Global and Local Processing of Hierarchical Visual Stimuli in Tufted Capuchin Monkeys (*Cebus apella*)

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Capuchin monkeys' (*Cebus apella*) relative accuracy in the processing of the global shape or the local features of hierarchical visual stimuli was assessed. Three experiments are presented featuring manipulations of the arrangement and the density of the local elements of the stimuli. The results showed a clear advantage for local level processing in this species, which is robust under manipulations of the density of the local elements of the stimuli. By contrast, the density of the component elements linearly affected accuracy in global processing. These findings, which support those from other studies in which a local superiority emerged in animals, challenge the generality of early claims concerning the adaptive value of global advantage in the processing of hierarchical visual patterns.

On the basis of his findings concerning the perceptual processing of visual stimuli, Navon (1977, 1981) argued that the human perceptual system processes the global features of a visual scene before proceeding to a more fine-grained analysis of local details. This hypothesis, termed the *global dominance* or *global precedence hypothesis* (Navon, 1977), was supported by the results of a series of experiments in which adult subjects were presented with hierarchically structured stimuli consisting of large letters made up of small letters. Navon observed that the accuracy and latency for visual detection response were better and shorter, respectively, when participants had to attend to global aspects of compound stimuli than when they were required to attend to their local features. Furthermore, in conditions in which attention had to be directed to local features, but not in conditions in which attention had to be directed toward the global form of the stimuli, the identity of the global level letter did affect subjects' discriminative responses. Global characters that conflicted with the local ones (e.g., a large *S* made of small *H*s) slowed down the perception of local level stimuli, whereas the identity of the local elements did not affect the recognition of global level hierarchical patterns. Navon interpreted this global-to-local interference as evidence for his global precedence hypothesis.

Navon's (1977, 1981) original proposal stimulated research on the basic nature of human visual perception, giving rise to an extensive literature on this topic. Although the global precedence phenomenon has been replicated in several studies, empirical evidence suggests that global processing priority may be affected by various structural properties of the stimuli, such as the density of local elements, the visual angle, or the familiarity with the stimuli (Dukette & Stiles, 1996, 2001; Hughes, Fendrich, & Reuter-Lorenz, 1990; Kinchla & Wolfe, 1979; Martin, 1979). For example, manipulating the number of local letters used to make up the global letter, Martin (1979) found a global-processing priority for many-element stimuli but a local-processing priority for few-element stimuli. Moreover, other lines of evidence suggest that the global-to-local advantage may also depend on attentional mechanisms, as shown by the human ability to shift attention back and forth between global and local levels of visual analysis (Kinchla, Solis-Macias, & Hoffman, 1983; Robertson, 1996; Robertson & Lamb, 1991; Ward, 1982).

Recently, some studies have begun to address the issue of whether nonhuman primates perceive, like humans, the global configuration of the objects prior to analyzing their details or instead integrate the global shapes of the objects from their component parts (Deruelle & Fagot, 1998; Fagot & Deruelle, 1997; Fagot & Tomonaga, 1999; Fagot, Tomonaga, & Deruelle, 2001; Hopkins, 1997; Horel, 1994; Tanaka & Fujita, 2000). Testing baboons in a matching-to-sample task, Fagot and Deruelle (1997) reported a strong local advantage in the processing of hierarchically structured stimuli. This local-to-global precedence persisted even when some physical aspects of the stimuli were manipulated, such as their shape or the connectedness of their local elements. In contrast, human subjects tested with the same compound stimuli used with baboons showed the typical global advantage initially reported by Navon (1977). To shed light on what factors could account for the differences in processing strategies of humans and

baboons, Deruelle and Fagot (1998) carried out a new series of experiments using a visual search procedure in which a target stimulus was presented in a display containing various distractors. Once again, they found an advantage for local processing in baboons and the global precedence effect in humans. Moreover, in the global but not in the local condition, baboons' response times increased linearly with the display size, suggesting that the monkeys were using a more effortful, attentional strategy to detect global targets and a more automatic procedure in perceiving local targets (Deruelle & Fagot, 1998, Experiment 1). In addition, other data from this study (Deruelle & Fagot, 1998, Experiment 4) revealed that changes in stimulus density affected baboons' performance at a global but not at a local level, an effect not found in humans. Monkeys exhibited a local advantage for processing sparse stimuli but no significant global or local advantage for processing dense stimuli, suggesting that they had difficulty in grouping the local elements of hierarchical patterns into a single percept.

A similar effect of the sparsity of local elements on the global perception of compound forms was also reported in chimpanzees by Fagot and Tomonaga (1999). Using the same stimuli and visual search procedure used with baboons (Deruelle & Fagot, 1998, Experiment 4), these authors found in their two subjects an advantage for processing the local shape in the sparse-stimulus condition and no advantage in the dense-stimulus condition. However, the local advantage of chimpanzees turned into a global advantage when the adjacent local elements of the sparse stimuli were connected by line segments. By contrast, in a recent study with macaques, Tanaka and Fujita (2000) found, on the basis of latency measures, that their two monkeys exhibited, like human subjects, a significant global precedence effect as shown by a shorter response time for global than for local tasks. However, a less clear-cut result was obtained in this study when accuracy scores were considered independently from response latencies: Only one of the two macaques showed a global advantage but neither local nor global advantage was observed for the other subject (Tanaka & Fujita, 2000). On the other hand, in the study by Fagot and Deruelle (1997) with baboons, the observed local advantage was reflected also in the lower level of accuracy shown by this species in the conditions requiring the processing of the global shape of compound stimuli, compared with conditions in which the processing of local features was required. Overall, these findings seem to suggest that nonhuman primate species differ in the way in which they process the global or the local form of hierarchical visual patterns.

