

The Relative Use of Proximity, Shape Similarity, and Orientation as Visual Perceptual Grouping Cues in Tufted Capuchin Monkeys (*Cebus apella*) and Humans (*Homo sapiens*)

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Recent experimental results suggest that human and nonhuman primates differ in how they process visual information to assemble component parts into global shapes. To assess whether some of the observed differences in perceptual grouping could be accounted for by the prevalence of different grouping factors in different species, we carried out 2 experiments designed to evaluate the relative use of proximity, similarity of shape, and orientation as grouping cues in humans (*Homo sapiens*) and capuchin monkeys (*Cebus apella*). Both species showed similarly high levels of accuracy using proximity as a cue. Moreover, for both species, grouping by orientation similarity produced a lower level of performance than grouping by proximity. Differences emerged with respect to the use of shape similarity as a cue. In humans, grouping by shape similarity also proved less effective than grouping by proximity but the same was not observed in capuchins. These results suggest that there may be subtle differences between humans and capuchin monkeys in the weighting assigned to different grouping cues that may affect the way in which they combine local features into global shapes.

Keywords: visual perception, grouping cues, nonhuman primates, *Cebus apella*

The visual world we perceive appears to consist of discrete objects of various shapes, sizes, and colors, which are seen against a background of different textured surfaces. To visually identify the objects and segregate them from the background, we must be able to group their component elements into a coherent perceptual whole.

The ability to organize sensory inputs into unitary percepts is fundamental to any organism equipped with a relatively sophisticated visual system. It is possible, thus, to suppose that the general principles regulating perceptual grouping in humans might pertain, to some extent, to all the species that depend to a great extent on vision for

their survival. This issue has recently generated a great deal of interest in comparative cognition in which attempts have been made to identify similarities and differences between the cognitive mechanisms underpinning visual perception in humans and in nonhuman animals.

Comparative studies using a variety of textured stimuli have shown that pigeons, like humans, readily and quickly detect the target region of multi-element displays on the basis of color and texture differences and ignore local feature changes (Cook, Cavoto, & Cavoto, 1996). These data imply that pigeons share with humans the early visual mechanisms responsible for identifying the global boundaries and surfaces of objects. However, experiments using hierarchical figures such as small local letters spatially arranged to form larger global letters (Navon, 1977), have shown that pigeons attend to the global aspects of the stimuli less readily than to the local ones (Cavoto & Cook, 2001). This finding contrasts with that reported for humans (Navon, 1977) who typically attend faster and better to the global aspect of the stimuli than to their local features. However, there is evidence that pigeons can selectively attend to either the global or the local stimulus level when specific testing procedures are employed (Fremouw, Herbranson, & Shimp, 2002; Fremouw, Walter, & Shimp, 1998), suggesting that the visual processing of hierarchical figures by pigeons can be sensitive to different levels of stimulus structure, at least in different tasks.

Interspecies differences in the mode of processing hierarchically arranged information also emerge when species taxonomically closer to humans, such as nonhuman primates, are considered. The visual system of nonhuman primates shares some important properties

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with that of humans. In fact, available data obtained from studies that have used two species of macaques (*Macaca nemestrina* and *Macaca mulatta*) as subjects, have demonstrated that the visual field of this Old World monkey species is about the same size (i.e., 200°) as that of humans (Wilson et al., 1989). In addition, humans and monkeys show a similar ability to detect fine details (visual acuity) and have a similar sensitivity to contrast (de Valois, 1971; Fobes & King, 1982). Furthermore, in both humans and monkeys, the visual pathways comprise two distinct channels that are sensitive differently to high and low spatial frequencies (Merigan & Maunsell, 1993), and recent fMRI studies have provided evidence that, in both monkeys and humans, the integration of local features into global shapes was mediated by similar neural mechanisms, which involved multiple-visual areas (Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003). Notwithstanding these similarities between the functioning of visual pathways of human and nonhuman primates, some comparative studies based on the global–local paradigm have shown that, in contrast with humans, 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) reliably discriminate the local components of the hierarchical patterns faster and more accurately than their global structure. Chimpanzees do not show a clear-cut advantage for global or local processing and do not always discriminate the local elements of the stimuli more quickly (Fagot & Tomonaga, 1999; Hopkins & Washburn, 2002) and as such, they seem to occupy an intermediate position between the two extreme modes of processing shown by monkeys and humans.

Differences between humans and monkeys in local and global processing cannot be easily explained on the basis of a different sensitivity to the particular visual angle subtended by the stimuli or to the number and relative size of their local elements. In fact, a local advantage in capuchin monkeys has been observed also in conditions in which the global shape of smaller stimuli subtended the same visual angle as that subtended by the local elements of larger stimuli (Spinozzi et al., 2006, Experiment 1), as well as in conditions featuring multi-element patterns (Spinozzi et al., 2006, Experiment 2), that is, patterns that in human perception relegated the local elements to texture and enhance a global advantage in both adults and children (Kimchi, 1990; Kimchi & Palmer, 1982). Moreover, recent data on pattern recognition show that the ability of capuchins to identify a complex visual pattern can be compromised when the spatial organization of all its components is disrupted, suggesting that these monkeys are as sensitive as humans to configural properties of visual stimuli (De Lillo, Spinozzi, & Truppa, 2007). This latter finding thus rules out the possibility that the lack of a global advantage in monkeys may be due to a deficit in encoding the spatial relations between the parts of a visual pattern.

One advantage in using hierarchical stimuli is that they can be constructed so that the same shape can be presented at the local and global level. As such, the observation of a local or global advantage in different primate species can be difficult to explain on the basis of the relative familiarity of a particular shape involved but has to reside in their specific abilities to group spatially separated elemental features into a coherent whole. This hypothesis is supported by the results of several comparative studies that have focused on the effect

of the stimulus density on global–local processing. Evidence from these findings suggests that the proximity of stimulus components plays an important role in the ability of nonhuman primates to group local features into a global coherent form. For example, data obtained with capuchins (De Lillo et al., 2005; Spinozzi et al., 2003), baboons (Deruelle & Fagot, 1998; Fagot & Deruelle, 1997), and chimpanzees (Fagot & Tomonaga, 1999) revealed that these species did not show a significant advantage for either stimulus level in conditions featuring stimuli composed of elements in close proximity to each other (dense stimuli), but they exhibited a strong local advantage in conditions involving stimuli with a larger interelement distance (sparse stimuli). By contrast, human adults showed a global advantage irrespective of variations in stimulus density (Deruelle & Fagot, 1998; Fagot & Tomonaga, 1999) and preschoolers, who performed equally well in local and global conditions, did not show an impairment of global processing when presented with sparse rather than more dense stimuli (De Lillo et al., 2005). An effect of the distance between elements on the global/local processing has been found also in cotton-top tamarins by Neiworth, Gleichman, Olinick, and Lamp (2006) who observed a global advantage in these monkeys when dense element displays were used. This finding contrasts with what has been reported for other nonhuman primate species (e.g., De Lillo et al., 2005; Deruelle & Fagot, 1998; Fagot & Tomonaga, 1999). Nevertheless, in the study by Neiworth and colleagues the global advantage shown by tamarins disappeared with sparse element displays. More interesting, the pattern of results observed in tamarins resembled that of children but differed from the results obtained with adult humans who showed a strong global advantage regardless of density. Despite some inconsistency in the density effect on the global–local processing, some of these findings strongly support the notion that nonhuman primates, compared to human adults, showed a different sensitivity to the proximity of the elements as grouping factor.

