Attention Allocation Modulates the Processing of Hierarchical Visual Patterns: A Comparative Analysis of Capuchin Monkeys (*Cebus apella*) and Humans

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Humans show a global advantage when processing hierarchical visual patterns, and they detect the global level of stimulus structure more accurately and faster than the local level in several stimulus contexts. By contrast, capuchins (*Cebus apella*) and other monkey species show a strong local advantage. A key factor which, if manipulated, could cause an inversion of this effect in monkeys is still to be found. In this study, we examined whether it was possible to induce attention allocation to global and local levels of perceptual analysis in capuchin monkeys and if by doing so, their local dominance could be reversed. We manipulated attentional bias using a matching-to-sample (MTS) task where the proportion of trials requiring global and local processing varied between conditions. The monkeys were compared with humans tested with the same paradigm. Monkeys showed a local advantage in the local bias condition but a global advantage in the global bias condition. The role of attention in processing was confined to the local trials in a first phase of testing but extended to both local and global trials in the course of task practice. Humans exhibited an overall global dominance and an effect of attentional bias on the speed of processing of the global and local level of the stimuli. These results indicate a role for attention in the processing of hierarchical stimuli in monkeys and are discussed in relation to the extent to which they can explain the differences between capuchin monkeys and humans observed in this and other studies.

Keywords: global–local, attention, primates, perception, *Cebus apella*

A central issue in visual cognition concerns the characterization of the factors involved in the processing of the relationship between wholes and their component parts. An extremely affluent body of literature indicates that in humans, the processing of the global configuration of a collection of elements precedes the analysis of the individual elements (e.g., Kimchi, 1998; Kinchla & Wolfe, 1979; Martin, 1979; see also Kimchi, 2003, for a review). Research on this topic has been fuelled by a now classic study by Navon (1977) carried out using hierarchical visual patterns featuring a larger global shape formed by the spatial arrangement of smaller elements. Navon found that human participants identified the global structure of stimuli faster and more accurately than their local components and that conflicting information between the global and the local level of stimuli produced asymmetrical global-to-local interference. These findings have been interpreted as supporting the notion that global processing precedes the more fine-grained perceptual analyses of details. Importantly, Navon (1977) proposed a number of general advantages for this order of processing, which include the "utilization of low-resolution information, the economy of processing resources and the disambiguation of indistinct details" (Navon, 1977, p. 381). He also suggested that the global precedence should be an inherent property of visual perception rather than of post-perceptual processes of selective allocation of processing resources (Navon, 1977).

These assumptions of general utility and automaticity of the global advantage encouraged the assessment of the generality of the global advantage from a comparative standpoint. The comparative study of global–local processing was pioneered by a study by Fagot and Deruelle (1997), which showed that, in contrast with humans, baboons (*Papio papio*) show an

advantage for the processing of the local level of hierarchical stimuli.

Comparative research in this area has now been conducted on a number of nonprimate species including fish (Truppa, Sovrano, Spinozzi & Bisazza, 2010) and pigeons (Cavoto & Cook, 2001; Goto, Wills & Lea, 2004; Fremouw, Herbranson & Shimp, 1998, 2002), with results indicating sometimes a local and sometimes a global advantage, as a function of the species and the experimental procedure used. Nevertheless, a more coherent pattern of results emerges from a review of the now substantial body of literature assessing global and local processing in primates.

The study of global–local visual processing is particularly important in nonhuman primates since they share very similar visual systems with humans (De Valois & De Valois, 1988; Fobes & King, 1982; Merigan & Maunsell, 1993). Moreover, given the phylogenetic relatedness of human and nonhuman primates, the comparison of primate species with a different degree of taxonomic distance from humans can potentially provide information about the emergence of human visual cognition. With some exceptions (Neiworth, Gleichman, Olinick & Lamp, 2006; Tanaka & Fujita, 2000; Tanaka, Onoe, Tsukada & Fujita, 2001), several monkey species, such as capuchins (De Lillo, Spinozzi, Truppa & Naylor, 2005; Spinozzi, De Lillo & Salvi, 2006; Spinozzi, De Lillo & Truppa, 2003), baboons (Deruelle & Fagot, 1998; Fagot & Deruelle, 1997), and macaques (Hopkins & Washburn, 2002), show a local processing advantage, which contrasts with the global advantage observed in humans. An intriguing piece of evidence, which emerges from the literature on global and local processing in primates, is that the presence of a local advantage is less clear in apes than in monkeys. To our knowledge, chimpanzees are the only apes tested with hierarchical stimuli, and some studies report a global advantage in this species (Hopkins & Washburn, 2002) while others have observed some individual variability, with one chimpanzee out of two showing a local advantage and no specific advantage observed in the other (Fagot & Tomonaga, 1999). The reasons for these inconsistencies in the results reported for chimpanzees are still unclear. They could be due to differences in the procedures used in different studies or they could be an expression of genuine interspecies differences, suggesting a trend in the emergence of a global advantage, which parallels the distance of common ancestors shared by humans and other primate species.

A potentially important factor for the explanation of the variability in the results obtained in different studies is the density (defined in terms of spatial separation between individual local elements) of the stimuli employed. Fagot and Tomonaga (1999) argued that the global advantage observed in chimpanzees may have been due to the high density of the stimuli used there. It has been argued that the global advantage occasionally observed in macaques also could be accounted for by this factor (see Fagot & Barbet, 2006 for a discussion). Dense stimuli were also used in the only study to date to report the emergence of a global advantage in a New World monkey species, the cotton-top tamarin (*Saguinus oedipus*), which nevertheless disappeared when more sparse stimuli were employed (Neiworth et al., 2006). However, the sensitivity to the spatial separation of the items cannot be the main explanation for the presence of a local advantage in monkeys.

Studies specifically aimed at addressing this possibility by systematically manipulating the density of the stimuli have confirmed a local advantage in baboons (Deruelle & Fagot, 1998) and capuchin monkeys (Spinozzi et al., 2006) and a robust global advantage in humans (Deruelle & Fagot, 1998; Fagot & Tomonaga, 1999; Neiworth et al., 2006).

