

Research report

Pattern recognition in tufted capuchin monkeys (*Cebus apella*): The role of the spatial organisation of stimulus parts

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Abstract

We report four experiments aimed at characterising the role played by the encoding of the spatial relationship between stimulus parts in pattern recognition in capuchin monkeys, as assessed by a matching to sample task. The results of the first experiment, which were also reliably replicated at different stages in the course of the study, indicated that the simultaneous rotation and/or translation of the four parts into which the stimuli were divided, but not a global rotation of the entire stimulus, impaired matching performance in capuchin monkeys. Experiments two and three showed that matching performance was not impaired following similar manipulations of a subset of one, two or three parts. In experiment four, the same task was presented to human subjects. The same pattern of results emerged for humans and monkeys in trials where all the four stimulus parts were presented. However, the matching performance of humans was affected more than that of capuchin monkeys when only a subset of stimulus parts was featured in the task. These results support the conclusion that the matching performance of capuchin monkeys is affected by the rearrangement of stimulus parts and, as such it seems to rely on global properties of the stimulus such as the spatial relationships of the component parts. However, the remarkable ability of capuchin monkeys to identify a stimulus on the basis of a subset of parts suggests that the reliance on the global properties of the stimuli may not be pervasive as it is in humans.

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Organisms, which rely on vision to identify relevant objects in their environment need to determine which parts of a visual scene belong together despite different possible interpretations of the pattern of light reaching their receptors. Some species reduce the complexity of this problem by identifying relevant items in the environment such as food, predators or conspecifics on the basis of a few distinctive features, which probabilistically lead to a correct interpretation of ambiguous stimuli. An example of such a strategy is provided by the classic study of aggressive behaviour in sticklebacks [26]. For this species, a single feature (a red patch) in a roughly specified position (ventral rather than dorsal) in basic two-dimensional patterns will evoke an aggressive response aimed at threatening an invader. By contrast, very detailed models preserving other features of a rival

stickleback will fail to trigger the relevant behaviour in absence of the critical red patch.

Organisms with a more sophisticated visual and cognitive system and a less rigid pairing of visual input and behavioural responses face the problem of having to integrate a number of more elementary stimulus parts into whole objects or patterns in order to identify and segregate meaningful figures from the background.

Pattern recognition in humans is achieved on the basis of stimulus representations containing both component parts and structural descriptions, which specify their spatial relationships [2]. Considering the similarity of the visual system of human and non-human primates, one would expect that similar processes and representations should underpin pattern recognition in humans and in non-human primates. Nevertheless, it has been suggested that capuchin monkeys may recognise and classify images by using a single relevant salient feature [4]. In fact, on the basis of an analysis of the errors performed by capuchin monkeys in a task requiring the discrimination of photographs

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containing humans from those not containing humans D'Amato and Van Sant [4] suggested the possibility that the animals were exploiting the systematic and spurious presence of a red patch which appeared in most photographs containing humans. Although D'Amato and Van Sant did not present their results as conclusive, their results have been interpreted by others (e.g. [21]) as supporting theories of pattern recognition and classification whereby the detection of one or more features is assumed to control the behaviour of the subject towards a stimulus regardless of their spatial arrangement. Even if it would be reasonable to assume that in some cases the reduction of a complex classification problem to the detection of a set or a single critical feature, as in the case of the capuchin monkeys tested by D'Amato and Van Sant [4], may reflect a strategy adopted by the animals rather than a limitation of their cognitive or perceptual systems, there are data indicating that there may be differences between humans and capuchin monkeys in their ability to integrate elementary features into global patterns.

One of our previous studies compared the performance of humans and capuchins in a task requiring the matching of whole visual patterns with some of their component parts obtained by segmenting the whole stimuli in various ways [23]. It emerged that humans were more accurate in this task when the stimulus parts were constructed by organising elementary features according to grouping principles based on spatial proximity, good continuation, symmetry and closure. By contrast, capuchin monkeys were consistently more accurate when the stimulus parts were not assembled on the basis of these principles and, for a human observer, consisted of a collection of disconnected features [23]. These results indicate that the type of segmentation that favours the detection of stimulus parts in humans hinders the solution of the same task in capuchin monkeys, and *vice versa*.

The results of comparative studies [6,8,25] obtained using hierarchical visual stimuli [20] indicate that these differences cannot be accounted for exclusively by the fact that some component parts of complex shapes may be more familiar to humans than to other species. Hierarchical stimuli are global shapes made up by the spatial arrangement of small local shapes. Typically, in studies with hierarchical stimuli, the same shape will appear at the local level in some trials and at the global level in other trials. This ensures that the emergence of an advantage in the processing of one of these levels cannot be accounted for by the particular shape used and by its familiarity. Studies using hierarchical stimuli show that in contrast with adult humans and children [6], who typically show a global advantage, different species of monkeys, including baboons [7,8], capuchins [6,25] and rhesus monkeys [14] show a local advantage.

Further studies [24] indicate that the preference shown by monkeys for the analysis of the local attributes of complex stimuli, rather than their global configuration, cannot be accounted for by a bias towards selectively attending to stimuli of a particular size (such as the specific size of the local elements of hierarchical stimuli). In fact, in monkeys the local advantage persists when the global shape of smaller stimuli is made of the same size of the local shape of larger stimuli [24].

Moreover, whereas the global advantage shown by humans is robust across variations of the spatial separation of the local

elements of a global configuration, the ability of monkeys to identify the global configuration is severely compromised by the reduction of the density of the stimuli [6,8,25].

These differences so reliably observed between the perceptual processes of humans and monkeys are particularly remarkable considering that the visual system of human and non-human primates is considered to be very similar [12,29]. The same visual pathways are present in both humans and monkeys [28] and an extensive amount of electrophysiological and neurophysiological research is carried out on non-human primates under the assumption that the visual system of monkeys represents a good model of the human visual system (see, for example [15]). These reasons make it worthwhile to carry out studies aimed at characterising the perceptual grouping processes of primates and their ability and limitations in the visual analysis of configurations of more elementary units.

Moreover, it is worth noting that some of the differences observed between humans and monkeys [6–8,25] are less clear-cut when great apes are considered. Chimpanzees tested on a successive matching to sample task with hierarchical stimuli show a global advantage [14]. In other studies where a local advantage has been observed in chimpanzees, it could easily be reversed using stimulus manipulations, which did not affect the local advantage shown by monkeys [9,10]. Thus, considering that the differences between humans and non-human primates in the processes responsible for perceptual organisation become more evident with the increase in their taxonomic distance, an additional value of research into these processes is that they tap dimensions of phylogenetic relevance and may shed light on the evolution of human high level perceptual skills.

Although it may seem relatively uncontroversial that any organism which is able to recognise patterns and objects must encode, at some level, the spatial relationship between stimulus parts, the comparative literature is not always in agreement concerning the extent to which all animal species equipped with a sophisticated visual system are equally dependent on the spatial arrangement of stimulus parts for pattern recognition.

For example, contradictory results emerge from the literature on avian species with some studies suggesting that pigeons may not be sensitive to the spatial relationships between the component parts of line drawings (e.g. [3]) and others indicating that pattern recognition in the same species can be compromised when the spatial organisation of stimulus parts are disrupted [16,17]. In fact, Kirkpatrick-Steger et al. [16,17] have shown that pigeons, trained to discriminate line drawings of different objects found it difficult to identify the objects when the spatial organization of their components was disrupted. Variations in the arrangement of local features of stimuli (obtained by scrambling their component parts) had a dramatic impact on the accuracy of recognition. This finding suggests that the spatial configuration of the components of objects plays a similarly important role in pattern recognition in pigeons and in humans [2].