There is also an indication that other grouping principles, which are pervasive in human perceptual organization, may not be deployed to the same extent by monkeys. In the study by Spinozzi, De Lillo, and Castelli (2004), capuchin monkeys and humans had to identify, in a matching-to-sample (MTS) task, which among different stimulus parts presented as comparison stimuli, belonged to a complex pattern presented as the sample. It emerged that humans found it much easier to identify the stimulus parts when they were formed by assembling elementary features on the basis of grouping principles such as closure and good continuation. By contrast, capuchin monkeys showed a remarkable advantage in identifying the parts when they were not assembled on the basis of these principles and to a human eye looked as a set of disconnected elements. A different sensitivity to some grouping cues has been reported also in other nonhuman species, such as rats (Kurylo, Van Nest, & Knepper, 1997) and Australian sea lions (Burke, Everingham, Rogers, Hinton, & Hall-Aspland, 2001) in tasks featuring bistable arrays of dots.

Taken together, these results can be seen as an expression of differences in at least some of the grouping processes used by humans and nonhuman primates as well as by other mammalian species. Given the importance of perceptual grouping in visual processing and visual recognition, a limited capacity at the level of perceptual organization has the potential to reduce the effectiveness of object recognition. Even in the very controlled context of an MTS task with hierarchical stimuli, it is likely that a variety of grouping factors play a role in the recognition of global shapes.

Nevertheless, the issue of the relative prevalence of particular grouping cues compared to others in different species has rarely been addressed systematically.

In the literature on human visual cognition, it has for a long time been assumed that perceptual organization is a unitary process, and grouping principles on which it is based operate pre-attentively, at the same stage of processing in early vision (Marr, 1982). However, more recent approaches to this problem suggest that perceptual organization is not a monolithic phenomenon but involves a multiplicity of processes that might vary in their attentional demands and might operate at different stages of visual processing (Behrmann & Kimchi, 2003; Kimchi & Razpurker-Apfeld, 2004). For example, there is evidence that proximity and similarity have a different impact in the unit formation, with grouping by proximity being perceived faster and with fewer errors than grouping based on similarity of luminance, shape, or orientation (Ben-Av & Sagi, 1995; Chen, 1986; Han & Humphreys, 1999; Han, Humphreys, & Chen, 1999; Quinlan & Wilton, 1998). In view of these findings, it seems important to assess empirically, how different grouping principles operate in other primate species, and their relative contribution to the perception of whole patterns and objects.

The aim of this study is to evaluate the relative weight given to specific grouping cues in the visual processing of humans (*Homo sapiens*) and capuchin monkeys (*Cebus apella*), using the same stimuli and similar experimental procedures based on a simultaneous MTS task. Previous findings demonstrated that, compared to humans, capuchin monkeys display a different sensitivity to proximity as grouping cue for the global processing of hierarchical stimuli (De Lillo et al., 2005). However, proximity is only one of the grouping cues used by humans and the global processing of hierarchical stimuli may be based on other grouping processes based on the shape similarity, continuity, or alignment of elements. Thus, it is possible to suppose that differences observed so far between humans and capuchins may be due to a different use of some of these grouping cues. In fact, other experiments based on embedded figure tasks have shown that capuchins are less dependent than humans on the organizational principles of closure or good continuation for the processing of complex visual patterns (Spinozzi, De Lillo et al., 2004). Moreover, because the human literature has suggested that some form of grouping and segmentation takes place early and effortlessly whereas others occur later and require controlled attentional processing (Behrmann & Kimchi, 2003), it can be hypothesized that differences in perceptual grouping of humans and capuchins may be due to differences in their attentional and other higher level cognitive mechanisms. However, the use of hierarchical stimuli does not allow us to disentangle the processes involved during the perception of integrated figures. Hierarchical stimuli are a powerful tool for obtaining information regarding the advantage offered by one level of globality over the other in the processing of stimuli specifically constructed so that the global and the local elements can be equally complex, recognizable, and codable (Kimchi, 1992). Nevertheless, this kind of stimuli is typically not designed to evaluate which and how many grouping cues are used to derive whole patterns as a function of the nature and the interrelations among the stimulus components. To understand how and to what extent different principles of perceptual organization interact in the perception of a visual pattern it is necessary to assess processes that operate within and between groups of elements (Quinlan & Wilton, 1998).

In the experiments reported here, we used a grouping and segregation task and texture displays as stimuli to assess the extent to which forms of global organization emerge in monkeys (Experiment 1) and humans (Experiment 2) on the basis of proximity, similarity of shape, and orientation of a subset of local elements. Our primary aim was to assess whether some of the observed differences between humans and capuchin monkeys in their mode of processing visual information could be accounted for by a different prevalence of these grouping cues in the two species.

Experiment 1

Experiment 1 aimed at evaluating the extent to which capuchin monkeys found some visual grouping cues easier to use than others. Using a simultaneous MTS task, the monkeys were presented with a white-filled shape on a black background as the sample, and two multi-element patterns on a background of local elements as comparison stimuli. The task for the subjects was to identify in which of the two comparison stimuli the global shape of the compound pattern matched the shape of the sample. In some conditions of the task, the proximity, the similarity of shape or orientation between the elements forming the compound pattern and the background elements was manipulated to provide the basis for the identification and the segregation of the global figure. The comparison of the levels of performance across different conditions of the task could reveal the relative importance of the different grouping cues in the visual perception of this species.

The investigation of perceptual grouping processes in humans typically involves compound stimuli, which comprise alphabetic letters or simple geometric forms such as squares or crosses, that is, stimuli that are highly familiar to the observer and/or with a high degree of regularity and symmetry. These stimuli have been widely used in comparative studies on perceptual organization of nonhuman animals (e.g., Cook et al., 1996; De Lillo et al., 2005; Deruelle & Fagot, 1998; Fagot & Tomonaga, 1999; Hopkins & Washburn, 2002; Kurylo et al., 1997; Spinozzi et al., 2006). In the experiments reported here, we used both letter-shaped figures and irregular abstract forms as stimuli, in case the use of one or the other type of stimulus should have affected visual grouping in different ways in the two species.

Method

Subjects

The subjects were six adult tufted capuchins (*Cebus apella*), four males (Gal, Pepe, Narciso, and Patè) and two females (Virginia and Pippi), ranging in age from 5.5 to 23.8 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 to 130 m² × 3 m high) at the Centro Primati, Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche (C.N.R.), Rome. Capuchins were tested individually in an experimental box (0.76 m long × 1.70 m wide × 0.73 m high), to which they had access through a sliding door from their adjacent indoor cage. Each subject was separated from the group solely for testing, just before each daily testing session. The research protocol for this study was approved by the Italian Health Ministry.

The animals were given food pellets ad lib before and after testing; fresh fruit and vegetables were provided after testing. Water was freely available at all times. All the monkeys were already familiar with the set-up because they took part in a variety of previous experiments on cognitive and perceptual processes. More specifically, five subjects had been previously tested with tasks involving the global–local processing of hierarchical stimuli (Gal, Pepe, Narciso, Virginia, and Pippi: Spinozzi et al., 2006, 2003), the encoding of the spatial relationship between the stimulus components and the detection of a stimulus part embedded in a multicomponent pattern (Gal, Pepe, Narciso, Patè, and Pippi: De Lillo et al., 2007; Spinozzi et al., 2004). Moreover, four out of the six monkeys were tested and succeeded in a relational MTS task used to test the comprehension of abstract conceptual spatial relationship between objects (Gal, Pepe, Narciso, and Patè: Spinozzi, Lubrano, & Truppa, 2004). None of the subjects had been exposed to the stimuli used in the present study.