The relative readiness to process the global aspect of hierarchical visual patterns has been put in relation with different attentional requirements imposed by the processing of the global structure of stimuli in humans and monkey. In a visual search study with hierarchical stimuli, Deruelle and Fagot (1998) found that RT slopes were affected by the number of distracters in conditions requiring the processing of the global level of the stimuli in baboons but not in humans, and suggested that global processing may require attentional resources in monkeys but may occur preattentively in humans. This result would be consistent with those of other studies which have compared the ability of humans and capuchin monkeys to use visual grouping cues to segregate figures and backgrounds in a matching-to-sample (MTS) task (Spinozzi, De Lillo, Truppa & Castorina, 2009). There it emerged that humans used grouping by proximity seemingly without effort as their performance was similar when they were required to use this grouping cue and in conditions where no grouping was required. By contrast, capuchin monkeys performed less efficiently in conditions requiring grouping by proximity than conditions, which did not require any grouping. It is however not possible to estimate the extent to which these interspecies differences in grouping by proximity can be explained by the amount of attention required by the two species given the procedures used by Spinozzi et al. (2009), which were not designed to assess the role of this factor.

Several results reported in the literature on human visual cognition indicate that grouping by proximity in humans does require attentional resources (Ben-Av, Sagi & Braun, 1992; Mack, Tang, Tuma, Kahn & Rock, 1992), and it is possible that it does do so in monkeys. If this were the case, a different spontaneous use of attention allocation or a differential availability of attentional resources could also contribute to the differences between monkeys and humans in the processing of different structural levels of visual stimuli. To our knowledge, there are not any studies which have used procedures inducing the allocation of attention to one or the other of the two levels of hierarchical visual stimuli in monkeys. A comparative assessment of the role played by attention in this domain would be particularly useful as the possible participation of a number of other factors in the observed differences between humans and monkeys have now been ruled out. For example, we know that these differences cannot be explained by a preferential processing of stimuli of a particular size in the two species (Spinozzi et al., 2006) or a reduced ability in monkeys, compared to humans, to appreciate the spatial relationship between the constituent parts of visual patterns (De Lillo, Spinozzi & Truppa, 2007). In fact, in MTS tasks, humans and capuchin monkeys are both negatively affected by manipulations which disrupt the spatial relationships between stimulus parts but not by rotations of the stimulus which preserve these relationships (De Lillo et al., 2007).

In humans, the relative efficiency of global and local processing can be modulated by attention as the allocation of attention to one level of structure of hierarchical visual stimuli

can increase the speed of processing of that particular level (Kinchla, Solis-Macias & Hoffman, 1983; Lamb & Robertson, 1987, 1988; Miller, 1981; Robertson, Egly, Lamb & Kerth, 1993; Ward, 1982). Moreover, humans can repeatedly switch the focus of attention to the global and local features of stimuli as shown by faster responses to targets at either local or global levels following the priming of that level. Such priming effects have been examined with hierarchical stimuli by varying the proportion of trials which required attending to a particular level of stimulus structure within trial blocks (Kinchla et al., 1983; Lamb & Robertson, 1987), or by presenting a cue indicating that a target shape was more likely to occur at a particular level of stimulus structure (Robertson et al., 1993). The fact that attention can be allocated selectively to a particular level of a hierarchical structure (by enhancing processing at that level and/or hindering processing at the other level) has been interpreted as being due to a mechanism based on a spatial allocation of attention. Using the "spotlight" metaphor of attention, some investigators argued that the efficiency of responding to either levels of a compound pattern can be affected by variations in the diameter of the "spotlight" (Lamb & Robertson, 1988; Robertson et al., 1993; Ward, 1982). According to this hypothesis, the processing of global targets is facilitated when the attended area is relatively large (the size of a global form), whereas the processing of local targets is facilitated when the attended area is relatively small (the size of a local form). This has been referred to as *regional* selection (Robertson et al., 1993). Others have proposed the "zoom lens" as a more appropriate metaphor for describing the functional attributes of visual attention, which implies a change in the spatial extent of the visual field at which attention is focused (Eriksen & St. James, 1986; Stoffer, 1993, 1994). Both accounts claim that processing resources are distributed in such a way that the stimulus level within the focus of attention benefits from more attentional resources than the stimulus level outside it.

The use of visual search paradigms has been commonly used in animal studies to assess whether the processing of particular stimuli or level of processing is attention demanding or not (Blough, 1993; Deruelle & Fagot, 1998; Tomonaga, 2001; Washburn & Tagliatella, 2006). More recent studies have attempted to induce directly the allocation of attention to particular levels of stimulus structure using priming procedures. For example, Fremouw, Herbranson, and Shimp (1998) tested pigeons with Navon-type stimuli and showed that biasing targets at a particular level facilitated the processing of targets at that level. Further experiments (Fremouw et al., 2002) demonstrated that pigeons could display highly dynamic stimulus-driven shifts of local–global attention when a priming cue was presented before each trial, the color of which probabilistically predicted the level of the following target. Overall, these studies show that pigeons, like humans, can selectively attend to different stimulus dimensions and can shift attention between different levels of visual analysis.

The extent to which it is possible to induce monkeys to shift attention between levels of processing is still to be determined. More importantly, the question remains to be answered concerning whether the selective allocation of attention to particular levels of stimulus structure may determine a reversal of the local advantage systematically reported for some primate species.

The aim of this study is to evaluate the role of attention in the global–local processing of capuchin monkeys (*Cebus apella*) in comparison to humans (*Homo sapiens*). The use of capuchin monkeys for this investigation is particularly appropriate since their strong local advantage is well documented (De Lillo et al., 2005; Spinozzi et al., 2003; Spinozzi et al., 2006) and the search for a single key factor which may explain why this species shows a different processing mode to that of humans has proved difficult (De Lillo et al., 2007; Spinozzi et al., 2009). In fact, the local advantage in capuchin monkeys cannot be reversed or reduced by manipulations of some stimulus-related variables that are known to affect global/local processing in humans (Kimchi, 1998; Kinchla & Wolfe, 1979; Martin, 1979), such as the visual angle subtended by the stimuli or the number and relative size of the stimulus component elements (Spinozzi et al., 2006).

Asymmetrical properties in the allocation of attention to the global and local level of compound stimuli have been suggested as a mechanism for the explanation of the emergence of the global dominance in humans (Stoffer, 1993). It is therefore possible that they could affect the local dominance observed in this monkey species.

In the experiments reported here, we examined the ability to shift attention between different levels of hierarchical stimuli in monkeys (Experiment 1) and humans (Experiment 2) in a MTS task featuring manipulations of the relative frequency of trials requiring the processing of either the global or the local level of the stimulus within a testing session. Our aims were, first of all, to assess whether the observed differences between humans and capuchin monkeys in their mode of processing hierarchical forms could be understood better on the basis of a different capability in the allocation of attention to a particular level of hierarchical structure. Second, we aimed to assess whether the local advantage systematically observed in this species (De Lillo et al., 2005; Spinozzi et al., 2003; Spinozzi et al., 2006) could be reversed under appropriate conditions which affected the allocation of attention to a given level of processing.

