Research report

Local advantage in the visual processing of hierarchical stimuli following manipulations of stimulus size and element numerosity in monkeys (*Cebus apella*)

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Abstract

Previous studies suggest that monkeys process local elements of hierarchical visual patterns more quickly and more accurately than they process the global shape. These results could be indicative of differences between relatively high visual functions of humans and non-human primates. It is, however, important to rule out that relatively low-level factors can explain these differences. We addressed this issue with two experiments carried out on capuchin monkeys (*Cebus apella*) using matching-to-sample tasks featuring hierarchical stimuli. The first experiment assessed whether manipulations of stimulus size can affect the local advantage so far observed in this New World monkey species. An overall local versus global advantage still emerges in capuchins, irrespectively of the amplitude of the visual angle subtended by the hierarchical shapes. Moreover, a local-to-global interference, indicative of a strong local advantage, was observed for the first time. In the second experiment, we manipulated size and numerosity of the local elements of hierarchical patterns, mimicking procedures that in human perception relegate the local elements to texture and enhance a global advantage. Our results show that in capuchin monkeys, a local advantage emerges clearly even when these procedures are used.

These results are of interest since extensive neurophysiological research is carried out on non-human primate vision, often taking for granted a similarity of visual skills in human and non-human primates. These behavioural results show that this assumption is not always warranted and that more research is needed to clarify the differences in the processes involved in basic visual skills among primates.
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1. Introduction

The organization of local features and parts of visual stimuli into whole percepts is a central problem for visual perception that has been extensively investigated at both behavioural and physiological level. However, neurophysiological and neuropsychological studies present a varied and not always coherent picture of the neural structures and the psychological processes that are likely to be involved in assembling visual elements into larger figures [1,29]. Part of the confusion arises from a difficulty in specifying whether the

mechanisms responsible for the integration of local features into global shapes operate at relatively early, sensory stages of visual processing, or belong to higher, post-attentive cognitive skills [38]. Indeed, recent approaches to this problem suggest that perceptual organisation may involve processes that are less unitary than originally thought and rely on both lower and higher order visual areas, with the latter specifically involved in determining closure and shape formation [1].

The fact that elementary grouping principles have been considered traditionally as widespread perceptual functions, common to any organism equipped with a relatively advanced form of vision, has recently generated a great deal of interest in comparative cognition where attempts have been made

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to assess empirically whether basic mechanisms observed in humans also apply to other species [3,4,25]. Studies involving non-human primates are of particular interest here. Non-human primates and humans have a similar sensitivity to contrast and visual fields of a similar size [7,13]. Moreover, it is assumed that humans and non-human primates share very similar primary and secondary visual pathways [37] and recent evidence indicates that several areas in the human extrastriate cortex could be functionally similar to those observed in monkeys [36,39]. Functional differences between cortical visual areas in humans and non-human primates are more likely to be localised in more anterior areas [2]. As such, among primates, any obvious interspecies differences in the mode of processing of visual information may be indicative of differences in relatively higher visual functions.

There are, nevertheless, some surprising differences between the performance of human and non-human primates in relatively simple visual tasks. For example, we recently carried out a study where capuchin monkeys and humans had to match visual patterns with some of their parts [31]. In some conditions the parts were formed by grouping elementary features according to gestalt principles of organization and, in other conditions, they were an assemblage of disconnected elementary units. While humans were systematically better in the conditions featuring grouped parts, monkeys were systematically better in conditions featuring disconnected features. The matching performance of humans was also facilitated when the stimulus parts formed closed rather than open figures. The same effect was not observed in capuchin monkeys [31].

These results suggest that humans and non-human primates may differ in the relatively higher-level post-attentive processes that make the visual system sensitive to grouping principles such as closure. However, more parsimoniously, one could conjecture that grouped features may form closed shapes that happen to be more familiar to humans and that familiarity alone could explain the observed interspecies differences.

However, this type of objection cannot be easily applied to paradigms featuring the use of hierarchical visual stimuli, where larger global shapes are formed by the spatial arrangement of smaller local shapes and both the global and local levels of the stimuli are derived from the same set of shapes. As the same shape can feature at both the local and the global level of the stimuli, an advantage in processing one level over the other cannot be related to the specific shape involved.

The use of hierarchical visual stimuli was pioneered by Navon [28], who found that adult humans perceive the global configuration of visual patterns more readily than their local elements. Moreover, in conditions where the local elements differed in shape from the global configuration (inconsistent stimuli), the conflicting information between the global and the local levels exerted asymmetrical global-to-local interference. This latter finding has been interpreted as evidence of a general global advantage in human visual perception [28].

A tendency to attend more readily to the global configuration of visual stimuli should provide a number of benefits to the perceiver such as a facilitation in the use of low-resolution information, the maximization of the economy of processing resources and assistance in the disambiguation of indistinct details [28]. Given these postulated benefits and the above-mentioned similarity in the visual system of different primate species [7,13], one could expect that the global superiority, that has been reliably observed in humans, should pertain to non-human primates as well.