Apparatus

The apparatus consisted of a wooden panel (45 cm long \times 35 cm high \times 2 cm thick) with two symmetrical rectangular openings (5 cm long \times 9 cm high), each 10 cm from the center. The panel was fixed perpendicularly onto a wooden board (45 cm \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 lids (6 cm long \times 11 cm high \times 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 \times 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, 1 cm above the two openings and equidistant from them. A black wooden screen (50 cm long \times 40 cm high \times 1 cm thick) was used to cover the vertical panel between trials. The screen could be slid vertically along two parallel metal tracks mounted vertically onto the wooden board of the apparatus.

The apparatus was placed in front of the experimental box behind a transparent Plexiglas panel (45 cm long \times 40 cm high) mounted on the front wall of the experimental box. The Plexiglas panel had two symmetrical lateral armholes (15 cm long \times 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 to retrieve a peanut. The rectangular openings of the apparatus were positioned at the subjects' eye level.

General Procedure

The experiment was based on a simultaneous MTS task. Two experimenters administered the test. The first experimenter operated the apparatus while the second sorted the stimuli to be administered in each trial. The same two experimenters tested all the animals. At the beginning of each trial, the apparatus was placed in front of the experimental box, at a distance of about 30 cm. The first experimenter, while standing behind the trolley in a central position, covered the apparatus with the black sliding screen. Then

she 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. Finally, she 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. To avoid providing the monkey with spurious cues concerning the location of the reward, the experimenter performed the hiding procedure by moving both hands simultaneously behind the sliding lids. When the animal positioned itself in front of the apparatus (either in a seated or quadruped posture), the black sliding screen covering the apparatus was lifted. The monkey could obtain the reward only if it moved the lid featuring the matching stimulus (S+). Only one response, whether correct or incorrect, was allowed for each single trial. Once the monkey made a choice by sliding one of the two lids, the screen was lowered and the testing panel moved out of reach of the subject. Trials were separated by an interval of about 30 s, during which the second experimenter recorded the choice and selected stimuli for the next trial.

Stimuli

The monkeys were tested with three sets of stimuli. The first set (see Figure 1A), which was used in a preliminary test (see below), comprised three compound figures formed by the arrangement of small elements, and three figures filled in solid white color. The compound figures were composed of 69 unfilled heart-shaped elements arranged so that they created three different irregular forms. The overall size of these forms was about 6.5 \times 4.4 cm (i.e., 12.23° \times 4.34° of visual angle at a distance of about 15 cm). Each of their component elements measured 0.3 \times 0.3 cm (0.57°) and was separated by 0.22 cm (0.42°) from each adjacent element. The filled stimuli included single solid irregular forms that matched in shape and in size to the global configuration of the corresponding compound patterns.

The other two sets of stimuli (see Figure 1B) were used in the grouping cue test (see below). One set, from now on referred to as *irregular patterns*, included irregular figures formed by overlapping rectangles. The other set, to which we will refer to as *letters*, included letter-shaped figures. For each set, there were four subsets of stimuli, which included either figures filled in solid color, or compound stimuli that could be classified according to the grouping cues necessary to identify the global shape of a configuration of disconnected elements. They are described below in detail.

In the *filled figures* subset (Figure 1B.a), three filled white figures on a uniformly black background were used for each set. The overall size of the three filled figures belonging to the set with irregular patterns was about 7 \times 4.3 cm, whereas the size of the three filled figures of the set featuring letters was 7.5 \times 3.5 cm.

The other subsets consisted each of three compound figures on a background of elements. Each compound figure was composed of 69 local elements arranged to create three different global forms that matched in shape and in size the form of the corresponding filled figure in each set. The elements of the compound figures and the background elements were identical in size (0.3 \times 0.3 cm). In the *proximity* subset (Figure 1B.b), the elements of the compound figures ($n = 69$) and the elements

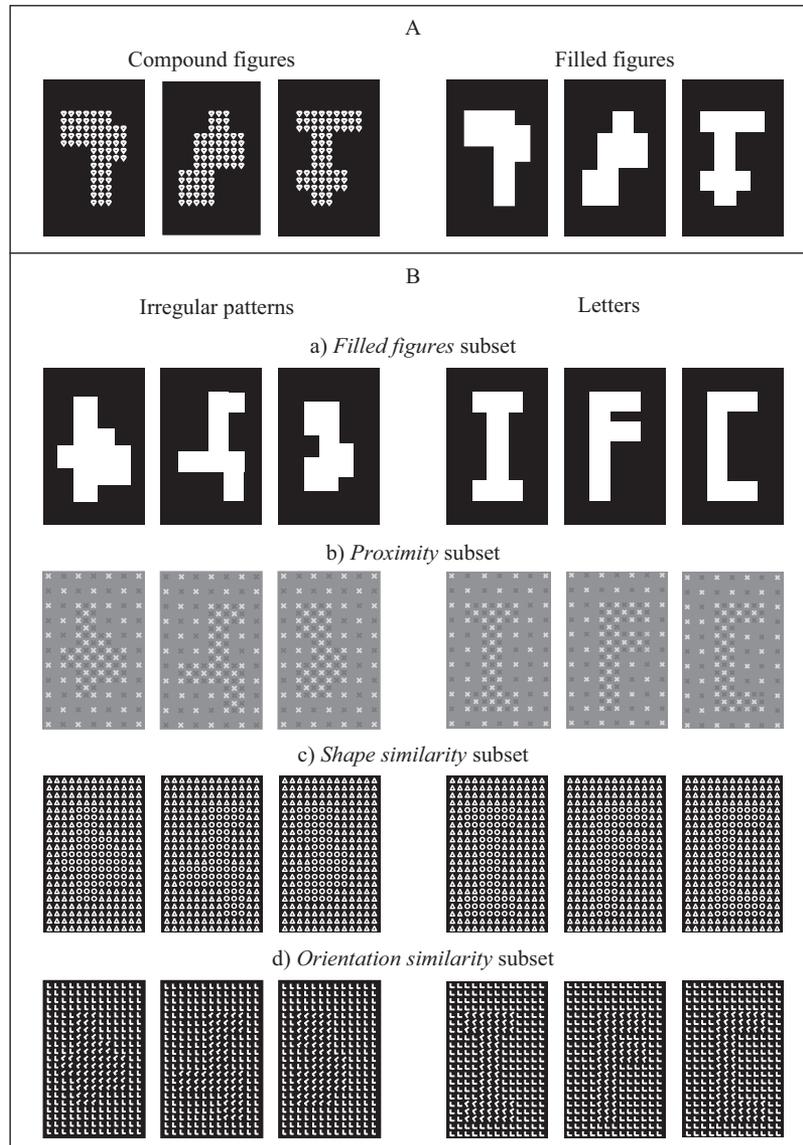


Figure 1. A: The stimulus set used in the preliminary test of Experiment 1; the set includes three filled shapes and three compound figures. B: The two sets of stimuli used in the grouping cues test of Experiments 1 and 2. The first set, “irregular patterns,” includes irregular figures; the second set, “letters,” includes letter-shaped figures. For each set, there are four subsets of stimuli. The first subset (a) includes three filled shapes; the other subsets (b, c, and d) consist each of three compound figures on a background of elements (see text for more details).

of the background ($n = 54$) were small crosses. Half of the crosses were colored in light gray and half in a dark gray. All the crosses were presented on a background filled with a shade of gray, which was intermediate between that used for the light and dark crosses. The use of shades of gray for this subset of stimuli was chosen to avoid that, by presenting white elements on a black background, the effect of grouping by proximity was confounded by the relative level of brightness of figure and background. The distance between the crosses of the compound patterns was 0.22 cm, whereas the distance between the crosses of the background was 0.74 cm. In the *shape similarity* subset (Figure 1B.c), a black background was used. The local elements

of the compound figures were 69 unfilled, white circles whereas the local elements of the background were 104 unfilled, white triangles. The distance between every two elements—circle–circle, triangle–triangle, circle–triangle—was 0.22 cm. In the *orientation similarity* subset (Figure 1B.d), white, equidistant (0.22 cm) L-elements differing in orientation were presented on a black background. The Ls were formed by two perpendicular segments of equal length (0.3 cm). The L-elements of the compound figures ($n = 69$) were rotated by 58° , while the background elements ($n = 104$) were upright Ls.