Experiment 1

Experiment 1 aimed at evaluating the extent to which capuchin monkeys were able to switch their attention between the different levels of hierarchical stimuli on a simultaneous MTS task. We tested the monkeys with the same set of stimuli used previously by Spinozzi et al. (2003) with capuchin monkeys and by De Lillo et al. (2005) in a comparative study of monkeys and preschool children. In order to examine the role of attention in the processing of hierarchical patterns, we varied the proportion of trials in which the information required to solve the task was at the local or the global level of the stimuli in different conditions. In one condition (local bias), trials requiring the local processing of the stimulus were more likely to occur than trials requiring its global processing and, in another condition (global bias), global processing was required more often than local processing. The comparison of the levels of performance between global and local trials under different bias conditions could reveal the relative ease, or the relative difficulty, in allocating attention to a particular level of the stimuli in this species.

Method

Subjects

The subjects were five adult tufted capuchins (*Cebus apella*), 4 males (Gal, Patè, Rubens and Vispo) and 1 female (Pippi) ranging in age from 7.5 to 28.0 years. All the monkeys were born in captivity. They lived in three social groups, each housed in an indoor–outdoor enclosure (indoor: 5 m² × 2.5 m high; outdoor: 40–130 m² × 3.0 m high) at the Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche (CNR), Rome. Capuchins were tested individually in an experimental cage (0.76 m long × 1.70 m wide × 0.73 m high), which they could access through a sliding door from their adjacent indoor enclosure. Each subject was separated from the group immediately before each daily testing session and only for the duration of the testing. 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.

Two monkeys (Gal and Pippi) had previously served in studies on the processing of hierarchical stimuli (De Lillo et al., 2005; Spinozzi et al., 2006). The remaining three subjects had never been presented with this type of visual pattern before. However, they were already familiar with the MTS procedure, having been previously tested on pattern discrimination and categorization problems using MTS (Spinozzi et al., 2009; Truppa, Spinozzi, Stegagno & Fagot, 2009). The research protocol for this study was approved by the Italian Health Ministry.

Apparatus

The apparatus is presented in Figure 1. It consisted of a vertical wooden panel (45 cm long × 35 cm high × 2 cm deep) with two lateral wooden walls (35 cm long × 35 cm high × 2 cm deep). It was fixed perpendicularly onto a wooden board (45 cm × 35 cm), which could be moved forward and backward on a support, which was mounted on a trolley (50 cm long × 50 cm wide × 55 cm high). The vertical panel had 2 symmetrical, rectangular openings (5 cm long × 9 cm high), each 10 cm from the center. Three
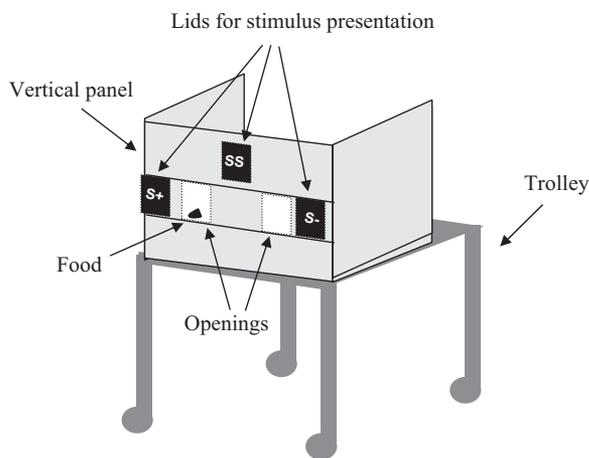

Figure 1. A schematic representation of the apparatus used in Experiment 1. See text for details.

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 two comparison stimuli were placed on these two sliding panels. The third lid, into which the sample stimulus could be placed, was fixed in the center of the vertical panel, between the two openings and equidistant from them. The apparatus was placed in front of the experimental box behind a transparent Plexiglas panel (45 cm long × 40 cm high) mounted on the front wall of the experimental box. The Plexiglas panel had two symmetrical lateral armholes (15 cm long × 5.5 cm high) at the level 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 order to retrieve a peanut. The rectangular openings of the apparatus were positioned at the subjects' eye level.

Stimuli

The stimuli used in this experiment are presented in Figure 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 the eight compound forms used by Fagot and Deruelle (1997) with baboons and subsequently by Spinozzi et al. (2003) with capuchin monkeys. The set of stimuli included large circles (C), squares (S), rhombi (R), or letter *X*s (X) made up of smaller circles (c), squares (s), rhombi (r), or letter *X*s (x). The shape of the global level could be identical (consistent stimuli) or it could be different (inconsistent stimuli) from the shape of the local level. All the stimuli measured about 4 × 4 cm at global level and had 12 local elements measuring about 0.5 × 0.5 cm. Capuchins viewed the stimuli from approximately 30 cm. At this distance, the stimuli subtended about 7° of visual angle at global level and 0.9° at local level.

Procedure

The experiment was based on an identity-MTS task. At the beginning of each trial, the apparatus was placed in front of the experimental box, at a distance of about 30 cm. The experimenter, while standing behind the trolley in a central position, placed the sample stimulus (SS) at the center of the panel and the two comparison stimuli, the matching stimulus (S+) and the nonmatching stimulus (S−), on the sliding lids covering the rectangular openings of the panel, in full view of the animal. Finally, he placed the reward behind the lid featuring the matching comparison stimulus (S+) and moved the panel within the subject's arm reach, at about 15 cm from the front wall of the experimental box.

The hands of the experimenter were always occluded by the apparatus and out of view of the subjects when placing the reward. Only the upper part of the body was visible to the animal. As a precaution measure, the experimenter moved both hands simultaneously behind the sliding lids when placing the bait, in the unlikely event that particular movements of the neck or shoulders could provide spurious cues to the animal concerning the location of the bait. The experimenter was trained to keep their head in a fixed position while looking ahead once the baiting had occurred
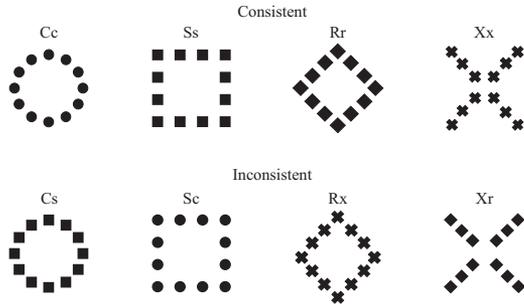
Figure 2. Set of stimuli used in the experiments.

and until the subject made a response. The monkey could obtain the reward only if it moved the lid featuring the matching stimulus (S+). After the monkey had moved one of the two lids with either hand, the panel was moved away from the box. Trials were separated by an interval of about 30 s, during which the experimenter recorded the choice and selected stimuli for the next trial.