However, when we tested capuchin monkeys (a New World monkey species) with hierarchical visual stimuli we observed that they show a pattern that is opposite to that observed with human subjects. In contrast with humans, capuchin monkeys were more proficient in processing the local features of visual stimuli than their global shape [32]. Interspecies differences in the processing of hierarchical stimuli emerged also when capuchin monkeys were compared with pre-school children [5]. These results are consistent with those obtained with Old World monkey species, such as baboons [6,9] and rhesus monkeys [16], that are also faster and more accurate when processing the local features of visual stimuli rather than their global structure. Chimpanzees show no clear-cut advantage for global or local processing and do not always discriminate the local details of the compound patterns more quickly [11,12,16] and as such seem to occupy an intermediate position between the two extreme modes of processing shown by monkeys and humans.

Overall, these findings indicate that human and non-human primates may differ in their readiness to group perceptually elementary visual components of hierarchical patterns into a global configuration. Nevertheless, caution is required when interpreting these differences in terms of higher cognitive skills, before having evaluated, within a comparative context, the possible effects of a number of low-level factors on the global/local processing of hierarchical visual stimuli.

In fact, although the phenomenon of global advantage has been replicated in a large number of studies in human perception and cognition [18], some researchers have identified various factors that can affect and even reverse this global advantage in humans. These include, among others, stimulus size [22,26], the paucity or sparsity of local elements [18,21,27]. For example, Kinchla and Wolf [22] found a global advantage for patterns subtending less than about 6° of visual angle, but a local advantage for larger patterns. Similarly, Martin [27] found a global advantage with dense stimuli and a local advantage with sparse ones.

In a detailed study of the role played by the size and quantity of the constituents of hierarchical stimuli in the emergence of global advantage, Kimchi [19,20] showed that patterns composed of many relatively small elements are perceived as textured global shapes. The local elements lose their function as individual parts of the form and are perceived as texture. By contrast, in patterns composed of a few, relatively large elements, these elements are detected more readily than their global arrangement.

Considering that the global dominance effect, so widely replicated in humans, can be affected by the manipulation of some properties of the sensory input, it cannot be ruled out that the difference in sensitivity to the local and global levels of visual stimuli observed in nonhuman primates may depend on basic properties of the stimulus and that interspecies differences in global/local processing may be related to relatively peripheral visual mechanisms rather than to higher visual functions.

In fact, there is evidence that, in pigeons, the local precedence observed in perceptual and classification tasks using hierarchical patterns can be reversed as a function of the relative salience of the local and the global features of the stimuli [4,15]. Moreover, it has recently been shown that pigeons can selectively attend either to the local or the global level of hierarchical patterns when specific testing procedures are employed. For example, Framwork et al. [14] found that their subjects can shift attention between wholes and parts following a presentation of priming cue signalling whether a target is at the global or local level in a given trial.

It is, therefore, important to assess empirically whether manipulations of appropriate stimulus factors can reverse or reduce the local advantage typically observed in monkeys.

In the present study, we report the results of two experiments designed to assess whether the relative salience of the local and the local levels of visual patterns can be affected in capuchin monkeys by the visual angle subtended by the global shape and by the number and the relative size of local elements as it has been reported for humans [18,22,26].

2. Experiment 1: manipulations of visual angle

In previous work with capuchin monkeys [32], a local advantage was found for stimuli whose global and local features subtended about 3.5° and 0.5° of visual angle, respectively. To assess whether the manipulation of the stimulus size could affect the global/local processing in capuchins, as reported for humans [22,26], in this experiment we used compound patterns subtending two different visual angles, of which one was about five times the size of the other, so that the size of local shapes in the large visual angle condition was the same as the size of the global shape in the small visual angle condition. Our reasoning was that, should a local advantage have emerged in both conditions, then the local advantage in this species is unlikely to be exclusively explained by stimulus size alone and other, possibly higher processes, need to be invoked in order to account for interspecies differences in local/global advantage.

We used a simultaneous matching-to-sample (MTS) procedure to test the monkeys with the same set of stimulus shape used previously by Spinozzi et al. [32] with capuchin monkeys and by De Lillo et al. [5] in a comparative study of monkeys and pre-school children.

2.1. Methods

2.1.1. Subjects

Six tufted capuchins (*Cebus apella*), three males and three females, ranging in age from 4.0 to 22.3 years, were used in this experiment. All monkeys were born in captivity. They lived in four social groups, each housed in an indoor–outdoor cage (indoor, 3.0 m long × 1.7 m wide × 3.0 m deep; outdoor, 2.5 m × 1.7 m × 3.0 m) at the Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche (C.N.R.), in Rome, Italy. Each subject was separated from the group solely for the purpose of testing, just before each daily testing session.