The stimuli of each set appeared as white shapes on a black background and were created using Microsoft PowerPoint®. Each

stimulus was printed on paper and was glued onto polyvinyl chlorides lids.

Design

The experiment featured the presentation of a preliminary test followed by the grouping cues test.

Preliminary test. This test was designed to gather baseline information on the ability of capuchins to discriminate visual patterns in which the global shape was defined by the spatial arrangement of a large number of identical elements. We used compound stimuli featured by minimal interelement spacing (0.22 cm) because previous findings revealed that capuchin monkeys find it difficult to perceive the global shape of compound patterns featured by a larger distance between the local elements (De Lillo et al., 2005; Spinozzi et al., 2003). The main goal of this preliminary test was to determine whether the chosen stimulus features (i.e., minimal interelement distance) were appropriate to induce the perception of a whole shape on the basis of a configuration of elements.

The monkeys were initially trained to discriminate the three filled stimuli shown in Figure 1A, using an identity MTS task. During the training, each of the monkeys received one daily session of 24 trials, for 5 consecutive days from Monday to Friday. Within the same session, the stimuli appeared as the sample an equal number of times in a pseudorandom order, so that no more than 2 consecutive trials could feature the same sample stimulus and the correct comparison stimulus could not appear on the same side more than twice consecutively. Each comparison stimulus appeared to the left and the right with equal frequency. Training sessions were repeated until the subjects satisfied a learning criterion of at least 75% ($p < .05$, binomial test) or more of correct responses in two consecutive sessions.

The test consisted of eight sessions of 24 trials per subject, one session a day, for a total of 192 trials. Half of the trials, referred to as the *grouping* trials, featured the presentation of the compound stimuli shown in Figure 1A. The other half of the trials, referred to as the *control* trials, featured the presentation of the same filled stimuli used in the training phase. These trials were administered to ensure that the subjects were still using a matching rule during testing. Each testing session contained 12 grouping trials and 12 control trials, pseudorandomly intermixed. Within each session, each of the six stimuli depicted in Figure 1A was presented four times as the sample in pseudorandom order with the same constraints as those mentioned for the training phase. Each comparison stimulus appeared on the left and the right with equal frequency. No physical restriction was imposed on the animals during the experiments. As in the training phase, subjects were tested for 5 consecutive days.

Grouping cues test. This test was administered immediately after the completion of the preliminary test. It consisted of two phases. In Phase 1, the monkeys were tested using the irregular patterns; in Phase 2, the subjects were tested using the letters (see Figure 1B).

In each phase, capuchins were initially trained to match the three filled stimuli depicted in Figure 1B.a using an identity MTS procedure. During the training, each monkey received one daily session of 24 trials. Within the same session, each of the three filled figures (Phase 1: irregular patterns; Phase 2: letters) was presented eight times in a pseudorandom order, so that no more

than two consecutive trials could feature the same sample stimulus and the correct comparison stimulus could not appear on the same side more than twice consecutively. Each comparison stimulus appeared to the left and the right with equal frequency. In each phase of the task, the acquisition criterion was 75% or more correct responses in two consecutive sessions.

During the test, a similarity MTS procedure was employed. In each phase, the sample stimulus, SS, consisted always of one of the three filled shapes used during the training (Figure 1B.a) whereas the two comparison stimuli, S+ and S-, varied according to the following matching conditions. In the *grouping by proximity* condition, the comparison stimuli included the cross-element arrays of the proximity subset (Figure 1B.b). In the *grouping by shape similarity* condition, the comparison stimuli included the circle-triangle arrays of the shape similarity subset (Figure 1B.c). In the *grouping by orientation similarity* condition, the L-element stimuli of the orientation similarity subset (Figure 1B.d) were used as comparison stimuli. In the *grouping* condition, the comparison stimuli included the compound figures made out of the crosses, circles, or Ls used in the previous three conditions but presented on a uniform background (i.e., without elements). This condition allowed the subjects to group by proximity, similarity, or both but did not require segregation from other elements. It was used as baseline measure of capuchins' ability to discriminate compound patterns differing with respect to the shape of their constituent elements. In the *identity-matching* (Id-MTS) condition, only filled shapes (Figure 1B.a) were used as comparison stimuli. This condition included trials identical to those presented during the training and was administered to ensure that subjects were still using a matching rule during the test. In each of the five testing conditions, only the global shape of the figure in S+ matched the shape of the sample. As in the preliminary test, only the selection of the matching comparison stimulus, S+, was rewarded.

In each phase, each subject performed 12 testing sessions of 30 trials each, 1 session a day, for a total of 360 trials. Each session included 6 trials for each matching condition, pseudorandomly intermixed. Within each session, each filled shape was presented 10 times as the sample in a pseudorandom order with the constraints that 2 consecutive trials could not feature the same stimuli and that the comparison stimuli appeared on the left and the right side of the sample with equal frequency. For each sample stimulus, there were 2 trials for each matching condition. All possible combinations of stimuli were balanced across sessions. No physical restriction was imposed on the animals during the task.

A summary of the different training and testing phases used in Experiment 1 is reported in Table 1.

Data Analysis

Because previous analyses, using the Kolmogorov-Smirnov test, showed that the group data did not deviate from a normal distribution, in this experiment and in the following experiment, we used parametric statistics to analyze and compare the accuracy scores in the different conditions of the tasks. For multiple comparisons, the False Discovery Rate method (FDR; Benjamini & Hochberg, 1995) was used. Accuracy was defined as the percentage of correct responses per test condition.

Table 1
Summary of Different Training and Testing Phases of
Experiment 1

Test	Stimulus set
1. Preliminary test	A
Training	
Testing	
2. Grouping cues test	B
(a) Phase 1	Irregular patterns
Training	
Testing	
(b) Phase 2	Letters
Training	
Testing	

Note. A = the stimulus set shown in Figure 1.A; B = the sets of stimuli shown in Figure 1.B.

Results

Preliminary Test

On average, it took capuchins 5.5 sessions to achieve 75% correct performance in the training phase, with a range between 2 sessions and 12 sessions (i.e., 48 to 288 trials). All the monkeys performed at a high accuracy level during the last 48 trials, with an average accuracy of 85.0% (range 79.2% to 89.6%).

The overall mean percentages of correct responses observed during the test ranged from 74.0% to 90.7%. One-sample *t* tests showed that the percentage scores obtained in each matching condition were significantly above the 50% expected by chance, grouping: $M = 80.4%$, 95% confidence interval (CI) = 70.6 to 90.2, $t(5) = 8.00$, $p < .001$; control: $M = 82.6%$, 95% CI = 78.2 to 87.1, $t(5) = 19.02$, $p < .001$. A paired-samples *t* test comparing percentages of correct responses obtained in the control and the grouping trials did not reveal a significant difference between these two conditions, $t(5) = .78$, $p > .10$. Overall, the results demonstrate that capuchins were successful at integrating elementary visual components to form a unitary percept. The fact that the subjects were able to perform at a high level of accuracy in the condition featuring multi-element patterns, and the fact that their level of accuracy in this condition did not differ from their level of accuracy in the control trials, demonstrates that the stimuli were appropriate for inducing the perception of a whole shape on the basis of a configuration of elements.