There were two types of identity-matching trials. In the *global trials,* S+ was identical to the sample and S− differed from the sample only at the global level. In the *local trials,* S+ was identical to the sample, but S− differed from the sample only for local elements. An example of global and of a local trial is presented in Figure 3.

Two different bias conditions were presented to the subjects. In the *global bias condition,* 85.7% of trials required the processing of the global level of the stimuli (i.e., global trials) and the remaining 14.3% of trials required the processing of the local level of the stimuli. In the *local bias condition,* these probabilities were reversed (i.e., 85.7% local trials, 14.3% global trials).

Each subject performed 16 sessions of 28 trials each, one session a day, for a total 448 trials. Either the global bias or the local bias condition was presented in each session, with trials requiring global matching (i.e., global trials) and local matching (i.e., local trials) randomly intermixed. For each condition, one half of the trials included consistent sample stimuli in which the local and global shapes were identical (Cc, Ss, Rr and Xx), and the other half included inconsistent sample stimuli in which the local and global shapes were different (Cs, Sc, Rx and Xr) pseudorandomly intermixed. This ensured that the same comparison could not be presented more than twice consecutively and that S+ and

S− appeared on each side equally often. The counterbalancing of left and right presentation of each type of comparison stimulus was obtained across sessions. Global bias and local bias conditions were alternated every 4 sessions. For two subjects, the first 4-session block was the local bias condition, whereas for the remaining monkeys it was the global bias condition.

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. In those testing sessions where the subject stopped responding during testing, the session was interrupted and the data of the whole session were excluded from the analysis. This only happened on five occasions. No physical restriction was imposed on the animals at any time.

Results

The percentage of correct responses recorded by each individual and by the group of animals in the different conditions of Experiment 1 is reported in Table 1.

One-sample *t* tests showed that the percentage scores obtained by the group of monkeys for each type of trials in the different conditions were significantly above the 50% expected by chance (local bias local trials, $t(4) = 13.26$, $p < .001$; local bias-global trials, $t(4) = 5.88$, $p < .01$; global bias-local trials, $t(4) = 3.86$, $p < .05$; global bias-global trials, $M = t(4) = 20.49$, $p < .001$).

Binomial tests carried out on the frequencies of correct responses observed in each individual for the global and the local trials, combining the two bias conditions, confirmed that all the subjects responded correctly above the .5 proportion expected by chance in both types of trials (all ps $< .01$). There were not obvious individual differences between the two subjects (Gal and Pippi) who had previously been involved in similar studies and the three subjects that had not been previously tested using this task (Paté, Rubens, and Vispo).

The graph presented in Figure 4 shows the bias condition, reported on the horizontal axis, and the overall percentage of correct responses recorded in the local and global trials as separate
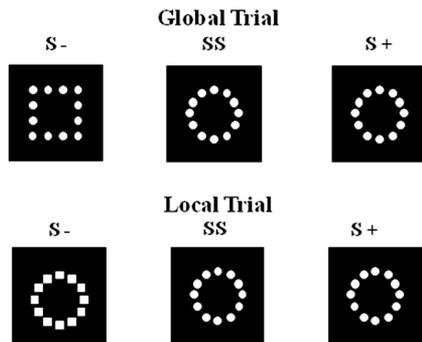

Figure 3. An example of a local and a global trial. See text for explanation.

Table 1

Percentages of Correct Responses Shown by Each Individual Monkey for the Global and Local Trials in the Local and Global Bias Condition

	Local bias		Global bias		Combined	
	Local trials	Global trials	Local trials	Global trials	Local trials	Global trials
Gal	85.4	75.0	59.4	82.3	72.4	78.7
Vispo	81.8	68.8	56.3	77.6	69.1	73.2
Pippi	86.5	81.3	77.8	81.5	82.2	81.4
Patè	81.8	71.9	62.5	75.5	72.2	73.7
Rubens	72.9	59.4	65.6	76.0	69.3	67.7
Mean	81.7	71.3	64.3	78.6	73.0	74.9

Note. The mean percentage of local and global trials obtained by combining the values for the two bias conditions is also shown.
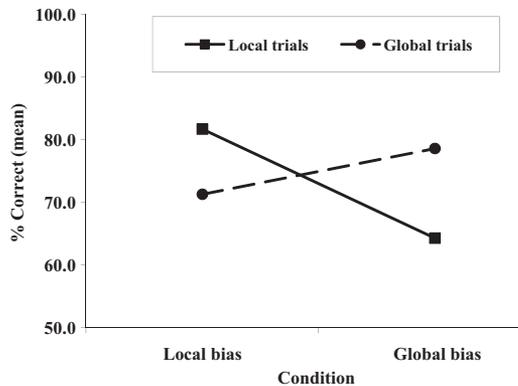
Figure 4. Percentage of correct responses recorded in the local and global trials, in the local bias condition and in the global bias condition performed by monkeys in Experiment 1.

lines. An inspection of the graph clearly shows a cross-over of the two lines, which suggests that attention bias had an effect. Moreover, Figure 4 provides a first graphical illustration, in the global bias condition, of a reversal of the local advantage that has so far been observed in capuchin monkeys.

This effect was confirmed by the results of a 2 × 2 × 2 [Bias Condition (global bias, local bias) × Level of Processing (global trials, local trials) × Stimulus Consistency (consistent, inconsistent)] repeated measures ANOVA. The ANOVA did not show any significant main effects. Crucially, however, it revealed a highly significant interaction between bias condition and level of processing [$F(1, 4) = 28.99$, $p < .01$, $\eta_p^2 = .879$]. None of the other interactions proved significant.

Post hoc comparisons (Fisher's LSD test) carried out to explain in detail the significant interaction bias condition by level of precessing, confirmed that accuracy scores were higher for local ($M = 81.7\% \pm 6.6$ CI) than for global ($M = 71.3\% \pm 10.1$ CI; $p < .05$) trials in the local bias condition, but they were higher for global ($M = 78.6\% \pm 3.9$ CI) than for local ($M = 64.3\% \pm 10.3$ CI; $p < .05$) trials in the global bias condition (see Figure 4).