The animals were given food pellets ad libitum before and after testing; fresh fruit and vegetables were provided after testing. Water was freely available at all times. Three monkeys had previously served in a study on the processing of hierarchical stimuli [5,32]. The remaining three subjects had never been presented with this type of visual pattern before. However, they were already familiar with the matching-to-sample (MTS) procedure, having been previously tested on pattern discrimination and categorization problems using MTS [31,33].

2.1.2. Apparatus

The apparatus was the same as that used in other previous studies [5,31,32] and consisted of a wooden panel (45 cm long × 35 cm high × 2 cm thick) with two symmetrical rectangular openings (5 cm long × 9 cm high), each 10 cm from the center. The panel was fixed perpendicularly onto a wooden board (45 cm × 35 cm), which could be moved forward and backward on a support, mounted on a trolley (50 cm long × 50 cm wide × 55 cm high). The apparatus is depicted in Fig. 1A. Three polyvinyl chloride lids (6 cm long × 11 cm high × 0.3 cm thick) were used for stimulus presentation. Two lids were placed in front of the rectangular openings of the vertical panel. They could be slid laterally in both directions along two parallel metal tracks (45 cm long × 1 cm high), which were mounted horizontally on the panel 1 cm above and below the openings. The third lid was fixed in the center of the vertical panel 1 cm above the two openings and equidistant from them. The set-up used for the presentation of the stimuli is shown in Fig. 1B.

The apparatus was installed outside the experimental cage (the indoor home cage) behind a transparent Plexiglas panel (45 cm long × 40 cm high) mounted on the front wall of the experimental cage. The Plexiglas panel had two symmetrical lateral armholes (15 cm long × 5.5 cm high) at the level of the bottom edge of the rectangular openings of the apparatus. The monkey had to insert an arm through one of the two holes and move one of the sliding lids covering the rectangular openings in the panel in order to reach for a peanut. The rectangular openings of the apparatus were positioned at the subjects' eye level.
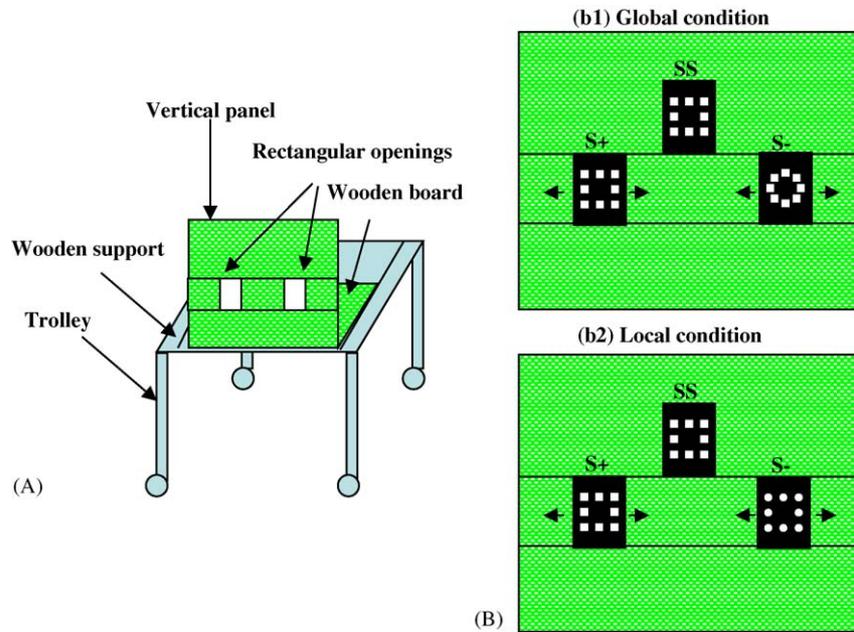
Fig. 1. (A) Apparatus; (B) an example of stimulus presentation in global (b1) and local (b2) conditions of Experiment 1.

2.1.3. Stimuli

The stimuli used in this experiment are presented in Fig. 2. They appeared as white shapes on a black background and were created using Microsoft PowerPoint. Each stimulus was printed on paper and was glued onto PVC lids.

The stimulus set comprised eight hierarchical shapes that varied in global and local size, and six filled shapes of different size (Fig. 2A). The hierarchical shapes included large circles (C) and squares (S) made up of smaller circles (c) or squares (s). The filled stimuli included single circles and squares (Fig. 2B); these patterns were used as control stimuli and served to assess the capuchins' ability to discriminate the size of single-element shapes per se, independently of hierarchical levels.