Grouping Cues Test

In the training phase, all capuchins learned to match the three filled stimuli relatively easily. In Phase 1 (irregular patterns), the overall mean number of sessions to criterion was 4.0 sessions, with a range between 2 and 7 sessions, and the accuracy levels in the last 48 training trials ranged between 79.0% and 85.4%. In Phase 2 (letters), all the monkeys reached the criterion in 2 training sessions, with an average accuracy of 92.1% (range 87.5% to 97.9%).

In the test phase, the overall mean percentage of correct responses recorded for irregular patterns ranged between 77.8% and 85.6%, whereas the average accuracy observed for letters ranged between 74.7% and 88.9%. One-sample *t* tests were conducted to

assess whether, in each phase of the task, the mean accuracy scores observed in each matching condition was significantly higher than the chance level of 50%. In the grouping condition, we collapsed data obtained for stimuli composed of different shaped elements (crosses, circles, or tilted Ls) because the results of preliminary one-way analyses of variances (ANOVAs) did not show evidence of a significant effect of the stimulus local features on capuchin's performance, irregular patterns: $F(2, 10) = 3.3$, $p > .1$; letters: $F(2, 10) = 0.54$, $p > .1$. The *t*-test analyses revealed that the accuracy level of the monkeys was significantly above the level expected by chance in all conditions, irregular patterns: Id-MTS, $M = 88.9%$, 95% CI = 82.9 to 94.9, $t(5) = 16.73$; grouping: $M = 81.0%$, 95% CI = 76.1 to 85.9, $t(5) = 16.17$; proximity: $M = 79.4%$, 95% CI = 75.7 to 83.2, $t(5) = 20.25$; shape similarity: $M = 79.9%$, 95% CI = 76.9 to 82.9, $t(5) = 25.51$; orientation similarity: $M = 73.6%$, 95% CI = 67.9 to 79.3, $t(5) = 10.65$, all $ps < .001$; letters: Id-MTS: $M = 93.1%$, 95% CI = 88.7 to 97.4, $t(5) = 25.68$, $p < .001$; grouping: $M = 88.2%$, 95% CI = 82.5 to 93.8, $t(5) = 17.36$, $p < .001$; proximity: $M = 85.6%$, 95% CI = 75.3 to 95.9, $t(5) = 8.89$, $p < .001$; shape similarity: $M = 83.6%$, 95% CI = 75.6 to 91.5, $t(5) = 10.79$, $p < .001$; orientation similarity: $M = 70.8%$, 95% CI = 62.9 to 78.7, $t(5) = 6.76$, $p < .01$. Thus, MTS performance was highly accurate both in conditions where the comparison stimuli featured solid figures (Id-MTS) and in conditions where the comparison stimuli were composed of multi-element patterns on different types of background.

An ANOVA was performed on the observed percentage of correct responses, with matching condition (Id-MTS, grouping, proximity, shape similarity, orientation similarity) and stimulus type (irregular patterns, letters) as repeated measures factors. A significant main effect was obtained for matching condition, $F(4, 20) = 20.75$, $p < .001$, $[\eta]_p^2 = .81$. Multiple comparisons (FDR method) revealed a higher percentage of correct responses in the Id-MTS condition (91.0%) than in the other matching conditions (grouping, 84.6%, $p < .05$; proximity, 82.5%, $p < .05$; shape similarity, 81.7%, $p < .01$; orientation similarity, 72.2%, $p < .01$), suggesting that shape identification was facilitated when no grouping operation was required. Moreover, the overall accuracy scores for the grouping condition, in which no background elements were present, were significantly higher than the accuracy scores observed for shape similarity ($p < .05$) and orientation similarity ($p < .01$) conditions. Furthermore, the percentages of correct responses observed in both proximity and shape similarity conditions were significantly higher than the percentages of correct responses observed in the orientation similarity condition (proximity vs. orientation similarity, $p < .01$; shape similarity vs. orientation similarity, $p < .05$). The effect of stimulus type was not significant (irregular patterns, 80.6%; letters, 84.3%). Likewise, the interaction between stimulus type and matching condition was not significant. Figure 2 shows the average performance of the monkeys for the five matching conditions. As stimulus type did not produce a significant effect, values for irregular patterns and letters have been combined in the figure.

Trial 1-response analyses were performed to assess the extent to which learning was required to match correctly the stimuli making up the samples and the alternatives in the different conditions of the task. The Id-MTS, proximity, shape similarity, and orientation similarity conditions featured the presentation of six compound stimuli (i.e., three irregular shapes and three alphabetic letters, see

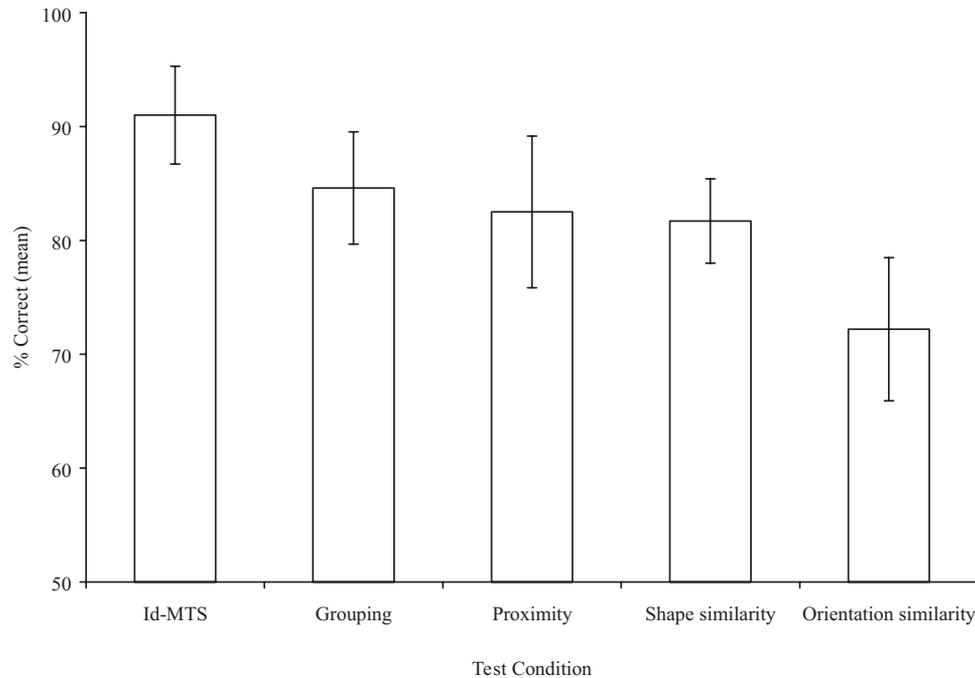


Figure 2. Mean percentages of correct responses (with 95% CI) by monkeys in each condition of the grouping cues test.

Figure 1B). Therefore, for each of these conditions, we considered the number of correct responses performed by the subject when presented with each of these patterns for the first time. In the grouping condition, 18 compound stimuli were used because each of the six compound patterns included figures composed of crosses, circles, or tilted Ls presented on a uniform background. Thus, a total of 18 responses per subject were included in the analysis. One sample *t* test revealed that the observed mean number of correct responses for the sample of monkeys on these initial trials was significantly different from the value expected by chance (i.e., nine correct responses for the grouping condition, three correct responses for the remaining four conditions) in all conditions, Id-MTS: $M = 4.8$, 95% CI = 4.0 to 5.6, $t(5) = 6.0$, $p < .01$; grouping: $M = 15.9$, 95% CI = 14.1 to 17.2, $t(5) = 10.85$, $p < .001$; proximity: $M = 5.5$, 95% CI = 4.9 to 6.1, $t(5) = 11.18$, $p < .001$; shape similarity: $M = 4.83$, 95% CI = 3.4 to 6.2, $t(5) = 3.38$, $p < .05$; orientation similarity: $M = 4.7$, 95% CI = 4.1 to 5.2, $t(5) = 7.9$, $p < .001$. This suggests that the correct responses of the monkeys were not the outcome of simple associative mechanisms such as learning a conditional discrimination by trial and error. Rather, it seems that the responses of the monkeys were informed by the particular matching relation between the sample and the comparison stimuli.