In order to assess whether attentional bias had a similar effect in both levels of processing conditions, post hoc comparisons between the two bias conditions for each level of processing trials were performed. Accuracy scores for local trials were significantly higher in the local bias condition than in the global bias condition ($p < .01$). However, the same effect was not observed for global trials. As shown in Figure 4, monkeys made more errors in the local bias than in the global bias condition when responding to the global aspects of the stimuli, but performance difference between conditions only approached significance ($p = .089$).

In order to assess if the amount of task exposure had an effect on the observed pattern of results, two separate repeated measure ANOVAs 2 (Bias Condition) × 2 (Level of Processing) were carried out for each of the two 4-session blocks.

The analysis carried out on the first block did not reveal any significant main effects. The interaction bias condition by level of processing was significant [$F(1, 4) = 54.59$ $p < .005$, $\eta_p^2 = .932$]. This significant interaction can be explained by the fact that, whereas there was a significant difference between the level of accuracy shown by the monkeys in the local and global trials in the

global bias condition (global trials $M = 76.25\% \pm 6.87$ CI; local trials $M = 57.50\% \pm 12.75$ CI, $p < .05$), this difference was not significant in the local bias condition (local trials $M = 80.21\% \pm 6.97$ CI; global trials $M = 75.00\% \pm 18.20$ CI, $p > .1$).

Moreover, as was observed in the ANOVA for the two blocks combined, the difference between local trials was different in the two bias conditions [local trials in global condition $M = 57.50\%$; local trials in local condition $M = 80.21\%$, $p < .05$], but the global trials were not significantly affected by attention bias [global trials in global condition $M = 76.25\%$; global trials in local condition $M = 75.00\%$, $p > .1$].

The analysis carried out in the second block of trials also showed that there were no significant main effects and a significant interaction between bias condition and level of processing [$F(1, 4) = 14.68$ $p < .05$, $\eta_p^2 = .786$].

However, interestingly in this second block of trials, significant differences emerged between the local and global trials in both the global bias condition (global trials $M = 80.71\% \pm 3.30$ CI; local trials $M = 70.75\% \pm 10.45$ CI, $p < .05$) and the local bias condition (local trials $M = 83.12\% \pm 6.36$ CI; global trials $M = 67.50\% \pm 11.51$ CI, $p < .05$).

Furthermore, in addition to a significant decrement of performance in the local trials in the global bias condition (local trials in global condition $M = 70.75\%$; local trials in local condition $M = 83.12\%$, $p < .05$), which resembled the results of analyses reported above, here it emerged that attention bias also affected the global trials (global trials in global condition $M = 80.71\%$; global trials in local condition $M = 67.50\%$, $p < .05$).

Discussion

This experiment demonstrates that the bias conditions were effective in producing performance trade-offs in capuchins. Monkeys showed a global advantage in the global bias condition but a local advantage in the local bias condition. This is the first evidence that the local advantage typically displayed by capuchin monkeys can be reversed under appropriate conditions. The effect of the bias condition was particularly evident in the local trials. The level of accuracy for local processing was very high when subjects were biased to direct their attention to the local features of the stimuli and deteriorated dramatically when they were biased toward the global structure of the visual patterns. This significant effect emerged in the first 4-session block and was present in the overall set of data with the two 4-session blocks combined.

The effect of the bias condition emerged less rapidly in the global trials. It was clearly present in the second of the two 4-session blocks where a significant change in accuracy was observed in the global trials as a function of attention bias. The percentage of correct responses in the global trials improved when they were presented as part of a global bias condition. This effect, however, was not significant in the first 4-session block and only approached significance when the two 4-session blocks were combined. Taken together, these findings indicate that there is a trade-off in capuchins as the probability of identifying the correct matching stimulus at a given level of processing changes as a function of the prevailing type of trials to which they are exposed during the task. This pattern develops more easily and is particularly robust in local trials.

Experiment 2

The aim of Experiment 2 was to collect data on humans, which would enable meaningful comparisons with the data collected on monkeys. We used the same stimuli and the same MTS task with humans in Experiment 2 as those used with monkeys in Experiment 1 and similar testing procedures. As experiments conducted on hierarchical stimuli in humans typically include response times (RTs) as a measure of the relative speed of processing of local and global properties of the stimuli, and given that the experimental set-up used with humans allowed us to do so, we also recorded RTs in this experiment and not just frequencies of correct responses.

Method

Participants

The group of human participants comprised 12 (5 males and 7 females) psychology undergraduates at the University of Leicester. They were paid a small fee for their participation. All participants had normal or corrected-to-normal vision and were naïve regarding the experimental hypothesis of the study.

Apparatus and Stimuli

The experimental set-up was composed of a PC (Intel Corel Duo CPU E8400 3.00GHz, 3.00GHz) with 19″ SVGA monitors with a resolution of 1024 × 768 pixel. The software used to run the experiments was developed at the University of Leicester, using E-Prime (Psychology Software Tools Inc.). It enabled the recording of the frequency of correct responses and RT with an accuracy of 1 ms.

Bitmaps of the stimuli used in Experiment 1 with monkeys were used for stimulus presentation on the computer screen. Thus, the stimulus set was composed of 8 hierarchical stimuli, which included 4 consistent (i.e., Cc, Ss, Rr, Xx) shapes and 4 inconsistent (i.e., Cs, Sc, Rx, Xr) shapes (see Figure 2). The size of the stimuli, as they appeared on the computer monitor, was double the size of the stimuli used with monkeys. The distance of the participants from the screen was controlled using a chin rest placed at a distance (60 cm) which was twice the distance of the Plexiglas panel separating the monkeys from the apparatus so that the visual angle subtended by the stimuli was kept approximately the same as that used with monkeys.

Procedure

Each participant sat in front of the computer screen in a testing room that had a similar level of fluorescent light illumination as that used in Experiment 1 with monkeys. Trials started with a stimulus sample displayed centrally at the top of the screen. Following a brief, randomly generated interval between 2 and 3 s, the two comparison stimuli appeared at the bottom left and right corners of the screen, respectively. The subject's task was to indicate, by pressing as fast as possible, the "L" or the "R" key, respectively located on the left end and right end of an array of keys of a response box, which of the two patterns (the one presented on the left or the one presented on the right of the screen)

was identical to the centrally presented pattern. All the three stimuli remained present on the screen until a response was made.