There were two types of hierarchical stimuli, referred to as *small* and *large hierarchical stimuli.* All the stimuli were formed using eight local elements. Capuchins viewed the stimuli from approximately 30 cm. At this distance, the small stimuli subtended $0.95°$ of visual angle at global level and $0.19°$ at local level. The large stimuli, featuring a proportional enlargement of the small ones, subtended about $4.9°$ of visual angle at global level and $0.95°$ at local level.

There were three types of filled patterns, the *small, medium* and *large filled stimuli,* subtending $0.19°$, $0.95°$, and $4.9°$ of visual angle, respectively.

2.1.4. Procedure

An identity MTS procedure was adopted. At the beginning of each trial, the apparatus was placed at a distance of 30 cm in front of the experimental cage. The experimenter placed the sample stimulus on the apparatus, above the two rectangular openings in the panel and equidistant from them, in full view of the subject. The experimenter then simultaneously placed the two comparison stimuli, the matching stimulus (S+) and the non-matching stimulus (S−), in front of the rectangular openings in the panel, below and to the right and left of the sample. The panel was, then, brought closer to the cage (about 15 cm), within reach of the monkey's arm. The monkey could obtain the reward only if it moved the lid with the matching stimulus glued on it. After the monkey moved a lid, the panel was moved away from the cage, and a new trial was set up.

Inter-trial interval was about 30 s following a correct response, and about 60 s following an incorrect response.

Regarding the hierarchical patterns, two identity-matching conditions were presented to the monkeys. In the *global matching condition,* S+ was identical to the sample and S− differed from the sample only at the global level (Fig. 1b1). In the *local matching condition,* S+ was identical to the sample, but S− differed from the sample only for local elements (Fig. 1b2). According to the size of hierarchical patterns, there were two global matching conditions, the *small-global* and the *large-global,* and two local matching conditions, the *small-local* and the *large-local.*

Regarding the filled patterns, there were three identity-matching conditions based on the size of the single-element shapes: the *small-identity,* the *medium-identity* and the *large-identity.*

Each subject performed 10 sessions of 22 trials each, one session a day, for a total of 220 trials. In each session, there were 16 trials including a combination of small and large hierarchical patterns, and six trials including the different sized filled patterns. In each session, each hierarchical stimulus (large-Cc, -Cs, -Ss and -Sc; small-Cc, -Cs, -Ss and -Sc) was presented as the sample two times in random order, and each comparison stimulus appeared to the left and right side of the sample with equal frequency; similarly, each filled stim-
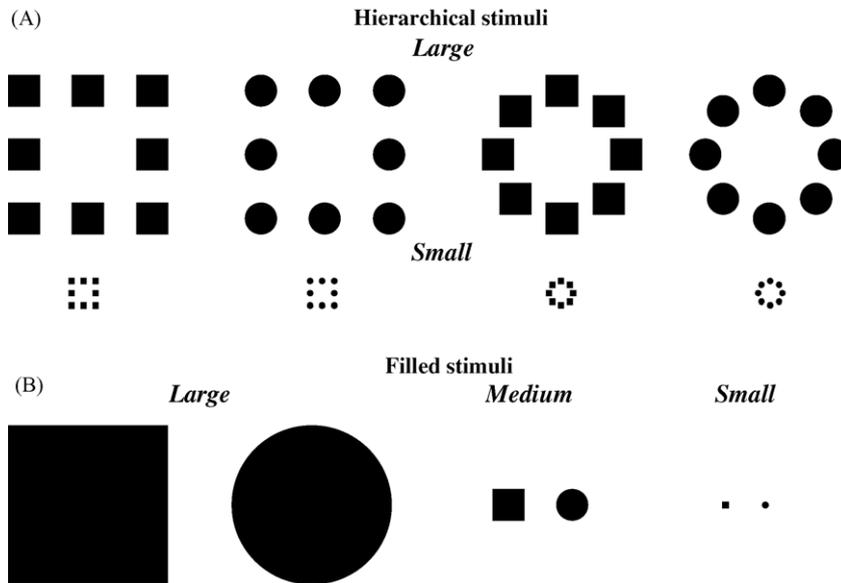
Fig. 2. (A) The hierarchical stimuli used in Experiment 1; (B) the non-hierarchical stimuli ("filled shapes") used as a control condition in Experiment 1.

ulus (large-, medium-, small-C and -S) was presented as the sample once.

Only the local or the global matching condition was presented within each session, with trials including consistent (i.e. local and global shapes were identical: Cc, Ss) and inconsistent sample stimuli (i.e. local and global shapes were different: Cs, Sc) randomly intermixed.

All daily sessions were preceded by nine practice trials, using an identity-MTS procedure and different stimuli from those used in the test (e.g. simple filled shapes such as arrow and heart shapes). These trials were used to assess the MTS performance level of each subject before each task. The criterion to be reached before the administration of the testing session was seven correct responses out of nine. No physical restriction was imposed on the animals during testing.