Discussion

Overall, these findings demonstrate that capuchin monkeys were able to identify the shape of compound patterns on the basis of the proximity, similarity of shape, or orientation of the elements that form them, as shown by the very high level of accuracy observed across the different conditions of the task. Thus, perceptual group-

ing in this species appears to be based on some of the grouping principles, which control perceptual organization in humans. Nevertheless, the ability of capuchin monkeys to integrate a subset of elements into a global form and segregate them from a background of other elements changed across conditions involving different grouping cues. Proximity proved a very effective grouping cue for our subjects. The level of performance of the monkeys in this condition did not differ from that observed in the grouping trials in which no segregation from background elements was required. This finding converges with the results of previous studies carried out on capuchins, in which the density of hierarchical stimuli was manipulated (De Lillo et al., 2005; Spinozzi et al., 2003) by showing that the spatial proximity of the elements plays an important role in facilitating the perception of the global form of discontinuous stimuli. In addition, the present data show that capuchin monkeys can perform at a very high level of accuracy also in conditions in which the identification and segregation of a multi-element pattern requires the analysis of shape similarity as a grouping cue. Moreover, the performance level of monkeys in this condition was indistinguishable from that observed in the proximity condition, indicating that these two grouping cues were equally effective for the identification of the shape of grouped elements. By contrast, grouping by orientation similarity proved more difficult. The identification of a whole figure in this condition requires the ability to segregate the foreground and the background on the basis of the slope of the elements. Capuchins were able to use this grouping cue because their accuracy scores were well above chance level. Notwithstanding this, the performance level of monkeys in this condition was significantly lower than that observed in conditions in which the segregation process could be performed on

the basis of proximity and shape similarity. It is interesting to note that the relative dominance of grouping by proximity and shape similarity over grouping by orientation emerged both in conditions featuring irregular shapes and in conditions featuring letter-shaped stimuli. This suggests that the differential effect of these grouping cues in the visual processing of monkeys was not specifically related to the particular stimuli used in the task.

Experiment 2

The aim of Experiment 2 was to collect data on humans, which enabled meaningful comparisons with data collected on tufted capuchin monkeys. To this end, we used the same stimuli and the same MTS paradigm used with monkeys. The design of the present experiment was similar to that adopted in the grouping cues task of Experiment 1 and featured the two sets of stimuli presented in Phase 1 (irregular patterns) and Phase 2 (letters) respectively. However, the order of presentation of the two phases was counterbalanced across participants.

Method

Participants

The participants were 12 first-year undergraduate students (4 men and 8 women) from the University of Leicester who took part in the study in exchange for course credits. They had normal or corrected-to-normal visual acuity and were naïve about the experimental hypothesis of the study.

Apparatus and Stimuli

The experimental setup was composed of Pentium PCs with 17" SVGA monitors with a resolution of 1024×768 pixels. A response box was connected with the PC and allowed the participant to make a choice by means of two response keys, respectively, located on the left and the right of the response box. The application used to generate stimuli on the computer screen and to collect the responses of the subjects was developed at the University of Leicester, using E-prime (Psychology Software Tools, Inc.).

Bitmaps of the stimuli previously used in the grouping cues task of Experiment 1 with monkeys were used for stimulus presentation on the computer screen. Therefore, the participants were tested with the set of stimuli featuring the irregular figures used in Phase 1 and the set of stimuli featuring the alphabetic letters used in Phase 2 of the Experiment 1 (see Figure 1B). The size of the stimuli, as they appeared on the computer monitor, was double the size of the stimuli used with the monkeys. The distance of the participants from the screen was about twice the distance used with the monkeys so that the visual angle subtended by the stimuli was kept approximately the same as that used with the monkeys.

Procedure and Design

Each participant sat in front of the computer screen at a distance of approximately 30 cm. At the beginning of each trial, a stimulus sample was displayed centrally at the top of the screen. After a brief, randomly generated interval, lasting between 2 and 3 s, the two comparison stimuli appeared at the bottom left and right corners of the screen, respectively. The task for the participants

was to indicate which of the two comparison stimuli was identical or more similar to the sample stimulus, by pressing one of two keys (the left and the right arrow to signal the selection of the stimulus on the left or right, respectively) on the computer keyboard. All three stimuli remained present on the screen until a response was made.

The order of presentation of the two sets of stimuli (irregular patterns and letters) was counterbalanced between participants. Half of the participants received the set irregular patterns first and then the set letters; the other half received the set letters first and then the set irregular patterns. For each set of stimuli, each participant performed a session of 180 trials, which included the five matching conditions (Id-MTS, grouping, proximity, shape similarity, orientation similarity) featured in Experiment 1 with monkeys. For each stimulus set, each matching condition comprised 36 trials, which were presented in a pseudorandom order so that two identical trials could not appear consecutively.

Results

Grouping Cues Test

The overall mean percentage of correct responses recorded for irregular patterns (Phase 1) ranged between 84.4% and 99.1% whereas the average accuracy observed for letters (Phase 2) ranged between 86.1% and 99.1%. One-sample *t* tests were conducted to assess whether, in each phase of the task, the mean percentage of correct responses observed for each matching condition was significantly higher than the chance level of 50%. In the grouping condition, data obtained for patterns composed of small crosses, circles, and tilted Ls on a homogeneous background were collapsed because previous analyses revealed no significant effect of the element-shape variable, irregular patterns, $F(2, 22) = 0.47$, $p > .1$; letters, $F(2, 22) = 2.42$, $p > 1$. The analyses revealed that the accuracy level of the participants was significantly above the level expected by chance in all conditions, *irregular patterns*: Id-MTS: $M = 99.3\%$, 95% CI = 98.2 to 100.4, $t(11) = 98.13$; grouping: $M = 94.0\%$, 95% CI = 92.2 to 95.8, $t(11) = 57.79$; proximity: $M = 95.3\%$, 95% CI = 93.6 to 97.0, $t(11) = 61.69$; shape similarity: $M = 86.5\%$, 95% CI = 82.7 to 90.3, $t(11) = 24.73$; orientation similarity: $M = 86.6\%$, 95% CI = 82.5 to 90.7, $t(11) = 23.04$; all $ps < .001$; *letters*: Id-MTS: $M = 99.5\%$, 95% CI = 98.8 to 100.2, $t(11) = 157.43$; grouping: $M = 96.4\%$, 95% CI = 95.2 to 97.6, $t(11) = 89.5$; proximity: $M = 96.3\%$, 95% CI = 95.1 to 97.5, $t(11) = 89.5$; shape similarity: $M = 86.9\%$, 95% CI = 80.7 to 93.12, $t(11) = 15.15$; orientation similarity: $M = 88.6\%$, 95% CI = 83.5 to 93.7, $t(11) = 19.36$; all $ps < .001$.