Each participant received 4 blocks of 112 trials, with a break of at least 5 minutes between blocks: two blocks featured the local bias condition (i.e., 85.7% local trials and 14.3% global trials) and two blocks the global bias condition (85.7% global trials, 14.3% local trials), with local bias and global bias blocks being alternated. Half of the participants started with a local bias block of trials and the other half with a global bias block. In each block, half of the trials included consistent sample stimuli, in which the local and global shapes were identical, and the other half included inconsistent sample stimuli in which the local and global shapes were different.

Both correct responses and RTs were recorded. Only RTs for correct responses were included in the analyses.

Results

Accuracy

The overall mean percentage of correct responses was very high (97.5%), ranging from 92.2% to 100.0%.

The percentage of correct responses recorded in the local and global trials, in the local bias condition and in the global bias condition performed by humans in Experiment 2, is reported in Figure 5a. An inspection of the figure suggests that in global trials, humans performed at a particularly high level of accuracy that was maintained irrespectively of the bias condition within which these
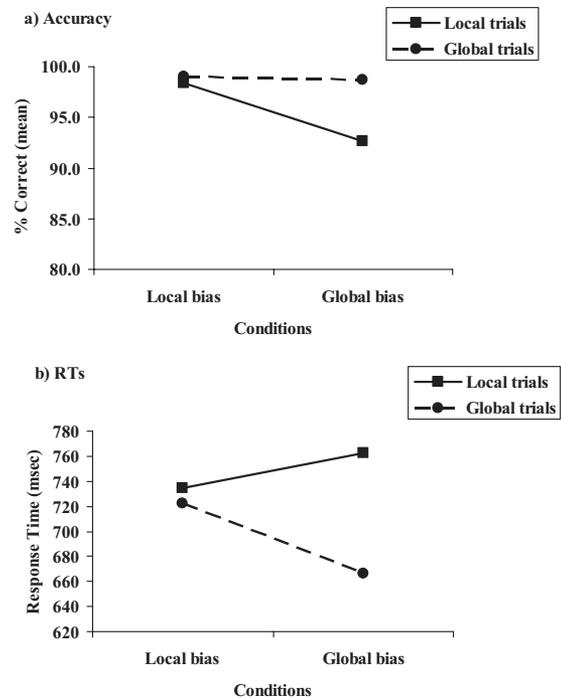

Figure 5. a) Percentage of correct responses recorded in the local and global trials, in the local bias condition and in the global bias condition performed by humans in Experiment 2; b) Response Time (RT) recorded for correct responses performed by humans in Experiment 2 in the local and global trials, in the local bias condition and in the global bias condition.

trials were presented. A similar level of high performance can be observed in the local trials. However, performance in the local trials seems more vulnerable as the figure shows it deteriorating in the global bias condition.

The above observations were confirmed by a 2 (Bias Condition) × 2 (Level of Processing) × 2 (Stimulus Consistency) repeated measures ANOVA carried out on the percentage of correct responses obtained in this experiment. The ANOVA revealed significant main effects for bias condition [$F(1, 11) = 8.27$, $p < .05$, $\eta_p^2 = .429$], and level of processing, [$F(1, 11) = 17.2$, $p < .01$, $\eta_p^2 = .610$].

The overall accuracy scores were higher for the local bias ($M = 98.7\% \pm 0.65$ CI) than for the global bias ($M = 95.7\% \pm 3.2$ CI) condition, and for global ($M = 98.8\% \pm 0.85$ CI) than for local ($M = 95.5\% \pm 2.0$ CI) trials. By contrast, the main effect of stimulus consistency was not significant [$F(1, 11) = 1.18$, $p > .1$, $\eta_p^2 = .097$]. The mean percentage of correct responses was 97.7% for the consistent and 96.7% for the inconsistent stimuli.

Importantly, the Bias Condition X Level of Processing interaction was significant [$F(1, 11) = 7.49$, $p < .05$, $\eta_p^2 = .405$]. Post hoc comparisons (Fisher's LSD test) showed that, in the global bias condition, the percentage of correct responses was significantly lower for local than for global trials (92.7% ± 4.1 CI vs. 98.7% ± .95 CI, $p < .01$). Conversely, in the local bias condition, percentages of correct choices were similar for both local (98.4% ± .75 CI) and global (99.0% ± .95 CI) trials. Moreover, performance level for local trials was significantly higher in the local bias (98.4%) compared with the global bias condition (92.7%, $p < .01$). By contrast, the percentage of correct choices for global trials was nearly identical in both conditions (local bias condition, $M = 98.7\%$; global bias condition, $M = 99.0\%$, $p > .1$). These results are reported in Figure 5a.

Response Time Analysis

This analysis was carried out on the human sample only as the apparatus used for the administration of the task to the monkeys did not allow the collection of RTs. Only latencies for correct responses were analyzed. The average RT observed in the local and global trials in the two bias conditions is presented in Figure 5b. From the figure, it can be seen that the participants were always faster in the global trials. RT appears to be dramatically reduced in the global trials in the global bias condition. Moreover, there seems to be an indication that a local bias reduced the time required to process the local level of the stimulus. This effect of attention bias, however, is not as evident as it is in the global trials. Average RT were subjected to a 2 (Bias Condition) × 2 (Level of Processing) × 2 (Consistency) repeated measures ANOVA. The analysis revealed a significant main effect for level of processing [$F(1, 11) = 27.84$, $p < .001$, $\eta_p^2 = .717$], with faster responses to global trials ($M = 694.2$ ms, ± 47.35 CI) than responses to local trials ($M = 748.8$ ms, ± 43.15 CI). The main effect of stimulus consistency was also significant, $F(1, 11) = 8.05$, $p < .05$, $\eta_p^2 = .423$, indicating that responses to consistent stimuli ($M = 706.3$ ms, ± 43.7 CI) were faster than those to inconsistent ones ($M = 736.7$ ms, ± 47.05 CI). The main effect of bias condition was not significant [$F(1, 11) = 1.04$, $p > .1$, $\eta_p^2 = .087$ (local bias, $M = 728.5$ ms; global bias, $M = 714.5$ ms)]. Interestingly, the interaction bias condition by level of processing proved significant [$F(1, 11) = 70.86$, $p < .001$, $\eta_p^2 = .866$], indicating that bias played a role in the speed of processing of the stimuli. None of the other second order or third order interactions was significant. Post hoc comparisons (Fischer's LSD test) revealed that responses to local trials were faster in the local bias than in the global bias condition (734.8 ms, ± 46.95 CI vs. 762.9 ms, ± 45.55 CI; $p < .01$), whereas responses to global trials were faster in the global bias than in the local bias condition (666.2 ms, ± 45.35 CI vs. 722.3 ms ± 53.9 CI, $p < .001$). Thus, variation in the proportion of trials requiring the processing of a particular level (global or local) of the stimulus produced a change in the speed of responding at that level. Moreover, there was a highly significant difference ($p < .001$) between the speed of responding to the global and local trials in the global bias condition but not in the local bias condition (see Figure 5b).