The main aim of the present study is to assess whether capuchin monkeys (*Cebus apella*), are able to recognize a visual pattern when it is decomposed into parts and the spatial organization among its component parts is modified. Also, by manipulating different aspects of the spatial organisation of

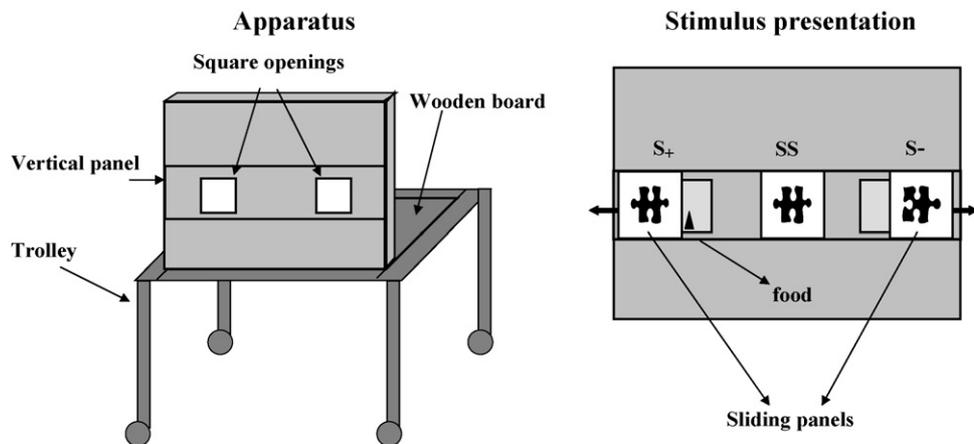


Fig. 1. Scheme of the apparatus used in this study.

stimulus parts in a matching to sample task, we aimed to perform a detailed assessment of the relative importance of different dimensions for the successful identification of two-dimensional patterns in capuchin monkeys and humans. In order to minimise the influence of other factors such as stimulus familiarity and the possibility, for humans, to use verbal descriptions of the stimuli and their parts, we used a set of patterns shaped as different jigsaw pieces (see Ref. [18]). In fact, for this type of stimuli ready made labels and verbal descriptions of the internal relationships of their parts should not be available.

1. Experiment 1

The aim of Experiment 1 was to assess to what extent pattern recognition in capuchin monkeys relies on the spatial organisation of the stimulus parts. Using a similarity matching to sample (MTS) task, subjects were presented with a visual pattern as the sample and had to choose which one of two comparison stimuli was more similar to the sample. According to the different conditions of the experiment, in some trials, the spatial organization of the component parts of the stimulus were altered whereas, in other trials, the orientation of the whole stimulus was modified keeping the internal relationship between the parts unchanged. If the spatial organization of the parts played an important role in the recognition of the figure, the monkeys should have found the first type of trials more difficult than the second.

1.1. Method

1.1.1. Subjects

The subjects were six adult capuchin monkeys (*C. apella*), four males (Narciso, Patè, Pepe, Gal) and two females (Brahms, Pippi), with an age range of 11.03–21.07 years ($M = 16.02$). The monkeys lived in four social groups, each housed in an indoor–outdoor cage (indoor: 3.0 m long \times 1.7 m wide \times 3.0 m deep; outdoor: 2.5 m \times 1.7 m \times 3.0 m) at the Istituto di Scienze e Tecnologia della Cognizione, Consiglio Nazionale delle Ricerche (C.N.R.), in Rome, Italy. Each subject was separated from the group solely for the purpose of testing, just before each daily testing session. Food pellets were freely available before and after testing. Fresh fruit and vegetables were provided after testing. Water was always available. All the monkeys were familiar with the MTS procedure but were naïve with respect to the specific test featured in this study.

1.1.2. Apparatus

A schematic representation of the apparatus used for the experiment is presented in Fig. 1. It consisted of a wooden panel (45 cm long, 35 cm high and 2 cm deep) with two square openings (5 cm \times 5 cm), symmetrically placed at 10 cm from the centre and roughly at the eye level of the subjects. 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, 50 cm wide, 55 cm high). Three polyvinyl chloride PVC lids (6 cm long, 7 cm high and 0.3 cm deep) were used for stimulus presentation. Two sliding lids were placed in front of the square openings of the vertical panel. The third lid was fixed in a central position between the other two. The apparatus was installed outside the experimental cage (the indoor home cage), behind a transparent Plexiglas panel (45 cm long, 40 cm high) mounted on the front wall of the experimental cage. The Plexiglas panel had two symmetrical lateral arm holes (15 cm long, 5.5 cm high) in positions corresponding to the square openings covered by the sliding lids on the apparatus. The monkey had to insert its arm through one of the two holes, move laterally one of the sliding lids covering the panel square openings, in order to retrieve a peanut.

1.1.3. Stimuli

The stimulus set used in the present study is shown in Fig. 2. It included three different black figures shaped as jigsaw pieces (labelled A, B, C, respectively), and their parts. The parts (labelled p1, p2, p3, p4) were created by dividing the whole figures into four quadrants (see Fig. 2). The size of the whole stimuli was 4.0 cm \times 4.0 cm and the size of each component part was 2.0 cm \times 2.0 cm. The stimuli were created using Microsoft PowerPoint, printed on white paper and glued onto PVC lids.

1.1.4. General procedure

A simultaneous MTS procedure was adopted. At the beginning of each trial, the apparatus was placed at a distance of 30 cm from the experimental cage. The experimenter placed the sample stimulus (SS) between the two square openings of the panel, in full view of the subject. Then, the experimenter simultaneously placed the two comparison stimuli, the correct (S+) and the incorrect (S-) comparison stimulus, on the sliding lids of the panel. When the animals positioned themselves in front of the apparatus (either in a seated or quadruped posture), the panel was moved within the subject's arm reach at about 15 cm from the cage. The monkey obtained the reward only if it selected and moved the lid featuring the correct comparison stimulus (S+). After the subject had moved a lid, and in the case of successful choices retrieved the reward, the panel was moved away from the cage, and a new trial was set up. The inter-trial interval was about 30 s, following a correct response and about 60 s, following an incorrect response.

1.1.5. Training

Before testing for the ability to process the stimulus parts and their organization, the monkeys were trained to discriminate the three intact stimuli (A, B, C, see Fig. 2) using a simultaneous identity MTS procedure. During this training phase, each monkey received daily testing sessions of 24 trials each.

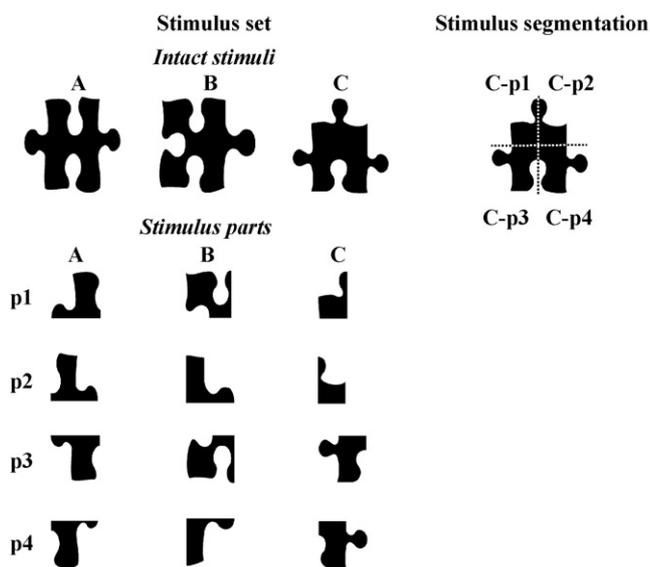


Fig. 2. The three stimuli (A, B, and C) featured in this study and the four component parts (P1, P2, P3 and P4) into which they were divided. In the example on the right-hand side of the figure stimulus C is divided into four quadrants, each containing part C-P1, C-P2, C-P3 and C-P4. Stimuli A and B were divided into parts in a similar way. See text for more details.

The acquisition criterion was 75% or more correct responses in two consecutive sessions. The overall mean number of trials performed by the monkeys to meet this criterion was 80 (range 48–168).

1.1.6. Testing

The test began for each monkey after reaching the criterion in the training phase. In each trial, SS always included one of the three intact figures (A, B or C) whereas S+ and S– varied according to the following matching condition.

- (a) *Identity-matching* (Id-MTS): S+ was identical to the sample, while S– included one of the two other intact figures (e.g. SS=A, S+=A, S–=B). These trials were identical to those presented during the training phase and were administered to ensure that the subjects were still using a matching rule during testing.
- (b) *Global rotation* (GR): S+ featured a 90° clockwise rotation in the frontal plane of the whole sample stimulus, which preserved the spatial intersections and interrelations of its parts.
- (c) *Four-part rotation* (4PR): S+ featured a 90° clockwise rotation in the frontal plan of each stimulus part, which preserved the internal spatial relationship between them. In this condition each stimulus part appeared in the same quadrant where it appeared in the sample stimulus. However, the contour of the figure as well as the spatial intersection of the parts was disrupted.
- (d) *Four-part translation* (4PT): S+ featured a diagonal translation of the stimulus parts. In this condition the quadrant in which each part appeared in S+ was different from that in which it appeared in the sample stimulus. Moreover, the contour of the figure, as well as the spatial intersection of the parts was disrupted. However, the orientation of each single part was preserved.
- (e) *Scrambled-four-part rotation/translation* (S-4PRT): S+ featured both a rotation and a translation of the stimulus parts.