In the present study, we examined the issue of global versus local advantage in tufted capuchins' (*Cebus apella*) accuracy in the processing of hierarchical stimuli. There is evidence that capuchins' search behavior in large-scale environments is affected by the overall spatial configuration of objects to be explored (De Lillo, Aversano, Tuci, & Visalberghi, 1998; De Lillo, Visalberghi, & Aversano, 1997). This species seems also able to process (as other species of nonhuman primates) abstract relations, such as identity or oddity, in conceptual learning tasks (see Adams-Curtis, 1990, for a review; Meador, Rumbaugh, Pate, & Bard, 1987; see also Tomasello & Call, 1997). However, there is some indication that these New World monkeys have a propensity to process the local rather than the global aspects of visual stimuli. For example, in their study of natural concept formation, D'Amato and van Sant

(1988) reported that capuchin monkeys classify stimuli (slides) into person and nonperson categories at least partially on the basis of absolute local features, such as a flesh-colored patch detected in the picture.

In the present study, we conducted three experiments examining how tufted capuchins processed compound stimuli, using a matching-to-sample task. To allow direct cross-species comparisons, we tested our monkeys with the same hierarchical stimuli as those used with baboons (Deruelle & Fagot, 1998; Fagot & Deruelle, 1997) and chimpanzees (Fagot & Tomonaga, 1999).

Experiment 1

The aim of Experiment 1 was to assess capuchins' ability to process the global and local aspects of hierarchical visual stimuli. We used a simultaneous matching-to-sample task in which the subjects were required to displace a sliding lid to retrieve an item of food.

Method

Subjects. The subjects were three adult tufted capuchins (*Cebus apella*), 2 males, Gal and Pepe, and 1 female, Pippi, ranging in age from 10.10 to 19.05 years. The monkeys lived in two social groups, each housed in an indoor–outdoor cage (indoor: 3.0 m long $\times$ 1.7 m wide $\times$ 3.0 m deep; outdoor: 2.5 m $\times$ 1.7 m $\times$ 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 had food pellets freely available before and after testing; fresh fruit and vegetables were provided after testing. Water was freely available at all times. None of the subjects had previous experience with similar tasks.

Apparatus. The apparatus consisted of a wooden panel (45 cm long $\times$ 35 cm high $\times$ 2 cm thick) with two symmetrical square openings (5 $\times$ 5 cm), each at 10 cm from the center (see Figure 1). The panel was fixed perpendicularly onto a wooden board (45 $\times$ 35 cm), which could be moved forward and backward on a support, mounted on a trolley (50 cm long $\times$ 50 cm wide $\times$ 55 cm high). Three polyvinyl chloride (PVC) lids (6 cm long $\times$ 7 cm high $\times$ 0.3 cm thick) were used for stimulus presentation. Two lids were placed in front of the square openings of the vertical panel. They could be slid laterally in both directions along two parallel metal tracks (45 cm long $\times$ 1 cm high), mounted horizontally on the panel, 1 cm above and below the openings. The third lid was fixed on the panel's tracks, equidistant from the two openings. The apparatus was installed outside the experimental cage (the indoor home cage), behind a transparent Plexiglas panel (45 cm long $\times$ 40 cm high) mounted on the front wall of the experimental cage. The Plexiglas panel had two symmetrical lateral arm holes (15 cm long $\times$ 5.5 cm high) at the level of the bottom edge of the square 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 panel square openings to reach for a peanut. The square openings of the apparatus were positioned at subjects' eye level.

Stimuli. The set of hierarchical stimuli comprised eight compound forms similar to the ones used with baboons and humans by Fagot and Deruelle (1997, Experiment 1). It included large circles, squares, rhombi, or letter *X*s made up of smaller circles, squares, rhombi, or letter *X*s (see Figure 2). We label these stimuli as Cc, Cs, Ss, Sc, Rr, Rx, Xx, 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). All the stimuli measured 4 $\times$ 4 cm at global level and had 12 local elements measuring 0.5 $\times$ 0.5 cm. Stimuli appeared as white shapes on a black
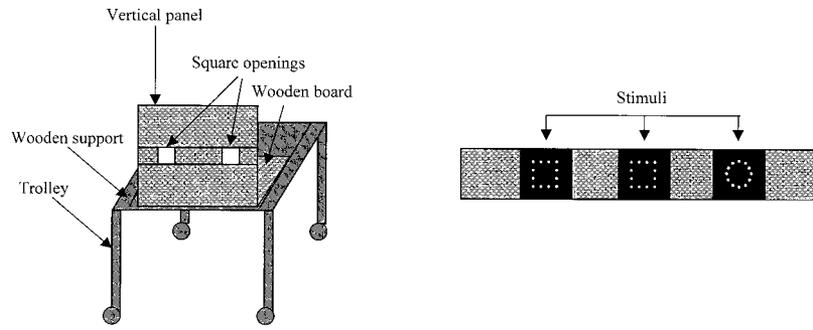
Figure 1. Apparatus (left) and an example of stimulus presentation (right).

background and were created using Microsoft PowerPoint. Each stimulus was printed on paper and was glued onto PVC lids.