A mixed-model ANOVA was performed on the percentage data, with matching condition (Id-MTS, grouping, proximity, shape similarity, and orientation similarity) and stimulus type (irregular patterns, letters) as within-subjects factors, and presentation order (letters first, irregular patterns first) as between-subjects factor. The ANOVA revealed a significant main effect for matching condition, $F(4, 44) = 7.83$, $p < .001$, $\eta_p^2 = .42$, but not for stimulus type (irregular pattern, 92.3%; letters, 93.5%) and for presentation order (letter first, 92.5%; irregular pattern first, 93.3%). Multiple comparisons (FDR method) carried out on the mean accuracy scores recorded in the five matching conditions revealed a significant difference between the level of accuracy

observed in the Id-MTS condition (99.4%) and all the other conditions (grouping, 95.2%, $p < .01$; proximity, 95.8%, $p < .05$; shape similarity, 86.7%, $p < .01$; orientation similarity, 87.6%, $p < .01$). Moreover, the grouping and the proximity conditions did not differ from each other, but performance in both these conditions was different from that registered for the shape similarity and orientation similarity conditions (all $ps < .05$). The latter two conditions did not prove different from each other. The interactions were not significant.

A second 2×5 (Species \times Matching Condition) mixed ANOVA was carried out to evaluate in more detail the pattern of differences observed in the performance of humans and capuchin monkeys in the different grouping conditions. Because stimulus type (letters or irregular patterns) did not yield significant effect in the previous analyses, this variable was not taken into consideration. The ANOVA revealed a significant main effect for species, $F(1, 16) = 65.44$, $p < .001$, $\eta_p^2 = .80$ (humans, 92.9%; monkeys, 82.4%), and matching condition, $F(4, 64) = 26.06$, $p < .001$, $\eta_p^2 = .62$. Moreover the interaction Species \times Matching Condition proved significant $F(4, 64) = 7.68$, $p < .001$, $\eta_p^2 = .32$. Multiple comparisons (FDR method) replicated the pattern observed separately in each species. In both humans and capuchin monkeys, the accuracy scores for the Id-MTS condition were significantly different from those observed in all other matching conditions, whereas no significant difference emerged between grouping and proximity conditions. However, while in humans a significantly higher choice accuracy was obtained in the proximity condition compared to both shape similarity and orientation conditions, in monkeys a significantly lower choice accuracy was obtained in the orientation similarity condition compared to both the proximity or shape similarity conditions (see Figure 3). Moreover, interspecies comparison revealed that, in all matching conditions, the accuracy scores of humans were significantly higher

than the accuracy scores of monkeys (similarity conditions, $p < .005$; all the other conditions, $p < .001$).

Discussion

Overall, the results of Experiment 2 show that human participants performed at a very high level of accuracy in all conditions of the task. The results of the analysis carried out on trials featuring the presentation of multi-element patterns showed that humans successfully organized disconnected elements into coherent wholes using proximity, similarity of shape, and orientation as grouping cues. However, we found that these grouping factors had a different impact in the unit formation. In fact, although the matching performance of the participants were highly robust, their accuracy at detecting the shape of compound stimuli was consistently better when the figure-ground segregation process required the use of proximity than when it required the use of similarity of shape and orientation grouping cues. This finding is in agreement with evidence from other studies suggesting that proximity plays a predominant role in the perceptual organization of humans and is more salient than similarity as a perceptual grouping cue (Ben-Av & Sagi, 1995; Chen, 1986; Han & Humphreys, 1999; Han et al., 1999; Quinlan & Wilton, 1998). The relative dominance of proximity over similarity by shape and orientation emerged for both alphabetic letters and irregular figures, that is, for two sets of stimuli that differed with respect to the degree of familiarity to human participants, suggesting that this variable did not play a significant role in this task.

A direct comparison of humans' and capuchins' data revealed some similarities in the matching performance of the two species. Both humans and capuchins were on average better at identifying the matching comparison stimulus in conditions featuring the presentation of filled shapes (i.e., Id-MTS) compared to conditions

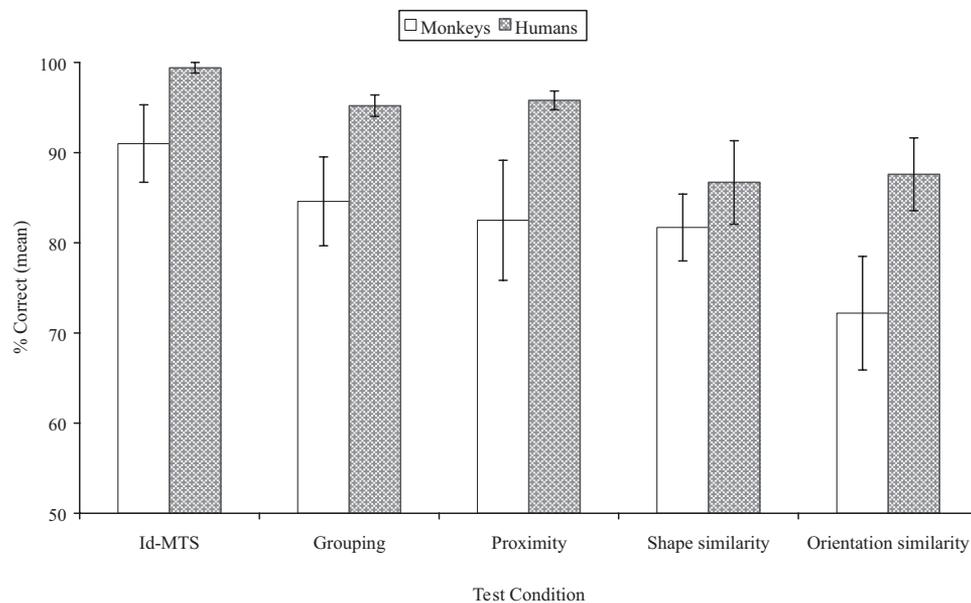


Figure 3. Mean percentages of correct responses (with 95% CI) by humans and monkeys in each condition of the grouping cues test.

featuring multi-element figures on different types of backgrounds. This shows that, in both species, the perception of a visual pattern was facilitated when no grouping operation was required.

A similarity between the modes of processing of the two species emerged also in their differential use of proximity and orientation similarity as grouping cues. Participants' mean accuracy scores in the orientation condition, although above chance level, were significantly lower than those recorded in the proximity condition, revealing that orientation was a less effective grouping factor for both humans and capuchin monkeys. This is consistent with other studies conducted in adult humans in which it has been found that items similar in shape but different in orientation are difficult to group together (Beck, 1966), whereas items placed at different distances are readily grouped together on the basis of their relative spatial proximity (Han et al., 1999).

On the other hand, some differences between humans and monkeys emerged in the use of shape similarity as a perceptual grouping cue. In fact, although for humans the detection of an integrated figure was carried out less efficiently when it required shape similarity than proximity grouping, for capuchins shape similarity was as effective as proximity in defining the form of multi-element patterns.

It could be argued that differences between humans and capuchin monkeys in the different degree of reliance on the grouping cues examined in the present study might be related to differences in the testing procedure that we used with the two species. For example, whereas humans were instructed verbally to select the comparison stimulus that was the most similar or identical to the sample stimulus, capuchins needed a long training period to learn to solve the MTS task on the basis of a matching rule (see Spinozzi et al., 2003). It is, however, difficult to envisage how such procedural differences could explain the fact that humans performed better in particular conditions and monkeys performed better in others, especially considering the overall high level of accuracy shown by the two species.

Another difference in the testing procedure used with humans and capuchins concerned the reinforcement schedule. Humans were never given feedback concerning whether their responses were correct or not. By contrast, capuchins were selectively reinforced for every correct response. Such procedural difference may have differentially affected overall performance, but it cannot explain why similarity grouping was processed differently by the two species.

General Discussion

This study featured a comparative investigation of the relative weight given to proximity, similarity by shape, and orientation as perceptual grouping cues by humans and capuchin monkeys. We used a figure-ground segregation task requiring the participants to identify the form of a multi-element pattern displayed on a background of other elements. If correctly identified, this form could be used by the participants to decide which of two comparison stimuli matched the sample in an MTS task. Performance in the MTS task gave us an indication of the extent to which the participant had been able to perceive a whole. According to the different conditions of the task, the proximity, the similarity of shape, or of the orientation between the elements of the compound patterns and the background elements was manipulated to provide different group-

ing cues as the basis for the unit formation leading to figure identification.