Consistent with the analysis carried out on monkeys in Experiment 1, we carried separate 2 (Bias Condition) × 2 (Level of Processing) ANOVAs for the two blocks of trials of Experiment 2, for both percentages of correct responses and RT. As the analyses revealed the same pattern of results in each of the two blocks and in the overall ANOVAs reported above, for brevity they are not presented in detail here.

Discussion

In terms of accuracy, three main findings emerged from the data collected on humans. First, the overall level of accuracy observed in the global trials was higher than that recorded for the local trials. Second, there was a global advantage in the global bias condition, but neither a global nor a local advantage emerged in the local bias condition. Third, whereas the accuracy level in global processing did not change as a function of bias, it did so for local processing. The absence of an overall effect of bias could be possibly due to a combination of effect of the interaction between bias and level of processing and the very high level of performance observed in the human sample overall.

The analysis of RTs is particularly informative given the widespread use of this measure in the determination of the presence of an attentional bias in human visual cognition. The results of this analysis revealed an overall global advantage in humans, which was consistent with the global advantage suggested by the accuracy analysis. Also, consistently with the accuracy results, we found that global processing was faster than local processing when subjects were induced to direct their attention to the global level of the stimuli. Nevertheless, neither local nor global dominance was observed when subjects were induced to allocate their attention to the local level of the stimuli. In fact, in the local bias condition, the latency of response in the local trials (734.8 ms) did not differ from the latency in the global trials (722.3 ms). These data suggest that attentional allocation to the local level was not sufficient to slow down global processing in humans.

Nevertheless, this result does not indicate an absence of a bias effect since responding was faster at the processing level coinciding with that to where the allocation of attention was induced in a particular condition. In fact, global processing was faster in the global bias condition whereas local processing was faster in the local bias condition.

General Discussion

The finding that monkeys, in contrast with humans, show a local advantage when processing hierarchical visual stimuli has attracted a considerable interest in comparative cognition (De Lillo et al., 2005; Fagot & Deruelle, 1997; Lea, Goto, Osthaus & Ryan, 2006; Spinozzi et al. 2003), and it has proved difficult to identify a key factor which can explain these differences (Fagot & Deruelle, 1997). In a study aimed at finding conditions that could affect the local advantage of capuchin monkeys, we documented that such advantage cannot be explained by a tendency in this species to process better stimuli of a particular size (Spinozzi et al., 2006). In that study, an MTS task with hierarchical stimulus was used, similar to the task used here but where the size of the stimuli was manipulated systematically. There, capuchins maintained a local advantage even when the size of the local elements was the same as that of the global shape of smaller stimuli that also produced a local advantage. Moreover, capuchins do not differ substantially from humans in their ability to process the spatial relationships of the component parts of visual patterns. In fact, as explained in the introduction, pattern recognition in this species is affected by the same transformations of the arrangement of stimulus parts that affect humans (De Lillo et al., 2007).

The present study was a further attempt to search for conditions under which local dominance in capuchin monkeys can be reversed, and by doing so, suggest possible mechanisms responsible for it. The specific aim of the study was to assess the role played by attention in the global and local processing of hierarchical visual stimuli in monkeys, using a procedure often used in the literature on human visual cognition to modulate attention allocation to different levels of hierarchical patterns (Kinchla et al., 1983).

The results obtained here provide a first indication that capuchin monkeys can reverse their local advantage in particular conditions. In fact, the monkeys showed an advantage for local over global processing in the local bias condition and an advantage for global over local processing in the global bias condition. Overall, there was an indication that the global advantage observed in monkeys in the global bias condition was accounted for mainly by a decrease in performance in the local trials in conditions where most of the trials during the experimental session required attending the global level of the stimuli. Nevertheless, with task practice, a symmetrical effect was observed in local and global trials with the latter also being affected by manipulations of attention bias.

There are some parallels between the shift from local to global dominance that we induced in monkeys, following manipulations of attention bias, and the reversal of the typical local advantage of children with autism in conditions of selective attention (Plaisted, Swettenham & Rees, 1999). This latter result was explained in terms of an increased ability to inhibit the influence of the irrelevant local level caused by the priming of the global shape of the stimuli induced by selective attention at that level. This conclusion was drawn because the shift of dominance was observed in parallel with clear effects of interference in conditions featuring inconsistent stimuli. In particular, children with autism showed a change from local-to-global interference in a divided attention task to a global-to-local interference in a selective attention task. With our procedure, we induced a global advantage in monkeys in absence of an effect of interference between levels of processing. For this

reason, we would be more inclined to interpret the beneficial effects of inducing the monkeys to allocate more attention to the global level of processing as being due to the additional resources required by grouping local elements into global shapes. This would be in accordance with results reported in the human literature that indicate that grouping by spatial proximity is attention demanding (Ben-Av et al., 1992; Mack et al., 1992). Moreover, this account would not be inconsistent with a possible interpretation of local advantage in monkeys in terms of weak central coherence, as proposed for explaining local dominance in autism (Frith, 1989).