General procedure. A simultaneous matching-to-sample procedure was adopted. At the beginning of each trial, the apparatus was placed in front of the experimental cage, at a distance of 30 cm from it. The experimenter placed the sample stimulus between the two square openings of the panel, in full view of the subject. Then, the experimenter placed simultaneously the two comparison stimuli, the matching stimulus (S+), and the nonmatching stimulus (S−), in front of the square openings of the panel, approximately 6 cm on the right and on the left of the sample. The panel was brought nearer to the cage (about 15 cm) within the subject's arm reach. The monkey could obtain the reward only if it moved the lid with the matching stimulus (S+) glued onto it. After the subject moved a

Experiments 1 and 2

Experiment 3

A) Dense

B) Sparse

Figure 2. Stimulus sets used in Experiment 1, Experiment 2, and Experiment 3.

lid, the panel was moved away from the cage, and a new trial was set up. The intertrial interval was approximately 30 s, following a correct response, and approximately 60 s, following an incorrect response.

Training. Before testing the global and local processing of hierarchical stimuli, the monkeys were trained on a simultaneous identity matching-to-sample task with only two noncompound stimuli, the shapes of which were different from those used in global–local experiments. The stimuli (explosion and crossing dart shapes) measured 3 × 3 cm and were printed as white shapes on a black background. During the training, which required several months, each monkey received one daily session of 24 trials, 5 days a week. Within a session, both stimuli appeared as the sample an equal number of times in a quasi-random order, and each comparison stimulus appeared to the left and the right side of the sample with equal frequency. During the early training sessions, a correction procedure was used in which an incorrect trial was repeated until the animal made a correct response. A correction session continued until 12 correct responses were accumulated. When the subjects performed a total number of 15 or less trials on a correction session, the noncorrection 24-trial sessions were administered. The acquisition criterion was 90% or more correct responses on 4 successive noncorrection sessions. The overall number of trials required to meet the acquisition criterion was 310 for Gal, 476 for Pippi, and 1,266 for Pepe.

Transfer tests. Each subject received two transfer tests, each consisting of eight 24-trial daily sessions. In each session, half of the trials were based on the old sample set (to assess the extent to which the original matching performance was maintained), and half on the new one (to assess the transfer), randomly intermixed. In the first test, the old stimuli were those used during the training phase, whereas the new ones were arrow and heart shapes. In the second test, the old stimuli included the new stimulus set used during the first transfer test, whereas the new set included hourglass and round-arch shapes.

In both tests, all the monkeys performed at a very high level of accuracy from the outset. The Stimulus Set × Session analysis of variance (ANOVA) performed on the percentage of correct responses during each transfer test showed that the overall performance level on the novel stimuli did not differ from that observed with the old ones (Transfer Test 1: novel stimuli, 96.2%; old stimuli, 96.9%; Transfer Test 2: novel stimuli, 96.9%, old stimuli, 97.6%).

Global–local test. The global–local test was administered immediately after the completion of Transfer Test 2. Two different 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 its global level. For instance, if the sample was a circle made up of small circles (Cc), S+ was a circle made up of small circles (Cc), whereas S− was a square made up of small circles (Sc). In the *local-matching condition*, S+ was identical to the sample, but S− differed from the sample only by its local elements. For example, when the sample was a square made of small
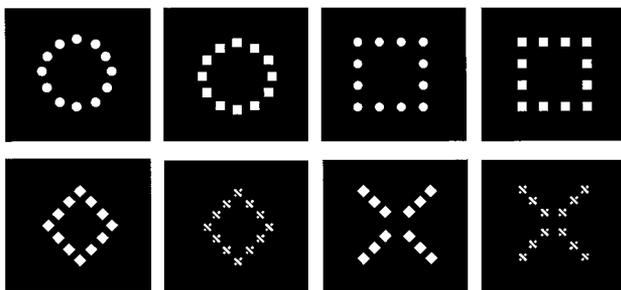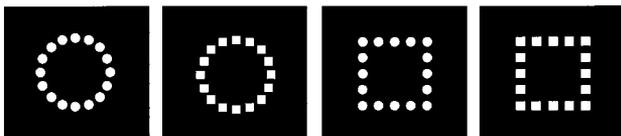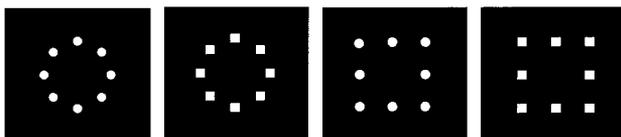
circles (Sc), S+ was also a square made up of small circles (Sc), and S− consisted of a square made up of small squares (Ss).

Each subject performed eight sessions of 24 trials each, one session a day, for a total of 192 trials. One half of the sessions included a combination of circles and squares (Cc, Cs, Ss, Sc), and the other half included rhombi and the letter *X* (Rr, Rx, Xx, Xr). In each session, each stimulus was presented six times as the sample in quasi-random order and each comparison stimulus appeared to the left and right side of the sample with equal frequency. Only the local or the global-matching condition was presented within each session, with trials including consistent sample stimuli (i.e., local and global shapes were identical: Cc, Ss, or Xx, Rr) and inconsistent ones (i.e., local and global shapes were different: Cs, Sc, or Xr, Rx) randomly intermixed. As in the training and transfer tests, no physical restriction was imposed on the animals during the task.

Data analysis. Accuracy scores were the dependent variable. Accuracy was defined as the percentage of correct responses per test condition. Interference between global and local levels was inferred by comparing trials with consistent sample stimuli with those including inconsistent sample stimuli.