Examples of trials of the different conditions are presented in Fig. 3.

Each subject performed six sessions of 30 trials each, one session a day, for a total of 180 trials. Each session included 6 trials for each matching condition (Id-MTS, GR, 4PR, 4PT, S-4PRT), with each stimulus appearing 10 times as SS. Trials of different conditions were presented in a pseudo-random order which ensured that two consecutive trials could not feature the same stimuli 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. No physical restriction was imposed on the animals during the task.

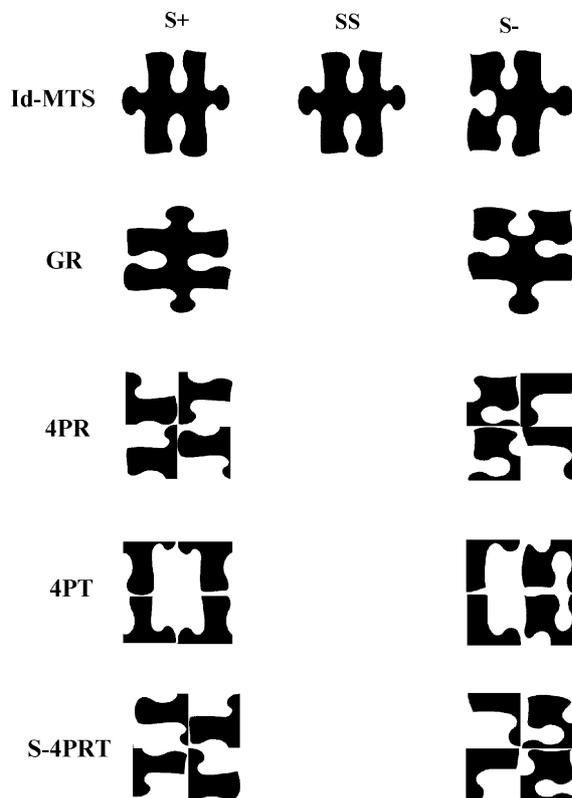


Fig. 3. Examples of trials of the different conditions used in Experiment 1.

1.2. Results

Table 1 reports the percentage of correct responses performed by each subject in each of the five testing conditions.

An analysis of variance (ANOVA) was performed on the percentages of correct responses, with matching condition (Id-MTS, GR, 4PR, 4PT, S-4PRT), and stimulus (A, B, C) as repeated measures factors. It revealed a significant main effect for Matching Condition, $F(4, 20) = 14.36, p < .001$. Post hoc comparisons (Tukey’s Honestly Significant Difference, HSD, test) indicated that performance levels for Id-MTS (89.9%) and GR (82.9%) did not differ from one another, but they were significantly higher than those for 4PR (61.6%), 4PT (62.5%) and S-4PRT (53.2%). The accuracy scores for the three latter conditions, all of which involved the rearrangement of stimulus parts (4PR, 4PT and S-4PRT), were not significantly different from each other. A bar graph of these results is presented in Fig. 4.

Table 1
Individual percentages of correct responses for each condition of Experiment 1

Subject	Id-MTS	GR	4PR	4PT	S-4PRT
Narciso	94.4***	100.0***	55.5	52.8	36.1
Patè	88.9***	86.1***	58.3	50.0	61.1
Pepe	91.7***	88.9***	69.4*	63.9	63.9
Brahms	83.3***	72.2**	72.2**	69.4*	41.7
Gal	91.7***	72.2**	50.0	72.2**	47.2
Pippi	89.8***	77.8***	63.9	66.7*	69.4*
Mean	89.9	82.9	61.6	62.5	53.2

* = $p < .05$; ** = $p < .01$; *** = $p < .001$.

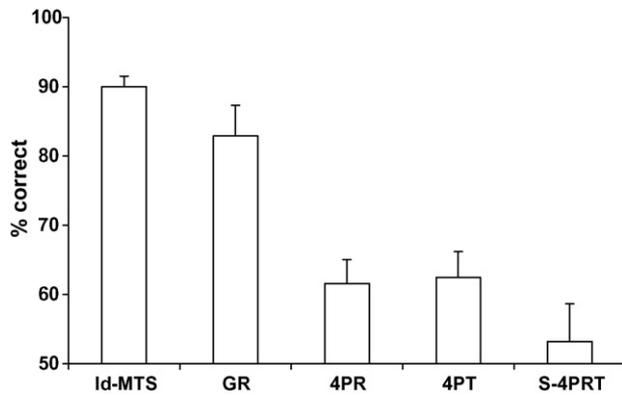


Fig. 4. Percentages of correct responses observed in the different conditions of Experiment 1. See text for more details.

The ANOVA also showed a significant main effect for stimulus type, $F(2, 10) = 7.24$, $p < .05$. Post hoc analysis indicated that the overall performance levels for stimuli B (72.8%) and C (74.4%) were significantly higher than the level of performance for stimulus A (62.8%, all $ps < .05$). The interaction between the two factors, however, was not significant. This lack of interaction suggests that the pattern of similarity and differences observed in different conditions was similar regardless of the particular stimulus involved.

One-sample t -tests were conducted to assess whether, for the group of monkeys, the mean percentage of correct responses observed for each matching condition was significantly higher than the chance level of 50%. The analyses revealed that the accuracy level of the monkeys was significantly above the level expected by chance not only for Id-MTS [$t(5) = 25.7$, $p < .001$] and GR [$t(5) = 7.4$, $p < .001$] conditions, but also for 4PR [$t(5) = 3.3$, $p < .05$] and 4PT [$t(5) = 3.4$, $p < .05$] trials. By contrast, the accuracy for S-4PRT condition did not differ from chance.

Finally, binomial tests were conducted to assess whether, for each condition, the number of correct responses performed by each subject was significantly different from that expected by a distribution with the 50% of correct responses and 50% of errors. The performance of all the subjects was highly accurate and above chance for both the Id-MTS (Narciso, $z = 5.2$; Paté, $z = 4.5$; Pepe, $z = 4.8$; Brahms, $z = 3.8$; Gal, $z = 4.8$; Pippi, $z = 4.5$; all $ps < .001$) and the GR condition (Narciso, $z = 5.8$, $p < .001$; Paté, $z = 4.2$, $p < .001$; Pepe, $z = 4.5$, $p < .001$; Brahms, $z = 2.5$, $p < .01$; Gal, $z = 2.5$, $p < .01$; Pippi, $z = 3.2$, $p < .001$). The number of correct responses was still above the level expected by chance for three subjects in the 4PT condition (Brahms, $z = 2.2$, $p < .05$; Gal, $z = 2.5$, $p < .01$; Pippi, $z = 1.83$, $p < .05$), for two subjects in the 4PR condition (Pepe, $z = 2.2$, $p < .05$; Brahms, $z = 2.5$, $p < .01$), and for one subject in S-4PRT condition (Pippi, $z = 2.2$, $p < .05$) (see Table 1).

1.3. Discussion

Overall, these results suggest that the spatial organization of the parts of a visual stimulus plays an important role in pattern recognition in capuchin monkeys. When S+ was subjected to a

global rotation which preserved both the contour of the global shape and the spatial relationships of the parts of the sample, the matching performance of the monkeys was very accurate and did not differ from that observed in the control condition (Id-MTS) which featured SS and S+ which were identical to each other. By contrast, the matching performance of the monkeys deteriorated following manipulations, which affected the spatial relationship of the stimulus parts.

However, notwithstanding their sensitivity to the spatial relationship of stimulus parts, the accuracy level of three individuals, albeit worsened, was still above chance following the translation of the stimulus parts (4PT) and the performance of two subjects was above chance despite the rotation of each stimulus part. Thus it is reasonable to conjecture that in those matching conditions, the successful monkeys were relying on more local characteristics of the stimulus, such as portions of the contour for the identification of the correct comparison stimulus.