2.1.5. Data analysis

The percentage of correct responses per test condition was used as the dependent variable. For hierarchical stimuli, the presence of interference between global and local levels was assessed comparing trials featuring consistent sample stimuli with trials featuring inconsistent sample stimuli. ANOVAs were used to compare accuracy in the different conditions and Fisher's LSD test was used for post hoc comparisons.

2.2. Results

Separate analyses were carried out to evaluate the percentage data obtained for filled and hierarchical visual patterns.

For filled stimuli, the overall mean percentage of correct responses ranged from 68.3% to 88.3% (see Table 1). One-sample t-tests showed that the mean percentage scores obtained for each type of filled stimuli were significantly above the 50% expected by chance

(small, $M = 80.0\%$, $t(5) = 9.49$, $p < .001$; medium, $M = 80.8\%$, $t(5) = 8.77$, $p < .001$; large, $M = 81.7\%$, $t(5) = 6.64$, $p < .01$). An analysis of variance (ANOVA) comparing percentages of correct responses obtained for small, medium, and large filled stimuli did not reveal a significant difference between these three levels of stimulus size, $F(1, 2) = 0.07$, $p > .1$.

For hierarchical stimuli, the overall mean percentage of correct responses ranged from 72.5% to 87.5% (see Table 1).

The ANOVA stimulus size (small, large) × matching condition (global, local) × stimulus consistency (consistent, inconsistent) failed to reveal a significant main effect of stimulus size (small = 79.8%, large = 81.0%), $F(1, 5) = 0.15$, $p > .1$, or stimulus consistency (consistent = 81.9%, inconsistent = 79.0%), $F(1, 5) = 3.6$, $p > .1$. However, the effect of matching condition was significant, $F(1, 5) = 16.6$, $p < .001$. The overall accuracy scores were higher for local ($M = 83.3\%$) than for global ($M = 77.5\%$) trials. Moreover, the interaction between matching condition and stimulus consistency was statistically significant, $F(1, 5) = 9.4$, $p < .05$ (Fig. 3). Post hoc comparisons (Fischer LSD test) revealed that in the global trials the level of performance was higher

Table 1
Individual percentages of correct responses for hierarchical and filled stimuli, according to different experimental conditions

Subject	Hierarchical stimuli				Filled stimuli		
	Small		Large		Small	Medium	Large
	Global	Local	Global	Local			
Robinia	70.0	85.0	67.5	75.0	75.0	70.0	60.0
Gal	77.5	87.5	87.5	82.5	75.0	90.0	85.0
Narciso	80.0	85.0	87.5	97.5	95.0	85.0	80.0
Pepe	70.0	82.5	80.0	90.0	80.0	90.0	95.0
Virginia	87.5	90.0	72.5	85.0	75.0	75.0	85.0
Pippi	65.0	77.5	76.5	71.0	80.0	75.0	85.0

for consistent than for inconsistent sample stimuli (82.1% versus 72.9%, $p < .05$); the same effect was not found in the local trials.

Furthermore, as revealed by post hoc analyses, the main effect registered in the global condition seems to be accounted for mainly by the lower level of performance observed in global trials (72.9%) compared to local trials (85.0%, $p < .01$) when the stimulus was inconsistent (Fig. 3). Stimulus size did not interact significantly with matching condition or with stimulus consistency; similarly the third order interaction between the three factors was not significant.

2.3. Discussion

We have previously reported a local advantage for stimuli subtending 3.5° of visual angle [5,32] in capuchin monkeys. In the present study, we used hierarchical stimuli both larger and smaller than those used in our previous experiments in order to assess whether stimulus size alone could explain the local advantage observed in this species. An overall local advantage emerged, irrespectively of the amplitude of the visual angle subtended by the hierarchical shapes.

Moreover, we found a significant effect of stimulus consistency when the global, but not the local level of the visual patterns had to be attended to. In particular, in the global matching conditions, our subjects responded to trials featuring an inconsistent sample stimulus at a lower level of accuracy than to trials featuring a consistent sample stimulus. This effect did not emerge in the local matching conditions: here, the monkeys were equally successful in trials featuring consistent and inconsistent patterns. The latter result can be interpreted in terms of a local-to-global interference and provides strong evidence for a superiority of local processing in capuchin monkeys. As far as we are aware this is the first time that this type of interference has been observed in non-human primates.

It may also be worth noting that this local advantage persisted with stimuli subtending less than 6° in visual

angle, which typically produce a global precedence effect in humans [22]. Since we designed our stimuli so that the local level of the larger stimuli was exactly the same size as the global level of the smaller stimuli, we should have observed an inversion of the local advantage in the conditions featuring smaller stimuli if size was an important factor in determining the mode of processing of these shapes, but we did not. Furthermore, evidence from control trials involving single filled patterns whose sizes were similar to either the local or the global aspects of hierarchical patterns, showed that capuchins were equally successful in discriminating large and small filled shapes. Overall, these results suggest that visual angle per se is not the critical factor responsible for the observed local advantage in capuchin monkeys.