Results

The overall mean percentages of correct responses were 79.2%, 87.5%, and 81.8% for Pepe, Pippi, and Gal, respectively (see Table 1, Experiment 1). Two-tailed binomial tests showed that, for each subject, the overall mean number of correct responses was significantly greater than the mean number of errors in both global (Pepe, $z = 3.4$, $p < .001$; Pippi, $z = 5.4$, $p < .001$; Gal, $z = 3.2$, $p < .01$) and local (Pepe, $z = 7.9$; Pippi, $z = 9.1$; Gal, $z = 9.1$; all ps $< .001$) conditions. Moreover, for each monkey, less errors were observed in the local trials than in the global trials: Pepe, $\chi^2(1, N = 40) = 12.1$, $p < .001$; Pippi, $\chi^2(1, N = 24) = 13.5$, $p < .001$; Gal, $\chi^2(1, N = 35) = 24.0$, $p < .001$.

An ANOVA was performed on the percentages of correct responses, with matching condition (global vs. local), stimulus consistency (consistent vs. inconsistent), and stimulus shape (circle–square vs. rhombus–letter *X*) as repeated measures factors. The ANOVA revealed a significant main effect for matching condition, $F(1, 2) = 51.3$, $p < .05$. The performance level was significantly higher on the local trials (94.8%) than on the global trials (70.8%). Other main effects and interactions were not significant.

Table 1
Percentages of Correct Responses for Each Subject in the Local and Global Conditions of Each Experiment

Subject and condition	Experiment 1	Experiment 2	Experiment 3 Dense	Experiment 3 Sparse
Pepe				
Local	90.6	93.7	85.9	87.5
Global	67.7	86.7	89.1	54.7
Pippi				
Local	96.9	90.6	92.2	87.5
Global	78.1	83.6	85.9	59.4
Gal				
Local	96.9	92.2	84.4	89.1
Global	66.7	87.5	96.9	59.4
Overall				
Local	94.8	91.9	87.5	88.0
Global	70.8	85.9	90.6	57.8

Discussion

This experiment demonstrates that capuchin monkeys process the local features more accurately than the global shape of hierarchical stimuli. The consistency of the sample stimulus did not affect the monkeys' performance because the local advantage was always evident regardless of whether the local and the global shapes of the sample were identical.

Overall, our findings concur with those observed by Fagot and Deruelle (1997, Experiment 1) in baboons tested with similar compound stimuli, but with a different matching-to-sample procedure (i.e., sequential matching-to-sample) and apparatus.

A notable finding of the present experiment is that notwithstanding the fact that the monkeys had a protracted exposure to the stimuli (while the tester mounted the stimuli and pushed the apparatus toward the subject) and therefore had plenty of time for visual analyzing and comparing them before responding, all three subjects exhibited a significantly greater difficulty to detect the global aspects of the compound figures. It seems that in capuchins the perception of the local elements of hierarchically organized visual patterns has a clear advantage over the perception of their global structure.

Experiment 2

Experiment 2 was designed to assess the robustness of the results of Experiment 1 by using different arrangements of the stimuli.

Method

Subjects, apparatus, and stimuli. Subjects, apparatus, and stimuli were the same as used in Experiment 1. However, the monkeys were tested with a different within-trial stimulus arrangement. In the global-matching condition, S+ matched the sample only at the global level, whereas S− differed from the sample at both the global and local levels. Thus, if the sample was a large circle made of small circles (Cc), S+ was a large circle made of small squares (Cs), but S− could be, for example, a large rhombus made of small letter *X*s (Rx). In the local condition, S+ matched the sample only at local level, but S− differed from the sample at both levels (e.g., if the sample stimulus was Rr, S+ included Xr, and S− could be Cc).

Testing procedure. Testing occurred immediately after completion of Experiment 1. Each subject performed eight sessions of 32 trials each, one session a day, for a total of 256 trials. Each session included all the eight stimuli quasi-randomly intermixed, with each stimulus being presented four times as the sample within each session and with the constraint that no more than two trials featuring the same sample could be presented consecutively. As in Experiment 1, the local and the global trials were presented in different sessions, with consistent and inconsistent sample stimuli randomly intermixed within each session.

Results

The matching-to-sample performance of each animal is shown in Table 1 (Experiment 2). Overall, each subject performed above chance level in both matching conditions (global condition: Pepe, $z = 8.2$; Pippi, $z = 7.5$; Gal, $z = 8.4$; all ps $< .001$; local condition: Pepe, $z = 9.8$; Pippi, $z = 9.1$; Gal, $z = 9.5$; all ps $< .001$).

The ANOVA (Matching Condition $\times$ Stimulus Consistency) revealed a significant main effect of matching condition, $F(1, 2) = 69.9$, $p < .05$. As in Experiment 1, capuchins showed a better

performance on the local (91.9%) than on the global (85.9%) trials. Moreover, a significant main effect of stimulus consistency was found, $F(1, 2) = 25.9$, $p < .05$. Overall, consistent sample stimuli produced a better performance (89.6%) than the inconsistent ones (88.3%). Finally, a significant Matching Condition × Stimulus Consistency interaction was found, $F(1, 2) = 75.3$, $p < .05$ (see Figure 3). This interaction can be explained on the basis of the results of post hoc comparisons (Tukey's honestly significant difference tests), which revealed that, whereas in the global trials the performance level was higher for consistent (88.5%) than for inconsistent sample stimuli (83.3%, $p < .05$), the same effect was not found in the local trials. Indeed, an inspection of Figure 3 indicates that, in the local condition, inconsistent stimuli were responded to more accurately than consistent ones; however, this difference was not significant. Further post hoc analysis (see also Figure 3) revealed that the main effect of matching condition seems to be accounted for mainly by the higher number of errors registered in the global (83.3%) trials compared with local (93.2%, $p < .05$) trials when the sample stimulus was inconsistent. By contrast, when the sample stimulus was consistent, the difference between global and local trials decreased and the monkeys' performance level became similar in the two matching conditions (local condition, 90.6%; global condition, 88.5%, $p > .10$).