In any case, most of the individuals showed a dramatic decrement in accuracy in all the conditions affecting the relationships between stimulus parts (i.e., 4PR, 4PT and S-4PRT). This suggests sensitivity to the internal spatial relationship of stimulus parts, in this species of monkeys. However, there are also possible alternative explanations for this result. It is possible that the monkeys had a specific deficit in the recognition of a stimulus on the basis of some of its parts and when those were rearranged they failed to recognize the individual parts as components of the shape presented as SS. In addition to this, the identification of individual parts may have been made particularly difficult in conditions featuring their spatial arrangement by the fact that by isolating the different quadrants of the stimuli additional visual cues were introduced by the new edges of the parts. Thus, a number of straight lines and 90° angles appeared in the rearranged figures which were not present in the original figure or in the figure subjected to a global rotation.

Therefore, rather than, or in addition to, the alleged disruptive effects of the rearrangement of the stimulus parts, there may have been an effect due specifically to a problem in detecting a stimulus part when disconnected from the rest of the stimulus and presenting additional straight edges. In other words, it is possible that the monkeys may have found it difficult to identify SS on the basis of a single part, as produced by our manipulations, even if this was not rotated and was presented in the same quadrant that it occupied in SS.

To evaluate this latter possibility, we carried out a new experiment where we tested the extent to which it was particularly difficult for the monkeys to identify the sample stimulus on the basis of the processing of a single part.

2. Experiment 2

Experiment 2 was designed to assess whether capuchin monkeys were able to identify whole figures by a component part when it was presented in the same quadrant and in the same orientation as in the sample and when it was subjected to manipulations which were similar to the manipulations performed simultaneously on all the four stimulus parts in Experiment 1.

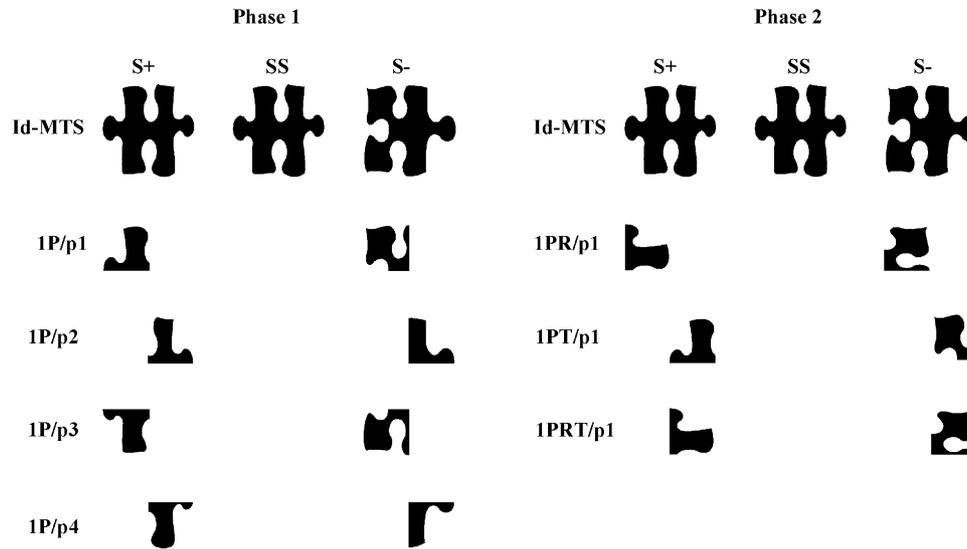


Fig. 5. Examples of trials used for the different conditions of Phase 1 (left) and Phase 2 (right) of Experiment 2. See text for further explanations.

Moreover, this experiment offered us the opportunity to evaluate the extent to which the presence of additional edges and angles generated by the process of isolating the parts in different quadrants contributed to make it difficult for the animals to match the stimuli by adding cues not present in the original figure.

2.1. Method

2.1.1. Subjects, apparatus and stimuli

Subjects, apparatus and intact stimuli were those used in Experiment 1. However, in Experiment 2, the monkeys were tested with a different arrangement of stimulus parts, following the design and procedure described below.

2.1.2. Design and procedure

The experiment consisted of two phases. Phase 1 tested whether the monkeys were able to recognize the test stimuli when three of their four component parts were removed. Using a simultaneous MTS, subjects were presented with an intact figure (i.e., A, B, or C) as the sample, and two single-part stimuli as comparison stimuli, with each single part being in the same location as it appeared in the corresponding intact figure. The task for the subjects was to identify which comparison stimulus was a part of the sample. Thus, if SS was the A-figure, S+ could include, for example, the part-1 (p1) of the A-figure, whereas S- could consist of the part-1 (p1) of the B- or C-figures. The single-part stimuli were created by deleting three parts from the original pattern (see Fig. 1, Stimulus Parts).

Each subject received two matching conditions. One condition, *Identity-One-Part* (Id-1P), featured trials with a single stimulus component (i.e., p1, p2, p3 or p4); the other condition, *Identity-matching* (Id-MTS), included trials with only intact figures and was used as a control.

Each subject received six daily sessions of 30 trials, for a total of 180 trials. Each session included six Id-MTS trials and 24 Id-1P trials (6 trials for each part type), with each of the three intact figures appearing 10 times as SS in a pseudo-random order. As in Experiment 1, the counterbalancing of trials for the left and right position of each single-part stimulus was performed across sessions. An example of trials of the different testing conditions is shown in Fig. 5 (Phase 1).

Phase 2 assessed the effect of the manipulation of the spatial position and/or orientation of a single stimulus part. As in Phase 1, Phase 2 also included always SS as one of the three intact figures (A, B or C); however, S+ and S- varied according to the type of matching condition. The following four matching conditions were employed: (1) *One-Part Rotation* (1PR), included the 90° clockwise rotation of the single part (i.e., p1, p2, p3, or p4); (2) *One-Part Translation* (1PT),

included a diagonal translation of the part; (3) *One-Part Rotation/Translation* (1PRT), included both the rotation and translation of the part; (4) *Identity-matching* (Id-MTS), featured trials with intact figures (A, B, C) as sample and as comparison stimuli and was used to monitor the matching behaviour of the subjects. An example of trials of the different testing conditions is shown in Fig. 5 (Phase 2).

Each subject received 16 daily sessions of 24 trials, for a total of 384 trials. Each session included 6 trials for each matching condition (1PR, 1PT, 1PRT, Id-MTS), with each stimulus appearing 6 times as the sample in a pseudo-random order with the constraint that two identical trials could not be presented consecutively. The counterbalancing of trials for stimulus type (A, B, or C), single stimulus part (p1, p2, p3, or p4), matching condition (1PR, 1PT, 1PRT, Id-MTS), and position (left and right) of each comparison stimulus was performed across sessions.

2.2. Results

2.2.1. Phase 1

The percentage of correct responses performed by each subject in each experimental condition (Id-MTS and Id-1P) is shown in Table 2.

For the Id-1P condition, the percentage of correct responses observed for each individual part of the stimulus is also reported. Binomial tests revealed that performance was above chance for each subject in each type of trial (all $ps < .001$, see Table 2).

Table 2

Individual percentages of correct responses for each condition of Experiment 2, Phase 1

Subject	Id-MTS	Id-1P			
		p1	p2	p3	p4
Narciso	88.9***	80.5***	86.1***	94.4***	77.8***
Patè	80.5***	97.2***	77.8***	83.3***	80.5***
Pepe	88.9***	83.3***	88.9***	88.9***	77.8***
Brahms	86.1***	83.3***	77.8***	80.6***	88.9***
Gal	91.7***	94.4***	80.5***	86.1***	88.9***
Pippi	86.1***	77.8***	91.7***	83.3***	80.5***
Mean	87.0	86.1	83.8	86.1	82.4

* = $p < .05$; ** = $p < .01$; *** = $p < .001$.

Table 3
Individual percentages of correct responses for each condition of Experiment 2, Phase 2

Subject	Id-MTS	1PR	1PT	1PRT
Narciso	97.9***	88.5***	96.9***	93.7***
Patè	94.8***	93.7***	92.7***	92.7***
Pepe	93.7***	89.6***	92.7***	91.7***
Brahms	92.7***	86.4***	88.5***	90.6***
Gal	96.9***	94.8***	96.9***	89.6***
Pippi	95.8***	96.9***	92.7***	92.7***
Mean	95.3	91.6	93.6	92.0

* = $p < .05$; ** = $p < .01$; *** = $p < .001$.

An ANOVA Stimulus Part (p1, p2, p3, p4) \times Figure Type (A, B, C), was carried out to assess whether or not, in the Id-1P condition, the percentages of correct responses obtained for the component parts of each figure component were different. The analysis did not show any significant effect of stimulus part [$F(3, 15) = 0.43, p > .1$ (p1, 86.1%; p2, 83.8%; p3, 86.1%)], figure type [$F(2, 10) = 0.19, p > .1$ (A, 84.7%; B, 83.3%; C, 85.8%)] or of the interaction between the two factors.