3. Experiment 2: manipulations of number and relative size of elements

Evidence from human literature suggests that the relative salience of global and local levels of hierarchical stimuli critically depends on the number and relative size of the elements. For example, Kimchi [19,20] found that when the arrangement of a few large elements formed a pattern, the local elements were perceived as more salient than the global figure; in contrast, in the case of patterns that were composed of many small elements, the global figure was perceived as more salient.

Experiment 2 was aimed at verifying whether capuchins would still exhibit a local advantage when the number and relative sizes of the elements of the hierarchical stimuli were manipulated.

3.1. Methods

3.1.1. Subjects, apparatus, and stimuli

Subjects and apparatus were the same as those used in the previous experiment. However, the monkeys were tested with a different set of stimuli. The shape and the density of the local elements of the stimuli were similar to those used by Kimchi [19] with humans.

All the hierarchical stimuli comprised large rhombi (R) and squares (S) made up of smaller rhombi (r) or squares (s). There were two sets of stimuli, which differed in the number and relative size of their elements. The *few-element* set consisted of stimuli composed of four relatively large elements. The *many-element* set consisted of stimuli made up of 16 relatively small elements. Each set contained two consistent stimuli in which the global and local shapes were identical, and two inconsistent stimuli in which the global and local shapes were different. All stimuli measured 3 cm × 3 cm at global level (2.9° of visual angle). Each individual element measured about 0.8 cm × 0.8 cm (i.e. 0.76°) in the few-element patterns and about 0.4 cm × 0.4 cm (i.e. 0.38°) in the many-element patterns (see Fig. 4).
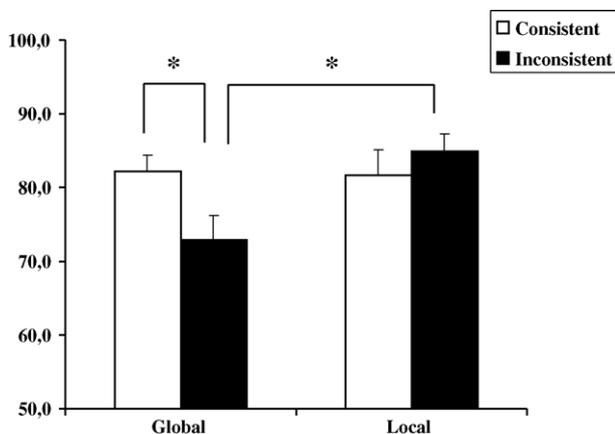

Fig. 3. Percentages of correct responses observed in global consistent, global inconsistent, local consistent and local inconsistent trials in Experiment 1.
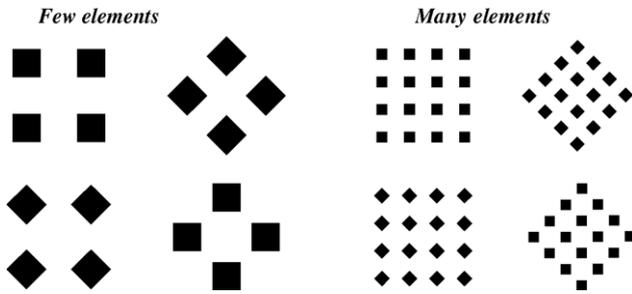
Fig. 4. Stimuli used in Experiment 2.

3.1.2. Procedure

In the present experiment, we used a similarity MTS procedure in which the monkeys were presented with a hierarchical pattern as the sample and had to choose which one of the two comparison stimuli was more similar to the sample. In the global condition, S+ matched the sample only at the global level, whereas S− differed from the sample at both global and local levels and was similar to S+ at local level. Thus, if the sample was a rhombus made of smaller rhombi (Rr), S+ was a rhombus made of small squares (Rs) and S− was a square made of small squares (Ss). In the local condition, S+ matched the sample only at local level, but S− differed from the sample at both levels and was similar to S+ at global level (e.g. if the sample was Rr, S+ included Sr, and S− was Ss).

Testing occurred immediately after completion of Experiment 1. Each monkey performed eight daily sessions of 32 trials each, for a total of 256 trials. One half of trials included few-element patterns, and the other half included many-element patterns. Each hierarchical stimulus was presented as the sample four times in a pseudorandom order, ensuring that two consecutive trials could not feature the same stimuli and that the comparison stimuli appeared to the left and right side of the sample with equal frequency. As in Experiment 1, the global and the local trials were presented in different sessions, with randomly intermixed consistent and inconsistent stimuli.

3.2. Results

Table 2 reports the individual percentages of correct responses for both few-element and many-element stimuli, in the global and the local conditions.