Experiments 1 and 2 differed regarding the arrangement of stimuli within sessions. To better evaluate the effects produced by the changes in the procedure adopted in the two experiments, we conducted an ANOVA to compare, for each matching condition and sample consistency type, the percentages of correct responses observed in Experiment 2 with those recorded in Experiment 1. This analysis revealed a significant main effect of matching condition, $F(1, 2) = 84.0$, $p < .05$, showing an overall advantage of the local ($M = 93.0\%$) over the global ($M = 78.3\%$) condition. Likewise, a significant Matching Condition × Stimulus Consistency × Task interaction was found, $F(1, 2) = 31.4$, $p < .05$. Intertask comparisons (Tukey test) showed that, in both experiments, the monkeys maintained a high performance level when the matching had to be performed at local level for both consistent and

Figure 3. Percentages of correct responses in local and global trials of Experiment 2 as a function of stimulus consistency.

inconsistent sample stimuli (Experiment 1: consistent sample = 95.1%, inconsistent sample = 93.1%; Experiment 2: consistent sample = 90.6%, inconsistent sample = 93.2%; all $ps > .10$). By contrast, performance level was higher in Experiment 2 than Experiment 1, when the monkeys had to match at global level both consistent and inconsistent patterns (consistent sample: Experiment 1 = 71.5%, Experiment 2 = 88.5%, $p < .01$; inconsistent sample: Experiment 1 = 70.1%, Experiment 2 = 83.3%, $p < .05$). Intratask comparisons confirmed the findings reported for each experiment.

Discussion

Overall, the results of Experiment 2 confirmed the local advantage in the processing of hierarchical stimuli observed in Experiment 1. However, in contrast with the results of the previous experiment, we found that the consistency of the sample stimulus affected the monkeys' performance in the global but not in the local trials. These latter results could be interpreted in terms of an effect of local-to-global interference (see Fagot & Deruelle, 1997) and, in the present case, would give further support to the evidence for a supremacy of local processing in capuchin monkeys.

However, because in the present experiment S− did not share any feature with the sample or S+, and considering the very high level of performance observed in the global consistent condition, it would perhaps not be unreasonable to interpret the effect of stimulus consistency in this condition more as a facilitative local-to-global effect than an interference effect. It is possible that, in the global consistent condition, the processing of the local elements of the sample (e.g., circles) primes the processing of the global shape of S+ (e.g., again a circle).

Moreover, we noted that the level of accuracy in the global condition was higher in Experiment 2 than in Experiment 1. By contrast, the level of performance observed in the local condition was not different in the two experiments. It is possible that the different stimulus arrangement used in Experiments 1 and 2 explains these differences in the results. In Experiment 1, the sample stimulus was always identical, at both local and global levels, to the matching comparison stimulus (S+). Moreover, the negative comparison stimulus (S−) was similar, at least in one level, to the sample stimulus. In particular, in the global trials of Experiment 1, S− shared the same local features as S+. Given the monkeys' local advantage in processing compound patterns, it is reasonable to hypothesize that the fact that the local elements of the three stimuli in the global condition were identical might, at times, have induced the animals to respond exclusively on the basis of the local features of the stimuli and therefore to confuse S+ and S−, which both shared these features with the sample.

By contrast, in Experiment 2, the sample stimulus shared only some features with the matching comparison stimulus (S+) and was completely different from S− at both the local and the global level. In the global trials of Experiment 2, therefore, the monkeys could only rely on the global aspects of the stimulus, and S− could not be chosen on the basis of its local features. In other words, in the global trials of Experiment 2, S− might have been a less powerful "distractor" for the animal and might have forced it to attend to the global shape of the sample and S+ (i.e., the only identity relationship between them). Conversely, in the global condition of Experiment 1, the negative comparison stimulus
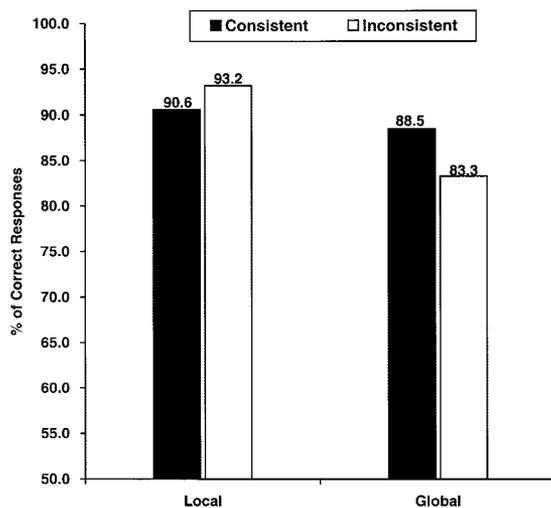
might have been a more powerful distractor, because the local elements were always identical to those of the other two stimuli.