A further ANOVA Matching Condition (Id-MTS, Id-1P) \times Figure Type (A, B, C) did not reveal significant main effects either. The mean accuracy scores were similar for both the Id-MTS (87.0%) and the Id-1P (84.6%) conditions [$F(1, 5) = 3.31, p > .1$]. Likewise, performance levels did not differ among figures [$F(2, 10) = 2.2, p > .1$; (A, 84.0%; B, 84.0%; C, 89.4%)]. The interaction Matching Condition by Figure Type did not prove significant.

2.2.2. Phase 2

The percentages of correct responses observed in Phase 2 are reported in Table 3.

Binomial tests revealed that performance was above chance for each individual in each condition (all $ps < .001$, see Table 3).

A repeated measure ANOVA with Matching Condition (Id-MTS, 1PR, 1PT, 1PRT) and Stimulus Type (A, B, C) did not reveal a significant main effect of matching condition: (Id-MTS, 95.3%; 1PR, 91.6%; 1PT, 93.6%; 1PRT, 92.0%), $F(3, 15) = 3.0, p = .072$, or stimulus type (A, 92.7%; B, 93.3%; C, 93.3%), $F(2, 10) = 0.14, p > .1$. The interaction also did not prove significant.

Moreover, a one-way ANOVA used to compare the percentage of correct responses obtained for each single component part (p1, p2, p3, and p4), when the different conditions (1PR, 1PT, 1PRT) were collapsed, did not prove significant [$F(3, 15) = .10, p > .1$]. This indicates similar accuracy levels in the processing of the different parts (p1, 92.4%; p2, 92.1%; p3, 91.9%; p4, 93.1%).

2.3. Discussion

The results of Phase 1 show that removing three parts from the original figure did not affect matching performance. The monkeys were able to identify the visual pattern presented as SS even when only a single stimulus part was available as S+. The high level of performance shown by the monkeys during the test, thus, suggests that they relied on the portions of figure

contour of each stimulus component for the identification of the pattern presented as the sample. Moreover, it indicates that the presence of additional straight lines generated by the isolation of a stimulus part cannot be a major factor in the deterioration of pattern recognition.

The results of Phase 2 show that the manipulation of spatial orientation and/or the quadrant in which a single stimulus component was presented did not have a significant effect on the matching performance of the monkeys. In fact, the accuracy scores for the conditions featuring a single part did not differ from the accuracy scores observed in the control condition (Id-MTS) where intact figures were presented. Therefore, the combined results of Phases 1 and 2 of this experiment suggest that capuchin monkeys can successfully use the visual characteristics of a single component part of the stimulus (such as its contour) to inform their matching choices, irrespectively of the position and orientation of the part in relation to the whole stimulus that contains it.

However, since this experiment was carried out after Experiment 1, it is possible that the task practice received by the monkeys was responsible for the high level of performance observed in all the conditions featured here and that it masked the effects of the experimental manipulations. As a consequence it is possible that the effects of the experimental manipulations that we observed in Experiment 1 would not have re-emerged if we tested the monkeys again at this stage.

In order to evaluate this possibility, we carried out an additional experiment where all the conditions used in Experiment 1 (i.e., Id-MTS, GR, 4PR, 4PT, S-4PRT) were presented again to the same animals. Moreover, as a control, we also included all the conditions featured in Phase 2 of Experiment 2 (1PR, 1PT, 1PRT). Each subject performed 3 sessions of 34 trials, one session a day, for a total of 102 trials. In each session there were 10 trials including the five matching conditions of Experiment 1, and 24 trials including the three matching conditions of Phase 2 of Experiment 2. The pattern of results obtained, was remarkably similar to that observed in Experiment 1.

A one-way repeated measures ANOVA performed on the percentage of correct responses observed in the different conditions produced significant results, $F(7, 35) = 26.51, p < .001$. Post hoc comparisons (Tukey's test) showed that, as in Experiment 1, the accuracy scores in the Id-MTS and GR conditions did not differ from one another and were significantly greater than the accuracy scores observed for 4PR, 4PT and S-4PRT conditions (all $ps < .001$). Moreover, the accuracy scores observed in conditions featuring the manipulation of the arrangement of the four stimulus parts (4PR, 4PT and S-4PRT) did not differ from one another. In addition, as in Phase 2 of Experiment 2, the accuracy scores observed for all the conditions involving the presentation of a single part in a different spatial location and/or orientation (1PR, 1PT, 1PRT) were similar to each other and did not differ from the accuracy scores observed in the Id-MTS and in the GR condition; moreover, they were significantly higher than the accuracy scores registered for the three conditions involving the rearrangement of the four parts (all $ps < .001$).

These additional data indicate that the results obtained in Experiment 1 are robust and that the decrement in matching

performance in conditions affecting the spatial relationship of four parts was not compensated by extensive exposure to a single component part received by the monkeys in Experiment 2. Moreover, the results obtained in the conditions featuring a single part replicated those obtained in Experiment 2, since no difference was obtained between the various conditions.

It is unclear, however, if the difference in the pattern of performance observed when one and four parts are presented is due to the difference between the presence of a single part compared to the presence of multiple parts in S+, irrespectively of the actual number of parts, or if, by contrast, the addition of one part at a time would make it progressively more difficult for the monkeys to process the stimuli following the manipulation of their spatial relationship. In other words, on the one hand, it is possible that the presence of more than one part produces a discrete increase of difficulty in the processing of rearranged comparison stimuli. On the other hand, it is possible that the addition of each single part produces a gradual increase in difficulty, which may be proportional to the number of parts present in the rearranged stimulus. This issue was addressed in Experiment 3.

3. Experiment 3

The aim of Experiment 3 was to evaluate the combined effect of the manipulation of the number of parts presented as comparison stimuli and of their spatial arrangement on the matching performance of the monkeys. In the present experiment, trials featuring comparison stimuli containing two and three parts of the sample were used. With this manipulation it was possible to determine if the negative effect of the presence of multiple rearranged parts in the matching performance of the monkeys was related to the number of parts of SS, which were featured in S+.

3.1. Method

3.1.1. Subjects, apparatus and stimuli

Subjects, apparatus and sample stimuli were those used in the previous experiments. The experiment was carried out in two phases. In Phase 1, we used comparison stimuli with two and three parts of the sample. Phase 2 featured comparison stimuli with four parts of the sample and was presented to monitor potential effects of task practice on the pattern of results observed in the previous experiments.

3.1.2. Procedure

3.1.2.1. Phase 1. In this phase, the monkeys were presented with an intact shape (i.e., A, B, or C) as the sample, and with a set of two or three parts of the original figures as comparison stimuli, with the parts appearing in a different location and/or orientation to how they appeared in the corresponding intact figure. As before, the task for the subjects was to identify which one of two comparison stimuli was more similar to the sample. Randomly interspersed trials of the following conditions were presented: *Two-Part Rotation* (2PR), included the presentation of two parts of the original figures, with a 90° clockwise rotation of each part; *Two-Part Translation* (2PT), included the diagonal translation of the two stimulus parts; *Scrambled-Two-Part Rotation/Translation* (S-2PRT), featured both a translation and a rotation of the two parts; *Three-Part Rotation* (S-3PR), included the presentation of three parts of the original stimulus, with a 90° clockwise rotation of each part; *Three-Part Translation* (3PT), included the diagonal translation of the three parts; *Scrambled-Three-Part Rotation/Translation* (S-3PRT), featured both the translation and rotation of the three parts; *Identity-matching* (Id-MTS), included trials with only intact figures; this