Table 2
Individual percentages of correct responses for few-element and many-element stimuli, in global and local conditions

Subject	Few-element		Many-element	
	Global	Local	Global	Local
Robinia	79.7	84.4	62.5	86.0
Gal	85.9	81.3	78.1	82.8
Narciso	79.7	89.1	73.3	90.6
Pepe	71.9	81.3	87.0	83.0
Virginia	70.3	76.6	73.3	75.0
Pippi	67.2	81.3	73.3	78.1

The overall mean percentages of correct responses ranged from 73.8% to 83.2%. A repeated-measure ANOVA (stimulus type (few-element, many-element) × matching condition (global, local) × stimulus consistency (consistent, inconsistent) was carried out to analyze the percentages of correct responses observed in the different conditions. The analysis revealed, once again, a significant main effect of matching condition, $F(1, 5) = 8.8$, $p < .05$ (see Fig. 5), with a higher level of accuracy for the local trials (82.4%) than for the global trials (75.2%). Thus, as in Experiment 1, the monkeys found it easier to identify the local than the global shapes of the hierarchical patterns. Moreover, the effects of stimulus type (few-element, $M = 79.0\%$; many-element, $M = 78.7\%$), and stimulus consistency (consistent, $M = 79.2\%$; inconsistent, $M = 78.5\%$) were not significant. However, in contrast with Experiment 1, the interaction between matching condition and stimulus consistency was not significant. Finally, neither the matching condition × stimulus type interaction nor the third-order interaction between the three factors was significant.

3.3. Discussion

The results of Experiment 2 indicate once again a significant overall advantage in the identification of the local shapes compared with the global ones. This local advantage was not related to the stimulus type, as it emerged regardless of the number and size of the elements which composed the visual pattern: capuchins' strong propensity for local over global processing was, in fact, evident not only for few-element patterns, but also for many-element patterns, that is, patterns that facilitate the perception of global structure in humans [18,19].

The current findings are thus congruent with the previous experiment, by showing that the processing strategy typical of this species is not affected by the structural properties of the stimulus.

We found that the consistency of the sample stimulus did not affect the monkeys' performance either in the local or in the global trials. In contrast with the results of the previous
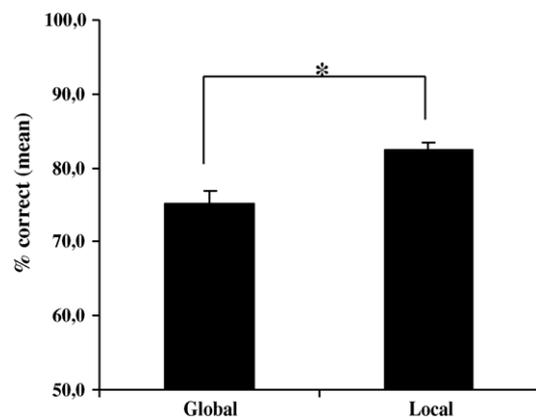

Fig. 5. Percentages of correct responses observed in global and local trials in Experiment 2.

experiment, capuchins' performance in the global trials was impaired irrespectively of degree of similarity of the local and the global shapes in the sample stimulus.

The differences in the patterns of results observed in Experiments 1 and 2 regarding the local-to-global interference could be due to the use of a different stimulus set. Experiment 1 involved the use of the Navon-type hierarchical stimuli, which produce a strong asymmetrical interference in humans. By contrast, Experiment 2 entailed the Kimchi-type stimuli, which do not always induce an asymmetrical interference in adult individuals, even though they produce either a local or a global advantage depending upon the number and relative size of their constituent elements [19].

It is worth noting that different MTS procedures were used in Experiment 1 (identity MTS) and Experiment 2 (similarity MTS). In the present experiment, the sample stimulus was always different from S− at both global and local level. Moreover, S+ matched the sample at only one level, but it shared with S− the other level. On the other hand, in Experiment 1, the sample and S+ were identical at both levels, and they shared properties at one level (either the global or the local one) with S−. In the global trials, therefore, S− shared the same local features with both the sample and S+. However, we find it difficult to explain from a theoretical point of view how these procedural differences may have accounted for the disappearance of the local-to-global interference in the second experiment. Nevertheless, the fact itself that a local advantage in capuchin monkeys is maintained despite these changes testifies, we believe, the strength and robustness of the finding and highlights the differences between this New World monkey species and humans in testing conditions that have been shown to induce a strong global advantage in the latter.

4. General discussion

Using a matching-to-sample procedure, we carried out two experiments to assess the effects of the manipulation of some stimulus properties on global and local processing of hierarchical visual stimuli in capuchin monkeys.