It is also worth noting that the very high level of performance in the local condition of Experiment 1 might have given rise to a ceiling effect and might have contributed to the lack of improvement in the local condition in Experiment 2.

Overall, these findings suggest that the presence of a neutral comparison stimulus aids or produces less interference with perceptual grouping operations in capuchins. Furthermore, with the experimental procedures adopted here, the consistency of local and global shapes of the sample facilitates the detection of the global aspects of hierarchical stimuli in capuchin monkeys.

Experiment 3

As some researchers have argued, some properties of the compound stimuli, such as the density of local elements may strongly affect visual discrimination in nonhuman primates (Deruelle & Fagot, 1998; Fagot & Tomonaga, 1999), an effect found also in humans (Dukette & Stiles, 2001; Martin, 1979). For example, both baboons and chimpanzees show a local advantage for the processing of sparse stimuli but no significant global or local advantage for the processing of dense stimuli. In Experiment 3, we investigated whether manipulations of the density of the local elements of compound stimuli would have affected capuchins' performance.

Method

Subjects, apparatus, and stimuli. Subjects and apparatus were the same as those in Experiments 1 and 2. The stimulus set is presented in Figure 2. It comprised Ss, Sc, Cc, and Cs stimuli varying in local element density. There were two different stimulus-type conditions: a *sparse-stimuli condition*, in which the compound stimuli were composed of 8 local elements and a *dense-stimuli condition*, in which the compound stimuli were composed of 16 local elements. The stimulus size at both local and global level was the same used in the previous experiments.

Testing procedure. Experiment 3 was carried out immediately after Experiment 2. The monkeys were tested using the same identity matching-to-sample procedure of Experiment 1, with S+ identical to the sample at both global and local level and S− differing from the sample either at the global (*global condition*) or local level (*local condition*). Each subject performed eight sessions of 32 trials each, one session a day, for a total of 256 trials. Within each session, half of the trials featured dense stimuli and half featured sparse stimuli, quasi-randomly intermixed, with each stimulus, dense or sparse, being presented four times as the sample within each session. As in Experiment 1, the local and the global trials were presented in different sessions, with consistent and inconsistent sample stimuli randomly intermixed within each session.

Results

Table 1 (Experiment 3) reports the individual performance level for both sparse and dense stimuli, in local and global trials. In the dense-stimulus condition, the monkeys' performance was above chance level in both global (Pepe, $z = 6.1$; Pippi, $z = 5.6$; Gal, $z = 7.4$; all $ps < .001$) and the local (Pepe, $z = 5.6$; Pippi, $z = 6.6$; Gal, $z = 5.4$; all $ps < .001$) matching condition. Conversely, in the sparse-stimulus condition, performance was above chance level in the local condition (Pepe, $z = 5.9$; Pippi, $z = 5.9$; Gal, $z = 6.1$; all $ps < .001$), but not in the global condition (Pepe, $z = 0.6$; Pippi, $z = 1.4$; Gal, $z = 1.4$; all $ps > .10$).

The ANOVA for Matching Condition × Stimulus Consistency × Stimulus Type (dense vs. sparse) revealed a significant main effect of matching condition, $F(1, 2) = 28.0$, $p < .05$, with an overall advantage for the local (87.7%) over the global (74.2%) trials. There was also a significant main effect of stimulus type, $F(1, 2) = 3,904.2$, $p < .001$. The mean percentage of correct responses was higher for dense stimuli (89.0%) than for sparse stimuli (72.9%). Moreover, the Matching Condition × Stimulus Type interaction was significant, $F(1, 2) = 75.3$, $p < .05$. Post hoc analyses (Tukey test) showed that the local advantage emerged for sparse stimuli (local = 88.0%, global = 57.8%, $p < .05$) but not for dense stimuli (local = 87.5%, global = 90.6%, $p > .10$). Furthermore, for the global, but not for the local-matching conditions, the sparse stimuli gave rise to the largest number of errors ($p < .05$). No other main effects or interactions were significant.

To further evaluate the role played by stimulus density on local–global processing, we compared capuchins' accuracy scores in Experiment 3 with those observed in Experiment 1, which involved a similar identity matching-to-sample procedure, but an intermediate density (labeled *medium*) of local elements compared with the sparse and the dense conditions used in the present experiment. A Matching Condition × Stimulus Consistency × Stimulus Type ANOVA (dense–medium–sparse) revealed a significant main effect of matching condition, $F(1, 2) = 1,067.0$, $p < .001$. Overall, a higher level of performance was observed in the local (89.9%) than in the global (73.1%) trials. Furthermore, a significant main effect of stimulus type emerged, $F(2, 4) = 56.0$, $p < .01$, showing that the rate of correct responses increased with higher stimulus density (sparse: 72.9% < medium: 82.5% < dense: 89.0%; see Figure 4). Moreover, a significant Matching Condition × Stimulus Type interaction was found, $F(2, 4) = 13.6$, $p < .05$. Post hoc analyses (least significant difference test) revealed a significant local advantage in the sparse (local = 88.0%, global = 57.8%, $p < .01$) and in the medium condition (Experiment 1, $p < .01$) but no significant difference between the local and the global trials for the dense condition (local = 87.5%, global = 90.6%). Additionally, separate trend analyses carried out for the local and the global trials on the three levels of stimulus density revealed that, in the global matching trials, the performance level decreased linearly with the sparsity of local elements, $F(1, 2) = 100.3$, $p = .01$. In particular, as revealed by post hoc tests, performance was better for dense stimuli than for medium ($p < .05$) and sparse stimuli ($p < .01$). Finally, an almost significant difference emerged between the percentage of correct responses for medium and sparse stimuli ($p = .052$, see Figure 4). By contrast, no significant linear trend was observed for the local trials.