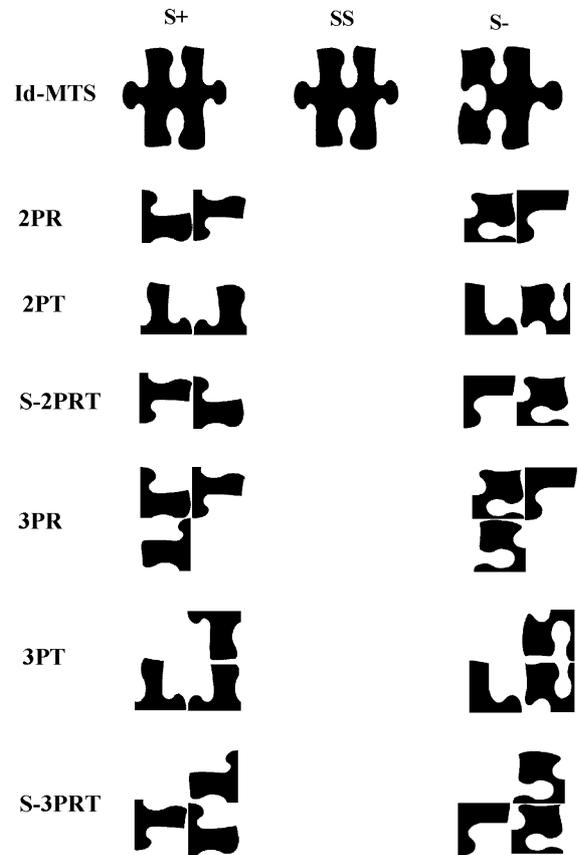


Fig. 6. Examples of trials used for the different conditions of Experiment 3.

latter condition, as before, was used to check that a high level of performance on a simple identity MTS task was maintained by the subjects. Each of the conditions where a manipulation of the spatial relationship between the stimulus parts was performed featured different combinations of the stimulus components. An example of trials of the different testing conditions is shown in Fig. 6.

Each subject performed six daily sessions of 36 trials each, for a total of 216 trials. Each session included six identity-matching trials, 18 trials with comparison stimuli containing two parts of the sample (6 trials for each matching condition), and 12 trials with comparison stimuli containing three parts of the sample (4 trials for each matching condition), with each of the three intact figures appearing 12 times as the sample in a pseudo-random order. As in the previous experiments, the counterbalancing of trials for stimulus type, matching condition, part combination, and position (left and right) of each comparison stimulus was achieved across testing sessions.

3.1.2.2. Phase 2. This phase featured randomly interspersed trials of four out the five matching conditions which were originally used in Experiment 1 (see Fig. 2): *Four-Part Rotation* (4PR); *Four-Part Translation* (4PT); *Scrambled-Four-Part Rotation/Translation* (S-4PRT), *Identity-matching* (Id-MTS).

Each subject received a total of 48 trials, administered in two daily testing sessions of 24 trials each. Each session included 6 trials for each condition (i.e., 4PR, 4PT, S-4PRT, Id-MTS). The balancing of trials for the position (left and right) of each comparison stimulus was achieved across sessions.

3.2. Results

3.2.1. Phase 1

The percentages of correct responses observed in Phase 1 are presented in Table 4.

One-sample *t*-tests revealed that the accuracy level shown by the monkeys was well above the 50% level expected by chance

Table 4
Individual percentages of correct responses for each condition of Experiment 3, Phase 1

Subject	Id-MTS	Two parts		Three parts			
		2PR	2PT	S-2PRT	3PR	3PT	S-3PRT
Narciso	94.4***	94.4***	88.9***	97.2***	95.8***	91.7***	87.5***
Patè	97.2***	100.0***	97.2***	94.4***	91.7***	95.8***	100.0***
Pepe	97.2***	97.2***	94.4***	100.0***	100.0***	95.8***	95.8***
Brahms	91.7***	91.7***	94.4***	94.4***	100.0***	95.8***	100.0***
Gal	97.2***	94.4***	100.0***	100.0***	95.8***	95.8***	100.0***
Pippi	94.4***	97.2***	97.2***	88.9***	95.8***	100.0***	95.8***
Mean	95.4	95.8	95.4	95.8	96.5	95.8	95.9

* = $p < .05$; ** = $p < .01$; *** = $p < .001$.

in all conditions (Id-MTS, 95.4%; 2PR, 95.8%; 2PT, 95.4%; S-2PRT, 95.8%; 3PR, 96.5%; 3PT, 95.8%; S-3PRT, 95.9%; all $ps > .001$).

Binomial tests revealed that performance was above chance level in all conditions for all subjects (all $ps < .001$).

A repeated measures ANOVA carried out on the percentage of correct responses observed in the different conditions (Id-MTS, 2PR, 2PT, S-2PRT, 3PR, 3PT, S-3PRT) was not significant. The monkeys responded with the same high level of accuracy in all conditions featuring the spatial rearrangement of stimulus parts and in the control condition.

3.2.2. Phase 2

The overall mean percentages of correct responses observed in Phase 2 ranged from 60.4% to 75.0%.

A repeated measures ANOVA performed on the percentage of correct responses observed in the different conditions revealed a significant main effect of matching condition, $F(3, 15) = 19.25$, $p < .001$. Post hoc analyses (Tukey test) showed that, as in the previous experiments, the mean accuracy scores recorded in all conditions featuring a rearrangement of the stimulus parts (4PR, 62.5%; 4PT, 65.3%; S-4PRT, 50.0%) were significantly different from the mean accuracy observed in the control condition (Id-MTS, 94.5%) (Id-MTS versus 4PR, $p < .001$; Id-MTS versus S-4PRT, $p < .001$; Id-MTS versus 4PT $p < .01$) but were not significantly different from each other.

One-sample t -tests performed on the mean accuracy scores obtained in each matching condition revealed that, as in Experiment 1, the level of accuracy of the monkeys was above the level expected by chance in the Id-MTS condition [$t(5) = 10.8$, $p < .001$], in the 4PR condition [$t(5) = 3.0$, $p < .05$] and in the 4PT condition [$t(5) = 3.4$, $p < .05$]. Conversely, in the S-4PRT condition the performance level for the group did not differ from the 50% expected by chance.

3.3. Discussion

Overall, the results of Phase 1 show that with comparison stimuli containing only two or three parts of the sample stimulus, the disruption of the spatial organization of the parts did not affect the ability of the monkeys to identify the sample stimulus and that their matching performance was similar to that observed in the identity MTS trials. Thus, the results obtained with comparison stimuli with two and three parts of the sam-

ple were similar to those previously obtained with comparison stimuli featuring only a single part. These results suggest that the monkeys relied mainly on the processing of the available parts, irrespectively of their arrangement. This contrasts with the results previously obtained with comparison stimuli featuring four parts, which showed that their spatial rearrangement had a dramatic effect on pattern recognition in this species.

The results of Phase 2, which was specifically designed to monitor the effects of task practice on the pattern of results obtained following the spatial rearrangement of four parts of the sample stimulus, allow us to rule out the possibility that the very high level of accuracy observed in conditions featuring two or three scrambled parts was due to general familiarity with the test stimuli. In fact, the results of Phase 2 confirmed those obtained in conditions similar to those used in previous experiments. They show that when the comparison stimuli contain four parts the spatial rearrangement of these parts produces a significant decrement in matching performance. We can conclude, therefore, that the high level of accuracy observed in Phase 1 in all conditions featuring only two or three stimulus parts and the absence of an effect caused by the manipulation of the spatial arrangement of the parts cannot be merely accounted for by a ceiling effect deriving from task practice and familiarity with the individual stimulus parts.

3.4. Conclusions from Experiments 1–3

Overall, the pattern of results of Experiments 1–3 allows us to draw the following conclusions. (A) The presentation of only one component part does not affect pattern recognition in capuchin monkeys. Moreover, a change in the absolute location and/or orientation of a single part had no effect on MTS accuracy. Thus, it seems that for the monkeys it is sufficient to rely on local characteristics, such as the contours of the individual parts, in order to produce a high level of matching performance. (B) The disruption of the spatial relationship within subsets of two or three parts does not produce significant effects on matching performance. Thus, the spatial relationship between two or three parts, when only two or three parts are present in the comparison stimuli, does not seem to be essential for the identification of a pattern. (C) Conditions where all the stimulus parts are presented and where their spatial relationships have been altered produce a detrimental effect on matching accuracy. Thus, the relationship between the different parts of a stimulus seems to exert