The results of Experiment 1 carried out on capuchins show that, although the monkeys were extremely proficient in all the conditions of the task, they were on average better at identifying the compound patterns when the segregation process was based on grouping by proximity and by shape similarity compared to conditions requiring grouping by element orientation.

The results of Experiment 2 with humans show that the accuracy level of the participants was significantly higher when the discrimination of the compound patterns required grouping by proximity than when it required grouping by similarity of shape and element orientation.

Our findings that humans do not give the same weight to proximity and similarity as grouping cues are consistent with those reported by previous research carried out with other stimuli and paradigms (Ben-Av & Sagi, 1995; Chen, 1986; Han & Humphreys, 1999; Han et al., 1999; Quinlan & Wilton, 1998). For example, Han et al. (1999) showed that the discrimination of compound patterns formed by proximity grouping was faster and more accurate than that of patterns formed by similarity grouping. The notion that proximity and similarity grouping cues may have a different status in human visual perception and may involve different processes is also consistent with recent electrophysiological evidence indicating that processes based on these different grouping cues have distinct neural substrates (Han, Ding, & Song, 2002).

The present results reveal that there are both similarities and differences between humans and capuchin monkeys in their relative use of different grouping cues. On the one hand, for both humans and monkeys, spatial proximity was a very effective grouping factor as it produced a higher level of MTS performance than orientation similarity in both species. On the other hand, some potential differences between the two species emerged in relation to the relative ease of use of shape similarity as a grouping cue. In fact, when the proximity cue was eliminated by equalizing the distance between all the local elements of the displays, differences in both shape (triangles vs. circles) and orientation (upright vs. tilted Ls) between the background elements and the stimulus component elements reduced to some extent the effectiveness of the segregation process in humans. By contrast, in capuchins, only grouping by orientation was less effective whereas grouping by shape similarity did not impair the segmentation of the compound pattern from the background. It is possible that the strong propensity typical of these monkeys to focus on the local details of visual stimuli (De Lillo et al., 2005; Spinozzi et al., 2006, 2003) enabled them to efficiently extract information about figure boundaries, facilitating local element grouping, but such ability seemed to depend on the features that defined the local items.

There is evidence from studies focusing on human participants (Field, Hayes, & Hess, 1993; Ledgeway, Hess, & Geisler, 2005) that suggests that the relative orientation of the elements defining a simple spatial contour has a strong influence on the segregation of that contour from a background of elements with a different orientation. For instance, Ledgeway et al. recently found that it was easier to detect contours when the element orientations were aligned with (parallel to) the contour axis. Performance was marginally worse when elements and contours are orthogonal. The most difficult conditions were those in which elements were ori-

ented obliquely with respect to the contour. In light of these findings, it is possible to suppose that the difficulty in using orientation as grouping cue observed in the present study in both humans and capuchin monkeys may be due to the fact that the local L-elements composing the figures were rotated by 58° with respect to the contours defining those figures. Such a misalignment might have hindered the discrimination of the stimulus features, such as line-slope differences, weakening to some extent the segregation process in both species.

However, it may be argued that in our study the differently orientated Ls, which were used to test orientation similarity, could have been perceived by the monkeys as elements differing in shape. In light of this hypothesis, the fact that the identification of a compound pattern in capuchins was easier in conditions featuring a group of circles in a background of triangles than in conditions featuring a group of tilted Ls in a background of upright Ls, suggests that several properties of the stimulus components can selectively affect perceptual grouping process of monkeys.

Studies using texture-segregation tasks have shown that, in humans, several features of the stimulus play an important role in visual perception. For example, disparity of element orientation does not always enable easy segregation between groups of elements: a group of Xs is not as easily detectable in a field of pluses as it is a group of diagonal lines in a field of vertical lines (Beck, 1982). The same is true for disparity of shape: A group of triangles is easily segregated from a group of arrows (Williams, 1992), but a group of upright Ts is less detectable in a field of upright Ls. In light of these findings, it seems important to carry out further experiments using displays with a variety of contrasting elements to assess whether and to what extent the manipulation of several properties of textured stimuli can differently affect perceptual grouping processes in capuchin monkeys.

Overall, the results of the present study seem to indicate that given the similarities observed in the two species, it is unlikely that the differences that have been reliably observed between humans and monkeys in the processing of the global shapes of complex stimuli are due to a failure in monkeys to use some of the visual grouping cues that are effective in humans.

Nevertheless, the difference in the relative influence of different grouping cues in the two species add more information to that provided by other comparative investigations that have found visual processing differences between humans and capuchin monkeys. For example, Spinozzi, De Lillo, and Casterlli (2004) compared the performance of humans and capuchin monkeys in tasks requiring the participants to identify a stimulus part embedded in a more complex pattern. It emerged that, in contrast with humans, capuchins found it easier to detect the local components of visual stimuli when they were segmented into relatively disconnected features rather than when they were grouped in conformity with particular principle of organization such as “closure” or “good continuation.” However, that study was not designed to assess the relative role of different grouping cues in the task and, in the conditions featuring grouped elements, several grouping cues could potentially operate at the same time. The present study provides further information that may help us to disentangle the complex pattern of interaction between the operation of different grouping cues in humans and capuchin monkeys.

Taken together, our research findings support the idea that some of the differences in the perception of whole patterns observed so

far between humans and capuchin monkeys may be, at least in part, accounted for by the relative dominance of some grouping cues in the two species. However, it is still unclear whether such differences in the processes underpinning visual perception would actually reflect differences in early vision (pre-attentive) mechanisms or in attentional mechanisms.

The question remains of whether differences between humans and capuchin monkeys lie in conspicuous differences in the neural bases of their visual processing of the grouping cues. Unfortunately, very little is known on the functional sensitivity of the visual system of capuchins. The available evidence suggests that, in many respects, the ability to see of this New World monkey species is similar to that of humans: Capuchin monkey’s visual acuity and sensitivity to brightness is equivalent to that of macaques and humans (Ankel-Simons, 2007; de Valois, 1971; Fragazy, Visalberghi, & Fedigan, 2004). However, capuchins appear to be polymorphic as far as their color vision is concerned, with males being dichromats and females having either dichromatic or trichromatic vision (Jacobs, 2007). Dichromatic individuals have difficulty discriminating red from orange that trichromats find it easy to differentiate. However, the differences between humans and monkeys observed in this study cannot be accounted for by a different capacity to perceive colors considering the fact that the stimuli used in our tasks featured white shapes presented against a black background.

A final note concerns the variations in the spatial-frequency components of the stimuli. It has been suggested that perceptual grouping could be achieved by the application of low-pass filtering of visual images (Beck, Sutter, & Ivry, 1987), and some researchers have suggested that similarity grouping depends on an analysis of higher spatial frequencies than does proximity grouping (Han et al., 2002). The clear advantage for shape similarity grouping shown by capuchins in our task may be due to a highly developed ability of these monkeys to process high-spatial frequency information. However, if it is the case, it remains unclear why, in capuchins, such a mechanism should facilitate grouping by shape similarity but not by orientation similarity. However, it is impossible to completely rule out the possibility that more subtle perceptual differences exist between the two species and might account for the findings. As recent neurophysiological data indicate that different cortical processes subserve different gestalt grouping operations in humans (Han et al., 2002), it is possible to speculate that some of the behavioral differences observed here map onto neurophysiological and neuroanatomical interspecies differences so far overlooked in the literature on primate visual systems.

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