As part of the weak central coherence hypothesis, the local advantage in autism is seen as a different style of cognitive processing (Happé, 1999) rather than an actual deficit as observed in neuropsychological conditions such as agnosia (Behrmann & Kimchi, 2003) or simultagnosia (Huberle, Driver & Karnath, 2010). Analogously, the interspecies differences between humans and monkeys should not be seen as a clear deficit in monkeys in the processing of the global shapes of the stimuli. In fact, our experiments demonstrate that monkeys can flexibly focus on different levels of stimulus structure as they were above chance, and in general highly successful, throughout the experiment which featured conditions always requiring a switch to responding to one level of stimulus structure to the other within a single testing session. In fact, in the present study, we did not have any condition assessing the level of performance in absence of a requirement to shift attention from one level to the other of stimulus structure in different trials. Yet, some information in this respect can be obtained from our previous studies carried out on capuchin monkeys using blocked testing sessions containing exclusively global or local trials using the same stimuli (e.g., Spinozzi et al., 2003; Spinozzi et al., 2006). The overall performance on global trials in the present study (74.9%) was not very different from that observed in the global trials of those previous studies (74.2% average of values observed in Spinozzi et al., 2003, Experiment 1, and Spinozzi et al., 2006, Experiment 1). However, the observed level of performance in the local trials was lower in the present study, compared to that of the previous studies (89.1% average of values observed in Spinozzi et al., 2003, Experiment 1, and Spinozzi et al., 2006, Experiment 1). This is possibly due to the requirement to switch between one level of stimulus processing to the other, even in those conditions where most of the trials were of the local type (local trials − local bias condition = 81.7%). The difference between the level of accuracy on the local trials observed in previous studies, as reported above, and in the present study (73.0%) is particularly evident when a global bias was induced by the presence of a higher percentage of global trials within the testing session (local trials − global bias condition = 64.3%). The decrement in performance was also present in the two subjects (percentage of correct responses observed in the local trials for Spinozzi et al., 2003 and Spinozzi et al., 2006 combined: Pippi = 85.6% and Gal = 91.0%) who had taken part in the previous two studies. These considerations confirm the suggestion that attention allocation using an MTS tasks affects mostly the processing of the local level in this species.

Humans, in our study, showed a global advantage in their accuracy in the global bias condition but no advantage was observed in the local bias condition. Here, the very high level of matching performance of participants in the local trials was indistinguishable from the performance level observed in the global

trials. Moreover, while accuracy for local processing was better when subjects were biased toward attending the local level of the stimuli than when they were biased toward attending the global level of the stimuli, the same effect was not observed for global processing: Accuracy level for global form detection appeared nearly identical during global and local bias condition.

Some additional considerations can be made on the basis of the RT data collected on humans. The analysis of RTs revealed that humans were faster when processing the global level of the stimuli when attention allocation was induced at that level. By contrast, when a local bias was induced, RTs were similar for the two levels of processing. Nevertheless, attention seemed to modulate both local and global processing in humans, as global processing was faster in the global bias condition and local processing was faster in local bias condition.

Although not possible in the present study, the collection and evaluation of RT data in capuchins would be of extreme value. In fact, results obtained with visual search for hierarchical visual patterns in baboons (Deruelle & Fagot, 1998) revealed steeper slopes in RTs as a function of number of distracters in global than in local processing condition, indicating that global processing is more attention demanding than local processing in that species. By contrast, a first consideration of our MTS accuracy data would suggest that local processing in capuchins is more attention demanding than global processing, as this level of processing is more vulnerable to changes in the context in which the trials are presented. Nevertheless, it is possible to envisage interpretative scenarios for our data which would be consistent with the notion that it is the detection of global aspect of the stimuli to require more attention in monkeys (Deruelle & Fagot, 1998; see also Parron & Fagot, 2007, for a similar account of the resistance to the effect of the Ebbinghaus visual illusion in monkeys). In fact, it is possible to conjecture that if global processing is particularly attention demanding in monkeys, conditions such as our global bias condition, featuring a large number of global trials, may detract a large amount of attentional resources from the task, thus producing a deterioration of performance in the local trials. By contrast, in the local bias condition, the fact that most of the trials require processing at the local level, which is not particularly attention demanding for the monkeys, may not deplete attentional resources to the same extent and thus fail to negatively affect performance on the few global trials present there. RT analyses of capuchins performance with the current and with visual search tasks would help to evaluate this possibility.

It is also possible that the asymmetrical effect of zooming down from global to local analysis or zooming up from local to global analysis as observed in humans (Stoffer, 1993) could explain the observed results on its own, or in addition to, a differential allocation of attentional resources to the two levels of processing. In fact, there is some evidence suggesting that, in humans, shifting attention in the global-to-local direction requires extra time and that only after attention has been reoriented to the local level can identification at this level begin (Stoffer, 1993, 1994). For example, Stoffer (1993, 1994) found longer RTs for local than for global identification, indicating that attentional zooming to the local level needs more time than zooming to the global level. It has been hypothesized that the RT differences between global and local identification is produced by the time necessary to refocus atten-

tion from an unintentional focusing at the global level to an intentional focusing at the local level (Stoffer, 1993, 1994).

It may be possible that monkeys share with humans an increased difficulty in moving attention from the global to the local level of the stimuli. Since most studies used blocked trials with one type of processing required in each session (e.g., Spinozzi et al., 2003; 2006), monkeys were not required to shift attention between levels of processing. In those conditions, monkeys would benefit from their tendency to focus on the local level of the stimuli in the local trials and do not have to perform costly shifts of attention from the global level of processing in the global trials. By contrast, in the global bias condition of the present study, monkeys are induced to engage attention at the global level and would find it difficult to disengage it when the occasional local trial is presented, thus causing a decrement in their performance in these latter trials. This account would also explain the decrement of performance observed in the local trials of the global bias condition in humans.

In sum, our results clearly indicate that it is possible to affect the allocation of attention in a MTS task with hierarchical stimuli in monkeys, at least as far as the local level of processing is concerned. A demonstration of this effect does not imply that differences in attention biases are the primary explanation of interspecies differences in this domain and does not tell us the origin of the specific biases exhibited by a given species. Nevertheless, they indicate that attention processes may have a prominent role for the characterization of important interspecies differences and are worthy of careful investigation.

Exactly on what components of the stimuli the attention bias operates remains to be determined. It is possible that it is via the priming of spatial frequency channels responsible for the detection of high and low spatial frequency, respectively. Several studies on the role of attention in global–local processing have indicated that, in humans, the allocation of attention to different levels of processing is mediated by a mechanism based on selection by spatial frequency (Lamb & Yund, 1993, 1996; Lamb, Yund & Pond, 1999; Robertson, 1996; Shulman & Wilson, 1987). We are currently investigating the extent to which attentional bias can be induced in capuchin monkeys by manipulating this factor.

Further investigations featuring the manipulation of the context in which global–local processing in monkeys and humans occurs, may highlight further differences (e.g., in terms of the differential allocation of resources to global and local processing) and potential similarities (e.g., in the preferred direction of the attentional zooming between stimulus levels) in the visual cognition of humans and monkeys. Thus, they could not only indicate which dimensions are important to consider if we want to trace the origins of human cognitive skills but also help in specifying the competences for which nonhuman primates can provide a plausible model of human cognitive neuroscience. Such information would be essential to the progress of neuro-scientific research on nonhuman primates.

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