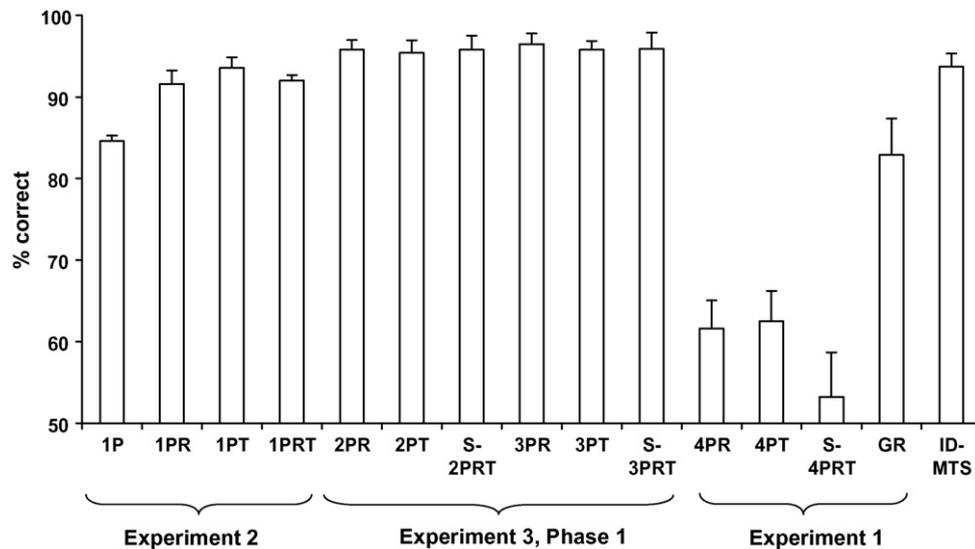


Fig. 7. Percentages of correct responses produced by monkeys in conditions featuring 1 stimulus part (Experiment 2, Phase 1 and Phase 2), 2 and 3 stimulus parts (Experiment 3, Phase 1) and 4 stimulus parts (Experiment 1). In the Id-MTS column the overall percentage observed in the control trials presented in Experiments 1–3 is reported.

a substantial control over the matching behaviour only when all the stimulus component parts are present in the comparison stimulus.

A graph summarizing the results obtained with monkeys in the conditions featuring a different number of stimulus parts in Experiments 1–3 is presented in Fig. 7.

4. Experiment 4

The aim of Experiment 4 was to assess whether the overall pattern of results observed in the previous experiments was specific to capuchin monkeys or pertained to humans too. This was particularly important to evaluate considering that previous studies indicated remarkable and sometimes unexpected differences between humans and capuchin monkeys tested with perceptual tasks [6,23–25]. To this end, we used the same stimuli and paradigms as those used with the monkeys. The design of the present experiment involved the presentation of all the relevant experimental conditions used in Experiments 1–3.

4.1. Method

4.1.1. Subjects

Twenty (10 males and 10 females) psychology undergraduates studying at the University of Leicester took part in the study in exchange for course credits. They ranged in age from 20 to 22 years and had normal or corrected-to-normal vision. They were all naïve in respect to the hypotheses tested in the present study.

4.1.2. Apparatus and stimuli

Humans were tested using Pentium PCs equipped with 15 in. SVGA monitors with a resolution of 1024 × 768 pixels. The software used to run the experiments was developed at the University of Leicester using E-prime (Psychology Software Tools Inc.). It enabled the presentation of the stimuli and the recording of the responses performed by the subjects.

Bitmaps of the stimuli previously used in the experiments with monkeys were used for stimulus presentation on the computer screen. 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 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.

4.1.3. Procedure

Fifteen matching conditions were used. Five conditions were identical to those used in Experiment 1 (i.e., Id-MTS, GR, 4PR, 4PT, and S-4PRT); four conditions featuring the presentation of only one stimulus part (i.e., 1P, 1PR, 1PT, 1PRT) were the same as those used in Experiment 2; and six conditions, involving the presentation of a subset of two and three component parts (i.e., 2PR, 2PT, S-2PRT, 3PR, 3PT and S-3PRT), were identical to those used in Experiment 3 (Phase 1).

Each trial started with the presentation of the sample stimulus, displayed centrally at the top of the screen. Following an interval of 2.5 s, the two comparison stimuli appeared at the bottom left and right corners of the screen, respectively. The subjects were required to indicate, 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, which of the two patterns resembled most closely the centrally presented pattern. All the three stimuli remained present on the screen until a response was made.

Each subject received 222 trials, according to the 15 conditions mentioned above. There were 36 trials for the Id-MTS condition, 18 trials for each of the three conditions involving the presentation of two parts subjected to a transformation of their spatial relationship (i.e., 2PR, 2PT, S-2PRT), and 12 trials for each of the remaining conditions (GR, 4PR, 4PT, S-4PRT, 1P, 1PR, 1PT, 1PRT, 3PR, 3PT, S-3PRT). Trials were presented in a pseudo-random order, which prevented two identical trials from being presented consecutively.

4.2. Results

The percentages of correct responses observed in the different conditions of Experiment 4 are presented in Fig. 8. A one-way ANOVA carried out to compare the percentage of correct responses observed in the 15 conditions proved highly significant [$F(14, 266) = 9.5; p < .001$]. In order to interpret the pattern of differences between the different conditions, separate ANOVAs were carried out to compare the percentage of correct responses observed for each of the conditions featuring the same number of parts in the comparison stimuli with the Id-MTS condition used as a baseline of matching performance.

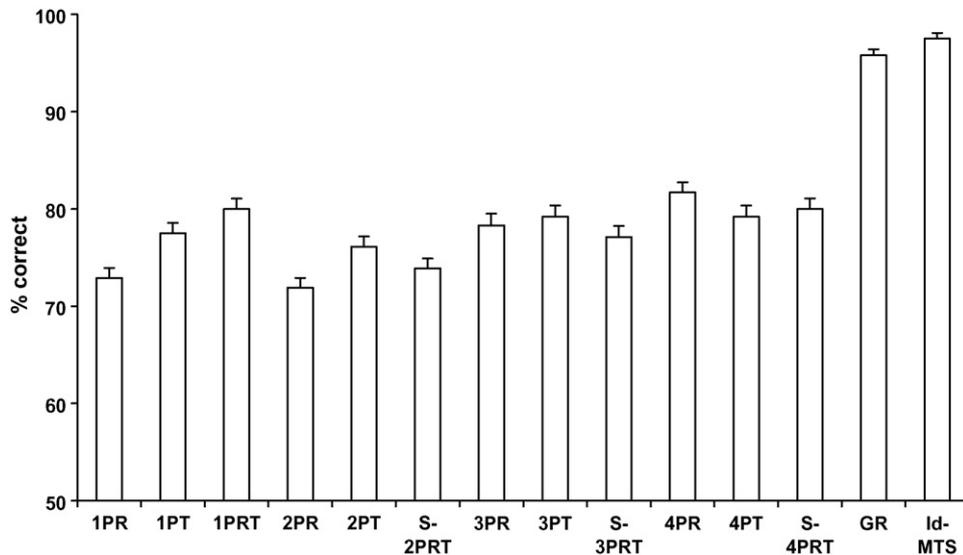


Fig. 8. Percentages of correct responses produced by human subjects in the different conditions of Experiment 4.

A one-way repeated measures ANOVA, used to compare the Id-MTS, GR, 4PR, 4PT and S-4PRT conditions, proved significant [$F(4,76) = 15.39$; $p < .001$]. Post hoc comparisons (Tukey's test) revealed that whereas the Id-MTS (97.5%, S.D. = 3.9) and the GR (95.8, S.D. = 6.9) conditions did not differ from each other, performance in both these conditions was different (all $ps < .001$) from that registered for the 4PR (81.7% S.D. = 13.4), 4PT (79.2%, S.D. = 15.9), and S-4PRT (80.0% S.D. = 15.4), the latter three conditions did not differ from each other. Binomial tests were carried out to identify the number of participants who performed above chance in each condition. They revealed that all 20 participants were above chance in the ID-MTS condition whereas 19, 12, 11 and 11 performed above chance in the GR, 4PR, 4PT and S-4PRT conditions, respectively (all $ps < .05$).

A one-way ANOVA carried out on the Id-MTS, 3PR, 3PT, S-3PRT also proved significant [$F(3, 57) = 16.12$, $p < .001$]. Post hoc comparisons revealed that performance in the Id-MTS condition was significantly different (all $ps < .001$) from that observed in the 3PR (78.3%, S.D. = 17.4), 3PT (79.2%, S.D. = 17.6), and S-3PRT (77.1%, S.D. = 17.1). The latter three conditions did not prove different from each other. Binomial tests revealed that out of the 20 participants who performed above chance level in the Id-MTS condition, only 10 performed above chance level (all $ps < .05$, at least) in the 3PR, 3PT and S-3PRT.

