* (same shape at both local and global levels of the stimuli, Fig. 2b) or *inconsistent* (different shapes at local and global levels of the stimuli, Fig. 2c). Inconsistent hierarchical stimulus pairs were created by switching the local elements of the two consistent stimuli of each pair. All stimuli consisted of white images presented on a black background (8 cm high × 8 cm wide, i.e. 28.0° of visual angle); they were created using Microsoft PowerPoint and then transformed into bitmap images for stimulus presentation on the computer screen.

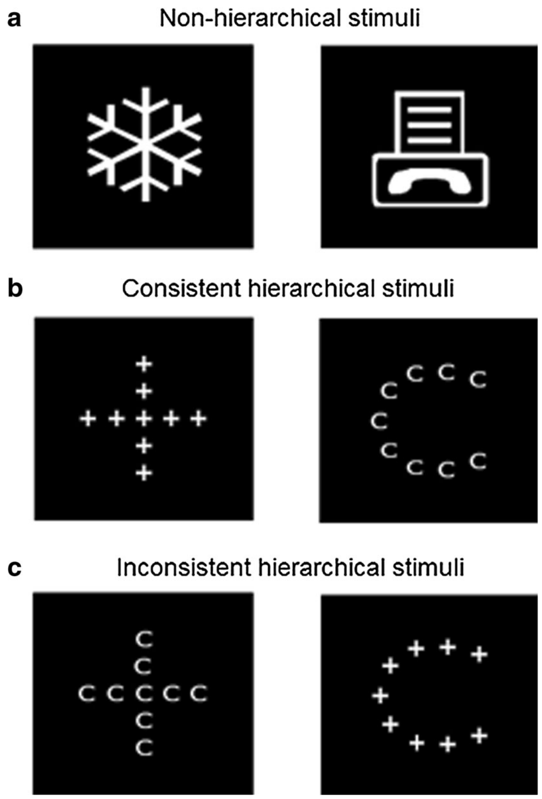


Fig. 2 Examples of **a** non-hierarchical stimuli used in both training and testing phases, **b** hierarchical consistent stimuli used in the training phase and **c** hierarchical inconsistent stimuli used in the testing phase

Design and procedure

The study included a training phase, a testing phase and a retesting phase (see Table 2). In order to avoid experimental sessions with a large number of different stimuli for the monkeys to memorise (training) and to recall (testing/retesting), the stimulus pairs were presented in two separate blocks of trials. Each block included 16 pairs of stimuli. The first 16 pairs (8 pairs of hierarchical stimuli and 8 pairs of non-hierarchical stimuli) were presented in a first training phase, followed by the corresponding testing and retesting phases. The other 16 pairs were presented in a second training phase followed by the corresponding testing and retesting phases.

Training phase

Subjects were trained to select the rewarded positive stimulus (S+) within a pair in a two-alternative forced-choice task. At the beginning of each trial, a white square (0.6 cm × 0.6 cm) appeared in the centre of the screen on a black background. When the monkey touched the square, two stimuli were simultaneously displayed to the right and left, at a distance of 5 cm apart. The initial touch of the central square was adopted to ensure that the monkey was looking at the screen when the stimuli appeared. The subject had to indicate its choice by touching one of the two stimuli on the screen; the touch-sensitive area included the entire stimulus surface, i.e. both the white figure and the black square background. The computer automatically recorded the choice and the response time (RT). RT was measured as the time between the appearance of the choice stimuli and the subject's choice (i.e. the touch of the selected stimulus). After the response, the display was immediately extinguished and, if the subject had selected S+, a food pellet was delivered. A correct response was followed by a 5-s inter-trial interval (ITI), whereas an incorrect response was followed by the 5-s ITI and an additional 10-s time out (TO). During the experimental trials and the ITI, the screen was light grey; during the TO, the screen was green. Monkeys received two 16-trial sessions per day. In each session, half of the trials included pairs of consistent hierarchical stimuli and the other half