Discussion

The results of Experiment 3 show that the capuchin monkeys' ability to process the global shape of hierarchical stimuli is affected by the density of their local elements. The monkeys did not exhibit any global or local advantage when the stimuli included several local elements (dense stimulus): In this condition, their discriminative performance was highly accurate at both levels. In contrast, the animals exhibited a clear local advantage when the stimuli involved fewer elements (sparse stimulus), basing their similarity judgments mainly on local level information. The com-
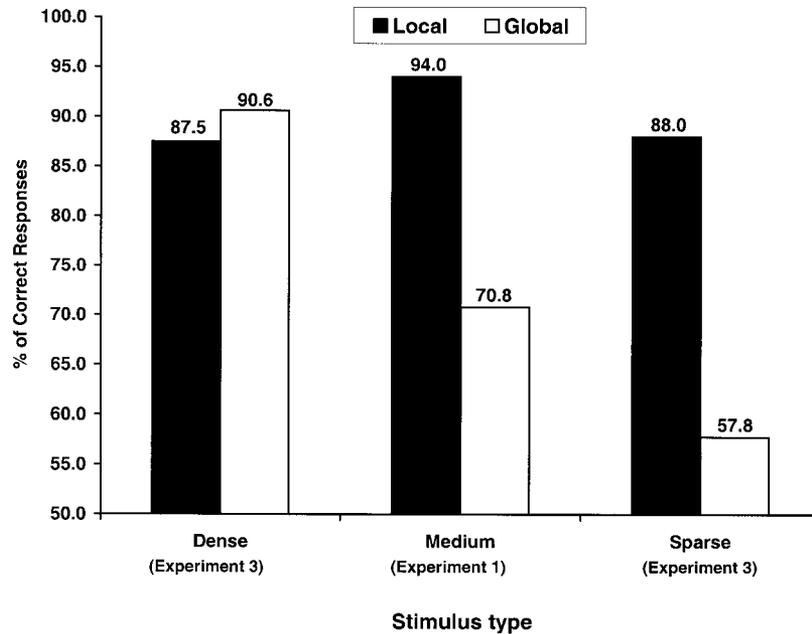
Figure 4. Percentages of correct responses in local and global trials as a function of stimulus density.

parison between Experiments 1 and 3 showed that the ability to attend to global shapes was linearly affected by increases in interelement distance of the component parts, suggesting that the processing of the global stimulus level involves a perceptual grouping operation. The observed local advantage in the processing of hierarchical patterns with fewer elements seems to reflect an increasing difficulty for capuchin monkeys in integrating the local parts into global coherent wholes.

General Discussion

We reported three experiments showing that the manipulation of the arrangement or the density of component parts of hierarchical stimuli strongly affected capuchin monkeys' ability to detect the global shape of the stimuli but not the accurate processing of their local elements. In Experiment 1, the monkeys exhibited a local advantage and no global-to-local or local-to-global interference in an identity matching-to-sample task, in which one of the two comparison stimuli was identical to the sample at both levels (local and global) and the other was different from the sample at one stimulus level only.

The results of Experiment 2, in which one of the two comparison stimuli was identical to the sample at either global or local level and the other did not share any similarity with the sample, confirmed the supremacy of local processing observed in Experiment 1. Moreover, in Experiment 2 a significant effect of stimulus consistency in the global trials emerged. In particular, trials featuring a consistent sample stimulus were responded to at a higher level of accuracy than trials featuring an inconsistent sample stimulus. Because in Experiment 2, S− did not share any feature with the sample or S+, it would be difficult to interpret this latter result in terms of a local-to-global interference leading to a decrement in performance in inconsistent trials. More likely, as we argued in the discussion of Experiment 2, the same result could be

interpreted as caused by a facilitative effect in the consistent condition, produced by the similarity between the shape of the local elements of the sample stimulus and the global shape of S+. According to this interpretation, the shape of the local elements of the sample stimulus would prime the global shape of S+. Given the very high level of performance observed in the global trials of Experiment 2 compared with the performance observed in the same trials in Experiment 1, we consider this second explanation more convincing. Regardless of which of these two interpretations is favored, the results of the first two experiments indicate a clear advantage in capuchin monkeys for the processing of the local features of hierarchical stimuli.

Because our results were based on accuracy measures, we discuss them in relation to other studies that reported accuracy scores on global–local processing in primates. The local advantage observed here in capuchins seems to be consistent with similar findings observed in baboons (Fagot & Deruelle, 1997). Moreover, it provides evidence for a local advantage in monkeys, which showed a high level of accuracy across the different conditions of the experiments. However, our results differ from those obtained by Tanaka and Fujita (2000) with two macaques. In this latter study, one monkey showed a global advantage in accuracy scores, whereas the other failed to show either a local or a global advantage. It is, however, worth noting that the global and local forms of visual stimuli used by Tanaka and Fujita (2000) differed in orientation rather than shape. Moreover, they were smaller at a local and global level than those used by us and by Fagot and Deruelle (1997), and the size of the stimuli might well play a role in the inversion of the processing advantage from one level to the other (see, e.g., Kinchla & Wolfe, 1979). A lack of global or local superiority has also been observed in chimpanzees that obtained very high levels of performance in both the local and the global condition of a visual search task (Fagot & Tomonaga, 1999,

Experiment 1) featuring hierarchical stimuli similar to those adopted here. As such, the different patterns of results obtained with monkeys and apes could be indicative of a cognitive difference between these taxa.