In particular, Experiment 1 evaluated the role played by variations in stimulus size. In fact, in the literature on human cognition, it has been reported that this variable can influence global processing in humans [22,26]. The importance of stimulus size emerges also from the analysis of dissociations reported in the literature on human neuropsychology. For example, an impairment of the ability to organise local parts into global wholes has been put in relation with neuropsychological patients, sharing some similarity with cases of integrative agnosia [17], who had specific difficulties in the processing of the global aspects of stimuli subtending large visual angles. This disorder has been referred to as "agnosia for larger figures" [30,34,35].

Considering that stimulus size can potentially affect perceptual organisation, it was important to assess whether the local advantage so far observed in capuchin monkeys could

have been explained on the basis of this factor alone. Our first experiment was designed so that the local level of larger stimuli was of the same size as the global level of smaller stimuli. If a local advantage observed with the larger shapes was due to stimulus size, then the effect should have been reduced or even reversed when the monkeys were faced with the smaller stimuli.

Although our subjects were very proficient in conditions requiring them to attend to the global aspect of the stimuli and in conditions requiring them to attend to the shape of the local elements, their level of performance was higher in the local conditions irrespectively of changes of the size of the stimulus. Moreover, a local-to-global interference was indicated by the finding that the consistency of the sample stimulus affected the monkeys' performance in global but not local trials. The fact that the global configuration of the stimuli was more difficult to process when it was different from the shape of the local elements mirrors symmetrically the finding in humans that inconsistent stimuli negatively affect the local but not the global level of the stimuli [28].

Taken together, the higher proficiency in processing the local level of the stimuli and the local-to-global interference observed here provide, to our knowledge, the strongest evidence of a local advantage in non-human primates.

In Experiment 2, we tested the extent to which the global/local discrimination in capuchins could be affected by a variation in the number and relative size of the stimulus constituent elements, a manipulation known to affect the relative ease of global and local processing in humans [18–20]. An overall local advantage emerged in capuchins regardless of the type of stimuli involved in the test. However, in contrast with Experiment 1, no local-to-global interference was found: the monkeys found it easier to process the shape of the local elements of the stimuli irrespective of whether the sample stimuli were consistent or inconsistent. This difference in the pattern of result between the two experiments is difficult to explain and may be related to the different stimulus types and/or MTS procedures used in the two experiments. Nevertheless, what emerges clearly from our results is that the local advantage observed in capuchin monkeys is very robust.

These findings provide clear evidence that for capuchin monkeys a pattern of results emerges that is different from that reported in the literature for human subjects [18,19]. Whereas the global advantage that characterizes human vision can be reduced and also turn into a local advantage as a function of manipulations of several stimulus-related variables [18,20,22,26,27], the same manipulations do not reduce or reverse the typical local advantage of capuchins.

The present study did not feature the direct comparison of monkeys and human subjects as human data for similar experiments have been reported in the literature [18,19,21]. In any case, the current results are consistent with results obtained in our previous studies where we compared humans and capuchin monkeys on their relative ability to integrate local elements into global shapes [5,32]. The ability to perceive the global configuration of a pattern consisting of elements is

considered to be a measure of grouping and element integration [8]. Assuming that the detection of a global configuration requires the capacity to group elements by proximity (and possibly by similarity as all the elements in the patterns were similar and close one to another), our data show that capuchins are indeed able to use this cue, since their level of performance in global trials is well above chance level. Nevertheless, the perceptual effect of this cue in capuchin monkeys does not seem to sufficiently powerful to produce the global advantage so often observed in humans.

We cannot exclude that a number of other factors can account for this difference quite apart from the relative sensitivity to element proximity of different species. However, an interpretation along these lines would be consistent with results of studies which have featured the direct comparison of human and non-human primates and have shown that for both monkeys and apes an increase in the separation of the elements of hierarchical visual patterns can be much more disruptive than for humans [5,6,10,12,32]. A diminished capacity for grouping by proximity, in comparison to humans, has also been reported in chimpanzees for tasks involving the processing of Kanizsa-illusory figures [11].

Results obtained in our previous studies suggested that other grouping principles may be stronger in humans than in capuchin monkeys. For example, we have recently identified some important differences in a direct comparison of the performance of humans and capuchin monkeys in tasks requiring the participants to identify a stimulus part embedded in a more complex pattern [31]. There emerged that, in contrast with humans, capuchins found it easier to detect the local components of visual stimuli when they were segmented into relatively disconnected features rather than organized on the basis of grouping principles, such as "closure" or "good shape"[23,24].

These results can be seen as an expression of differences in the perceptual grouping processes used by humans and non-human primates. As such, it would be extremely important to direct further research to the identification of the specific grouping cues that may be differentially used by humans and other primate species.

As research for the identification of new visual areas in the primate brain is currently very active, but it has proved difficult to pinpoint areas brain areas specialised in the use of specific grouping principles, we believe that behavioural studies pointing to intererspecies differences can provide illuminating complementary information regarding analogies and differences between the visual system of human and non-human primates and help avoiding overestimations of their similarity.

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