Table 2 Experimental design: sequence of procedures

Trial block	Phase	Stimuli used
1	First training phase	First block of stimulus pairs 16-trial sessions, each including 8 pairs of NHS + 8 pairs of CHS until achievement of the learning criterion
1	First testing phase	First block of stimulus pairs Four 10-trial sessions, each including 8 pairs of NHS + 2 pairs of IHS
1	First retesting phase	First block of stimulus pairs Four 10-trial sessions, each including 8 pairs of NHS + 2 pairs of IHS
2	Second training phase	Second block of stimulus pairs 16-trial sessions, each including 8 pairs of NHS + 8 pairs of CHS until achievement of the learning criterion
2	Second testing phase	Second block of stimulus pairs Four 10-trial sessions, each including 8 pairs of NHS + 2 pairs of IHS
2	Second retesting phase	Second block of stimulus pairs Four 10-trial sessions, each including 8 pairs of NHS + 2 pairs of IHS

For each animal, different pairs of stimuli were used in the two blocks of trials

NHS non-hierarchical stimul, *CHS* consistent hierarchical stimul, *IHS* inconsistent hierarchical stimuli

included pairs of non-hierarchical stimuli. Each S+ was presented an equal number of times in both the right and the left position. To reduce the possibility of biased results due to the particular shape of a given stimulus, half of the monkeys received one of the two stimuli in each pair as S+ , whereas the other half received the other stimulus as S+ . The trials were presented in random order. Sessions were administered 5 days per week. The learning criterion was achieved when subjects responded correctly in at least 7 out of 8 trials (87.5%, binomial test $P < 0.032$) during three consecutive sessions. The criterion was calculated separately for consistent hierarchical stimuli and for non-hierarchical stimuli. After achieving the learning criterion with both hierarchical and non-hierarchical stimuli, monkeys were tested with inconsistent hierarchical stimuli.

Testing phase

Each testing phase consisted of 4 10-trial daily sessions. Each session included two test trials with inconsistent hierarchical stimuli intermixed with eight training trials with non-hierarchical stimuli. Non-hierarchical training stimuli were included in order to check that the level of discrimination performance achieved during the training phase was maintained throughout the testing phase. The two inconsistent hierarchical stimuli presented in each test trial were both rewarded since each of them preserved one level (local or global) of the hierarchical stimulus reinforced during the training phase. Therefore, to avoid biases due to the reinforcement programme, only one test trial for each pair of hierarchical stimuli was presented. The trials were presented in random order. Sessions were administered 5 days per week.

Retesting phase

To determine whether or not any pattern of preference shown by capuchins during the testing was maintained after a long interval, a second trial for each block of pairs of inconsistent hierarchical stimuli was presented as a retest after five months from the end of the first testing phase. The stimuli, the number of sessions/trials and the procedure in the retesting phase were the same adopted in the testing phase. The long interval between the first (test) and the second (retest) presentation of the hierarchical inconsistent stimuli also helped to prevent biases due to the fact that those stimuli were always rewarded at the first presentation.

During both test and retest, control trials with non-hierarchical stimuli maintained the same reinforcing programme scheduled for the training phase.

Data analysis

The Kolmogorov–Smirnov test showed that all distributions of data did not significantly deviate from normality; therefore, we employed parametric statistics. Statistical significance was set at $P \leq 0.05$. In cases where no significant difference emerged with parametric statistical analyses, we conducted Bayesian statistics (Dienes 2014; Wagenmakers 2007) using JASP statistical software 0.7.5.6 (Love et al. 2015). According to Raftery (1995), a Bayes factor (BF_{01}) greater than 3 represents substantial evidence in favour of H_0 (i.e. that the effect investigated by the analysis does not occur), whereas a Bayes factor that falls within 1 and 3 means only weak evidence. Moreover, BF_{01} smaller than 1 indicates that the data are more likely under

H_1 (i.e. the effect investigated by the analysis does occur) than under H_0.