However, as a cautionary note, it is worth pointing out that whereas both our study and that of Fagot and Deruelle (1997) were based on a matching-to-sample task, Fagot and Tomonaga (1999) used a visual search task and Tanaka and Fujita's (2000) task was based on the presentation of a single compound stimulus. In this latter study, the monkeys had to learn, by trial and error, which stimulus level was relevant in a particular condition, and test trials occurred only after the monkeys had achieved a 90% correct learning criterion. Given the procedural differences between these studies, it would perhaps be premature to draw very strong conclusions about major interspecies differences.

The high level of accuracy observed in all the conditions of Experiments 1 and 2 suggests that, although capuchins show a marked superiority in the processing of local features of hierarchical stimuli, they successfully engage in global processing as well.

Because our experimental setup did not allow the manipulation of variables related to the duration of the presentation of the stimuli and did not allow the recording of response latencies, it is not possible to discuss the temporal order of processing of local and global information. However, given that the procedure adopted here involved a lengthy presentation of the stimuli in each trial, some inferences can be drawn concerning the relative stability of the local advantage in this species. The only study of which we are aware that addressed directly the problem of the stability of the priority of particular forms of processing in hierarchical stimuli in animals was recently conducted on pigeons and provided some evidence for a shift from local to global advantage when the duration of the stimulus presentation was increased from 750 ms to 5s (Cavoto & Cook, 2001). In our study, the duration of the presentation of the stimuli was much in excess of 5 s. It seems, therefore, that the local advantage exhibited by our subjects was relatively stable and immune from the variability that can be generated by the protracted exposure to the stimuli.

The extent to which the perception of the local and the global features of hierarchical stimuli was affected by the density of the local elements of the compound figures was evaluated in Experiment 3. There emerged again an overall advantage of local processing. However, it is interesting to note that, in the dense-stimulus condition, in which the spatial proximity and the number of local elements was increased, the superiority of local processing disappeared and the monkeys reached very high levels of performance in both the local and the global conditions. The disappearance of the local processing superiority when the density of the local elements is increased was also observed by Deruelle and Fagot (1998) in baboons tested with hierarchical stimuli in visual search tasks. However, when tested with hierarchical stimuli in a matching-to-sample task, the same animals (Fagot & Deruelle, 1997) showed a local superiority even when the global shape of the stimulus was emphasized by connecting the local elements of the figure with a continuous line. By contrast, our monkeys' sensitivity to the global aspects of the stimulus became similar to their sensitivity to the local features of the stimulus under the appropriate manipulations of stimulus density.

The other results obtained from Experiment 3 showed that the sparsity of the elements was critical for the detection of the global features of the hierarchical stimuli. In fact, in trials in which sparse stimuli were presented, the performance of the monkeys in the global condition fell to chance level. A decrease in performance in global processing for sparse stimuli has also been reported in chimpanzees (Fagot & Tomonaga, 1999), although this decrease resulted when using a different implementation of the task (visual search), and it was not as dramatic as the decrement in accuracy we observed here in capuchin monkeys.

When the results obtained in Experiment 1, which featured an intermediate stimulus density compared with the dense and sparse conditions of Experiment 3, were analyzed in conjunction with the results obtained from Experiment 3, a linear trend emerged in the monkeys' ability to detect the global features of the stimuli as a function of the density of their constituent elements. By contrast, the processing of the local features of the stimuli was robust enough to produce a high performance across variations of stimulus density.

These findings are compatible with recent comparative studies that revealed differences between humans and nonhuman species in their capacity for perceptual grouping. For example, when perceiving illusory figures such as the Kanizsa square, chimpanzees are much more sensitive than humans to element separation (Fagot & Tomonaga, 2001). Similarly, a reduced capacity for grouping by proximity has been reported in rats when bistable arrays of disjunct dots were used as stimuli (Kurylo, Van Nest, & Knepper, 1997).

In conclusion, our results support those of other studies in which a superiority for the processing of local information in hierarchical figures emerged in animals (Cavoto & Cook, 2001; Fagot & Deruelle, 1997). Although very convincing claims concerning the adaptive value of global precedence in the processing of visual information have been put forward (Navon, 1977), and there is clear evidence that priority is given to the processing of the overall spatial structure of the environment over the analysis of the featural details of the objects included in it (see, e.g., Cheng, 1986), results like ours (Cavoto & Cook, 2001; Fagot & Deruelle, 1997) challenge the generality of early claims concerning the adaptive value of global precedence in the processing of hierarchical figures (Navon, 1977).

It is indeed possible that the relative advantage in the processing of the spatial structure of a configuration of elements or the local features of the elements themselves is task specific and under the influence of ecological pressures experienced by particular organisms. Perhaps, for the cognitive evolution of some species it could have proved detrimental to renounce to the accurate identification of the constituent elements of, for example, seeds scattered on the ground in favor of the analysis of the global shape formed by their arrangement. A challenge for further research would, therefore, be the characterization of the range of circumstances and organisms to which a local or a global processing advantage pertain.

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