Training phase

All individual data obtained from the first and the second block of pairs were pooled and analysed together. We used two-tailed paired-samples *t*-tests to determine if performance in hierarchical and non-hierarchical conditions differed in: (1) the number of trials to achieve the learning criterion (i.e. learning speed); (2) the percentage of correct responses at the attainment of the learning criterion (i.e. accuracy level); (3) the RT at the attainment of the learning criterion.

Testing phase

A preliminary analysis demonstrated that the percentage of local choices of the first block of stimulus pairs (mean = 70.0%, SE = 10.90) was not significantly different from that of the second block of pairs (mean = 80.0%, SE = 3.06) [paired-samples *t* test, $t(4) = -1.09$, $P = 0.338$]. Therefore, data from the first and the second block of pairs were pooled and analysed together. We evaluated if: (1) the percentage of local choices was significantly higher than the 50% expected by chance (two-tailed one-sample *t* test); (2) the percentage of local choices differed between the two groups of subjects reinforced with different hierarchical figures (two-tailed independent-samples *t* test); (3) the RT differed between local and global choices (two-tailed paired-samples *t* test); (4) the percentage of correct choices for non-hierarchical stimuli was significantly above chance level (two-tailed one-sample *t* test).

Retesting phase

For the second presentation of the hierarchical inconsistent stimuli, we evaluated if: (1) the percentage of local choices was still significantly above chance level (one-tailed one-sample *t* test); (2) the percentage of local choices differed between the testing and the retesting phases (two-tailed paired-samples *t* test); (3) the percentage of correct choices for non-hierarchical stimuli was significantly above chance level (two-tailed one-sample *t* test); (4) the percentage of correct choices for non-hierarchical stimuli differed between the testing and the retesting phases (two-tailed paired-samples *t* test).

Results

All capuchins completed the scheduled experimental phases apart from the oldest female, Roberta. Roberta took a very long time to complete the training with the first 16 pairs of stimuli. After 2880 training trials with the second half of the stimuli, we interrupted the training because she had not approached the learning criterion for the discrimination of the hierarchical Navon-like figures. Therefore, the following analyses included data only for the first 16 pairs of stimuli for Roberta.

Training phase

More trials were required to achieve the learning criterion with hierarchical stimuli (mean = 1201.3, SE = 404.6) than with non-hierarchical stimuli (mean = 298.7, SE = 85.6) [paired-samples *t* test, $t(5) = 2.65$, $P = 0.045$, Fig. 3a]. However, once the capuchins had achieved the learning criterion there were no significant differences between hierarchical and non-hierarchical stimuli in either the percentage of correct responses [hierarchical, mean = 90.6%, SE = 1.17; non-hierarchical, mean = 91.3%, SE = 1.13; paired-samples *t* test, $t(5) = -0.38$, $P = 0.721$, Bayesian paired-samples *t* test, $BF_{01} = 2.53$; Fig. 3b] or RT [hierarchical, mean = 1034.41 ms, SE = 66.39; non-hierarchical, mean = 1134.52 ms, SE = 86.57; paired-samples *t* test, $t(5) = -1.64$, $P = 0.162$, Bayesian paired-samples *t* test, $BF_{01} = 1.10$, Fig. 3c].

Testing phase

At the first presentation of pairs of inconsistent hierarchical stimuli, the mean percentage of local choices was significantly higher than chance level [mean = 72.92%, SE = 5.74, one-sample *t* test, $t(5) = 3.99$, $P = 0.005$, Fig. 4]. However, capuchins had a similar mean RT in the local (mean = 1090.31 ms, SE = 124.55) and the global (mean = 1118.15 ms, SE = 135.93) choices [paired-samples *t* test, $t(5) = -0.25$, $P = 0.810$, Bayesian paired-samples *t* test, $BF_{01} = 2.61$]. No significant difference was found in the mean percentage of local choices between the two groups of subjects that were reinforced for choosing different stimuli [group 1: mean = 68.75%, SE = 9.55; group 2: mean = 77.08%, SE = 7.51; independent *t* test, $t(4) = -0.69$, $P = 0.530$, Bayesian independent-samples *t* test, $BF_{01} = 1.56$]. Finally, capuchins maintained a percentage of correct responses with the non-hierarchical stimuli that was well above chance level [mean = 96.88%, SE = 0.90; one-sample *t* test, $t(5) = 51.95$, $P < 0.001$].

Retesting phase

When capuchins were retested after five months, their mean percentage of local choices was still significantly higher than chance level [mean = 66.67%, SE = 6.78, one-sample *t* test, $t(5) = 2.46$, $P = 0.028$, Fig. 4]. Moreover, although the percentage of local choices made by the monkeys decreased, no significant difference was found between the percentage of local choices made immediately

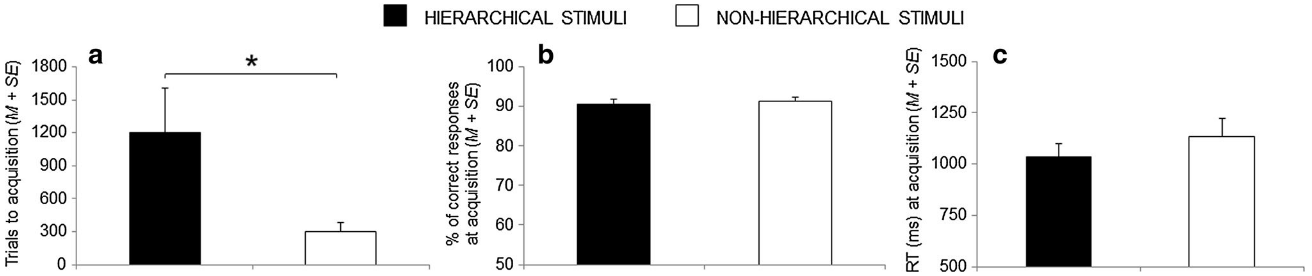


Fig. 3 Capuchins' performance (M + SE) in the hierarchical consistent stimuli and non-hierarchical stimuli used in the training phase in relation to **a** number of trials to achieve the learning criterion, **b** percentage of correct responses at acquisition and **c** RT in correct responses at acquisition. Dependent *t* test: $^{*}P < 0.05$

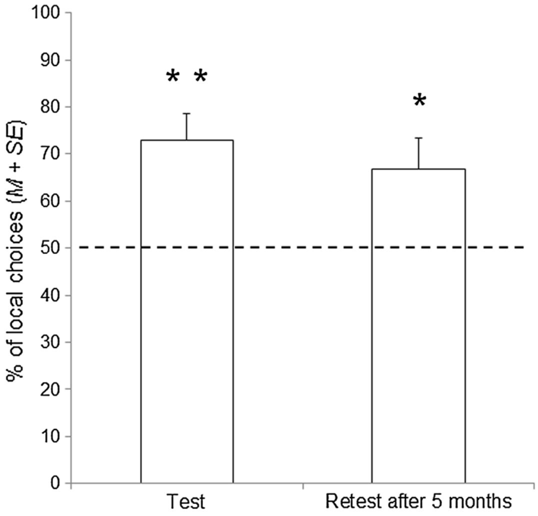


Fig. 4 Percentage of local choices (M + SE) in the testing phase right after the training phase and in the retesting phase after 5 months to the finish of the testing phase. One-sample *t* test: $^{*}P < 0.05$, $^{**}P < 0.01$

after training and after five months [paired-samples *t* test, $t(5) = 1.58$, $P = 0.175$, Bayesian paired-samples *t* test, $\mathrm{BF}_{01} = 1.16$]. Finally, the percentage of correct responses recorded for the non-hierarchical stimuli was well above chance level [mean = 89.84%, SE = 2.45; one-sample *t* test, $t(5) = 16.29$, $P < 0.001$] and did not differ from the percentage of correct responses observed in the testing phase administered immediately after the training [paired-samples *t* test, $t(5) = 2.16$, $P = 0.083$]. However, in this latter case the Bayesian analysis suggests a weak evidence in favour of H_1 [Bayesian paired-samples *t* test, $\mathrm{BF}_{01} = 0.55$]. This suggests that an increase in sample size could have resulted in a significant difference.

Discussion

This study shows that tufted capuchin monkeys rely on local elements in a conflict–choice task featuring Navon-type hierarchical stimuli. Monkeys were trained with consistent stimuli (same global and local shape). They were subsequently tested with inconsistent stimuli (different global and local shapes) obtained by exchanging the local elements between the consistent figures used in the training. In the testing phase, capuchins preferred figures which included the correct local elements even if they formed an incorrect global configuration, rather than figures with the correct global shape but formed by incorrect local elements. A local preference was also found in a retest presented after five months. These results are consistent with those of previous studies which showed that capuchins are more accurate when required to match hierarchical stimuli on the basis of the shape of their local elements in MTS tasks (De Lillo et al. 2011, 2012; Spinozzi et al. 2003, 2006; Truppa et al. 2016). The conflict–choice and the MTS tasks, therefore, provide converging results concerning capuchins' processing style despite the different memory load or other requirements of the two paradigms.

Capuchin monkeys have already proved to be more proficient in processing the local level of hierarchical stimuli in simultaneous MTS tasks without memory requirements (De Lillo et al. 2011, 2012; Spinozzi et al. 2003, 2006; Truppa et al. 2016) and in delayed-MTS tasks requiring the short-term retention (0.5–3.0 s) of the sample stimulus (Truppa et al. 2016). This latter study showed that whereas capuchins' recognition of local elements was above chance level with delays of up to 3.0 s, their recognition of global configurations was above chance level in simultaneous, 0.0- and 0.5-s delay conditions but not at delay intervals of 1.0 s or longer (Truppa et al. 2016). The present data on a conflict–choice task provide the additional important information that capuchins' choice of hierarchical stimuli is guided preferentially by the shape of their local elements, even when the stimuli have been retained for an extended period of time. Thus, a clear local dominance in capuchin monkeys is maintained even when the participation of integrative long-term memory processes mediated by the hippocampus (Kumaran et al. 2007; Sanderson et al. 2006) may have reduced it. The extent to which capuchins' propensity for the recognition of constituent parts of familiar rewarded stimuli rather than their configuration is caused by a less efficient encoding and/or recall of global information remains to be determined. Nevertheless, the fact that the local dominance in capuchins has been reported in several studies using simultaneous or 0-delay MTS (De Lillo et al. 2012; Spinozzi et al. 2003, 2006; Truppa et al. 2016) suggests that it emerges relatively early during visual processing and without requiring the participation of recall processes. At the same time, the finding that the local dominance of capuchin monkeys can be dramatically reduced by inducing an attention bias towards the processing of the global level of stimulus structure (De Lillo et al. 2011) suggests that it may not be an expression only of low-level, pre-attentive visual processes.

In our study, we used a larger number of stimuli than it has previously been done. An inspection of 18 studies from the comparative literature on global/local processing indicates that a range of 2–6 stimuli has been used typically, with a variety of experimental paradigms and classes of animals (insects: Avarguès-Weber et al. 2015; fish: Truppa et al. 2010b; birds: Cavoto and Cook 2001; Chiandetti et al. 2014; Fremouw et al. 1998, 2002; mammals: De Lillo et al. 2011; Deruelle and Fagot 1998; Fagot and Deruelle 1997; Fagot and Tomonaga 1999; Hopkins and Washburn 2002; Neiworth et al. 2006; Pitteri et al. 2014; Spinozzi et al. 2003, 2006; Tanaka and Fujita 2000; Tanaka et al. 2001; Truppa et al. 2016). In this study, we presented a total of 32 different hierarchical figures combined in 16 pairs to our subjects. The testing phase featured only a single presentation of each pair of inconsistent stimuli and a large number of stimuli were required to generate a sufficient number of testing trials. Although the use of a large number of stimuli was motivated mainly by this procedural requirement, it also allowed us to demonstrate that a spontaneous local preference in capuchins is present from their very first experience with a given compound stimulus. Moreover, the fact that the capuchins' local dominance was confirmed by using several different stimuli gives more weight to the results of previous studies that observed a similar pattern (e.g. De Lillo et al. 2011, 2012; Spinozzi et al. 2003, 2006; Truppa et al. 2016) and suggests that the local dominance of capuchin monkeys is not contingent upon the specific stimuli used there.

The present results together with previous findings suggest that capuchins' local dominance emerges both when they are free to choose between the two types of information, as in the conflict–choice task, and when they are required to attend the local or the global level of the hierarchical stimuli, as in the MTS task (De Lillo et al. 2011; Spinozzi et al. 2003, 2006; Truppa et al. 2016). It is important to note, however, that this local preference in capuchins is not due to an incapacity to process the global configuration of hierarchical stimuli. In fact, MTS studies show that although capuchins are more proficient in processing the local than the global level of the stimuli, they show a high level of accuracy when required to match the stimuli on the basis of their global configuration.

A further comment should be made on the implications of the procedure used in this study. We used an intermixed presentation of hierarchical and non-hierarchical stimuli within the experimental sessions. The use of non-hierarchical stimuli was motivated by the need to monitor capuchins' memory performance during the entire course of the experiment. This experimental design also gave us the opportunity to observe differences in the processing of hierarchical and non-hierarchical figures. In the training phase, capuchins learned to discriminate hierarchical consistent stimuli very accurately (90.6% of correct responses). However, they required significantly more trials to achieve the learning criterion with hierarchical than non-hierarchical stimuli. Learning speed was the only aspect of the performance that was affected by the type of stimuli presented. At the attainment of the learning criterion, the accuracy and RT of capuchins were similar for hierarchical and non-hierarchical figures. The fact that hierarchical figures needed a higher number of presentations to be accurately discriminated indicates that they are more difficult to encode and/or recall than non-hierarchical visual patterns. This suggests that, consistently with the results of other studies, capuchins' processing of hierarchical stimuli is not confined to the analysis of the shape of one level of stimulus structure only. In fact, if that were the case, the complexity of hierarchical stimuli could have been reduced to that of each of its individual elements. This, contrary to what has been observed here, should have resulted in a similar level of difficulty for the acquisition of the criterion for hierarchical and non-hierarchical stimuli.

The investigation of how part–whole relations within visual patterns are processed by different species yields important information concerning visual cognition. The observation of differences in visual processing style in species that share a similar visual system, for example, may suggest that they are mediated by higher cognitive functions. This suggestion is consistent with the evidence that top-down attentional processes modulate global/local processing in monkeys and humans (De Lillo et al. 2011). Particularly useful information can be obtained from the direct comparison of taxonomically related species, with a similar neuroanatomy and analogous ergonomic requirements. However, it is not always possible to carry out such comparisons in the same study. When comparing patterns of results obtained in different studies with a variety of organisms, it is thus crucial to ensure that any alleged interspecies differences cannot be accounted merely by methodological variations among the paradigms used. The present study, in conjunction with previous investigations of level of processing in capuchin monkeys, shows that the local advantage in capuchin monkeys is an extremely robust finding that can be replicated with different task variations reported in the comparative literature and provides a useful template for comparison across studies on animal visual cognition.

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Compliance with ethical standards

Ethical approval The research protocol for this study was approved by the Italian Health Ministry (Central Direction for the Veterinary Service, approvals n. 11/2011-C and n. DM132/2014-C to V. Truppa). All procedures were in accordance with the ethical standards of National Research Council of Italy, where the study was conducted.

Conflict of interest The authors declare that they have no conflict of interest.

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