A one-way ANOVA carried out on the Id-MTS, 2PR, 2PT, S-2PRT also proved significant [$F(3, 57) = 27.71$, $p < .001$]. Post hoc comparisons for the conditions featuring two parts replicated the pattern observed for the conditions featuring three parts. In fact, the Id-MTS condition was different (all $ps < .001$) from all the three conditions where a transformation of the relationship between the stimulus part was performed, i.e. 2PR (71.9%, S.D. = 12.7), 2PT (76.1%, S.D. = 16.5), S-2PRT (73.9%, S.D. = 13.8). The results of binomial tests indicated that 20, 13, 14, and 14 participants produced frequencies of correct responses significantly above chance level (all $ps < .05$) in the 2PR, 2PT and S-2PRT conditions, respectively.

Finally, a one-way ANOVA carried out on the Id-MTS, 1P, 1PR, 1PT, S-1PRT also showed a significant difference between the means of the different conditions [$F(4, 76) = 14.83$, $p < .001$]. Post hoc tests also revealed a significant difference between the level of accuracy observed in the Id-MTS condition and all the other conditions, 1P (81.7%, S.D. = 15.7), 1PR (72.9%, S.D. = 15.3), 1PT (77.5%, S.D. = 17.9), 1PRT (80.0%, S.D. = 15.5), all $ps < .001$. Binomial tests indicated that 14, 8, 12, and 8 participants were above chance ($p < .05$) in the 1P, 1PR, 1PT and 1PRT condition respectively compared to the 20 participants who were above chance in the Id-MTS condition.

None of the other comparisons between conditions yielded significant results.

4.3. Discussion

The results of the analysis carried out on the conditions featuring the transformation of the four parts of the stimuli show that, in humans, the global rotation of the whole stimulus which does not affect the internal relationship between the parts did not produce a decrement in the matching performance of the subjects. By contrast, whenever the spatial relationship between parts was affected by means of a rotation of each stimulus part and/or a translation of the stimulus parts, the performance of the participants suffered a dramatic decrement. These results show a remarkable similarity with those consistently obtained with the monkeys tested in analogous conditions such as those featured in Experiment 1, and Experiment 3 (Phase 2).

The matching performance of humans was affected by transformations of the stimulus parts also when less than four parts were featured in the comparison stimuli. This was indicated by both the comparisons of the percentage of correct responses observed in the different conditions and by the number of individuals who were successful in producing a number of correct responses, which was above the level expected by chance. The absence of some stimulus parts, even when no transformations of the stimulus were performed, such as in the 1P condition where

the single part presented as the comparison stimulus was in the same position and orientation as in the sample, also produced a detrimental effect in the matching performance of humans. These results seem to contrast with those obtained with monkeys in Experiment 2 and Experiment 3 (Phase 1), where the matching performance of monkeys was extremely robust and was not affected by similar manipulations. These differences could be interpreted as an indication that humans rely on the global properties of intact stimuli more than monkeys and their pattern recognition is more easily impaired whenever these properties are affected. However, caution is required before we can derive strong conclusions from these differences considering that monkeys overall received more trials with deteriorated stimuli than humans and perhaps this difference in the amount of task practice could explain, at least in part, the worsening of performance in humans, but not in monkeys in these conditions. However, it is important to point out that the extensive task practice that the monkeys received with conditions featuring four parts was not sufficient to overcome the negative effects due to the rearrangement of stimulus parts. This suggests that overall task practice may not have a very strong effect in presence of a genuine difficulty in dealing with particular types of stimulus transformation. For this reason, we may conjecture that the amount of task exposure may not have had a preponderant role in producing, on its own, the interspecies differences, which we have observed.

5. General discussion

In this article, we reported a series of experiments where we used a simultaneous MTS procedure to assess the type of information used by capuchin monkeys for the identification of a visual pattern. Our primary aim was to assess the extent to which pattern recognition in this species is dependent on properties of the stimulus, which include the spatial relationship among its parts. Moreover, we wanted to characterise more specifically the type of relationship among stimulus parts, which is most important for the identification of a visual pattern in this species.

The results of the first experiment, where the four parts into which the patterns were divided were all featured in the comparison stimuli, were clear-cut and have been reliably replicated in similar conditions presented as part of Experiments 2 and 3. The matching performance of monkeys was not affected by a manipulation, which involved a global rotation of the stimulus. This result is consistent with previous studies on mental rotation in non-human primates, which showed that baboons are able to process patterns subjected to rotations of different degrees with a high level of accuracy [27].

The global rotation of the stimulus in our study affected the quadrant in which each of the four parts of the stimulus was presented. However, both the internal relationship between stimulus parts and the whole contour of the pattern were preserved. Since the level of performance of capuchin monkeys with stimuli subjected to a global rotation was the same as that observed in trials featuring a simultaneous identity MTS, we can conclude that as long as the silhouette of the stimulus and the internal spatial relationship between parts of the stimuli are preserved the monkeys do not have any problems in identifying the relevant pattern.

The situation is dramatically different when the manipulation of the relationship between stimulus parts is affected such as in the four parts translation and the four parts rotation condition where a severe decrement in performance was observed. Conditions featuring the translation of stimulus parts affect the quadrant in which each of the stimulus parts is presented but also disrupt the contour of the stimuli. Thus, both the orientation and the position of the parts seem to be important for the recognition of a pattern in capuchin monkeys. The decrement of performance observed in the condition featuring the rotation of each single stimulus part clarifies these results. In fact, with this type of transformation the stimulus parts are presented in the same quadrant as in the sample but the rotation of each of the parts produces a disruption of the contour of the stimulus. As we know from the results of our global rotation condition that capuchin monkeys are able to cope with stimulus rotation, it seems unlikely that our subjects were using a strategy whereby they focused their attention on a single quadrant of the sample stimulus and tried to match it with the spatially equivalent quadrant of the comparison stimulus. If this line of reasoning is correct, then we should infer that the most detrimental consequence of all transformations which affected the relationship between the stimulus parts is the disruption of the contour of the stimulus. The disruption is so severe that it cannot be compensated for by task practice. In fact, we observed exactly the same pattern of results whenever we presented these conditions again at different stages of testing in the course of the present study.

Our results are therefore consistent with those indicating sensitivity to the spatial arrangement of stimulus part in pattern recognition in pigeons [16,17], the species on which research has typically been carried out in this area. It should however be noted that results obtained with pigeons have often supported alternative interpretations, some of which seem to indicate that pigeons do not process stimuli on the basis of structural descriptions specifying the spatial arrangement of stimulus parts [3,13]. As such it would be premature to draw similarities between how pigeons and monkeys process visual patterns.

The results obtained with our monkeys in conditions where the transformations of the stimuli presented as comparison stimuli involved all the four parts into which the patterns were divided show a remarkable similarity with the results obtained with humans in Experiment 4. This similarity of the pattern of findings obtained with monkeys and with humans indicates, first of all, that the results are extremely robust and that stimuli and procedure were suitable for a comparative analysis. More importantly, it shows that capuchin monkeys are as sensitive as humans to the internal relationship of spatial patterns. Thus, they allow us to rule-out that the differences previously observed between humans and capuchins [6,23–25] can be accounted for entirely by a deficit of capuchin monkeys in the encoding of the spatial relationships between the internal parts of the stimuli.

Surprising and interesting results, however, emerged in the conditions where not all the four parts in which the patterns were divided appeared in the comparison stimuli. The fact that monkeys were able to identify the sample stimulus on the basis of a single part even when it was subjected to a translation or a rota-

tion indicates that the decrement in performance observed when four parts were rearranged cannot be due simply to a difficulty in identifying parts when these are presented in isolation or disconnected from other parts (as it happens when they are rearranged). The fact that a single translated part was recognised with a level of accuracy indicated that MTS ability of the monkeys does not depend on a strategy consisting in attending exclusively to some portions of the relevant stimulus and using them for the comparison. Similarly, the fact the performance of the monkeys was equally robust following a 90° rotation of a single stimulus part provides a further indication of the flexibility of the matching behaviour in this species.

It is also of interest to note that for the monkeys, it was not important which particular part of the sample stimulus was featured in the comparison stimulus. This shows that the monkeys were equally attending to all the parts of the sample.

Thus, even if monkeys were able to attend to each of the four parts into which the sample stimulus was divided, and to identify the stimulus from which they were derived, even following its rotation or its displacement to a different quadrant, they had problems in attending to these same parts when they were all presented simultaneously as part of the comparison stimulus.

Considering the dramatic difference in performance observed following transformations of stimulus parts in conditions featuring four parts and those featuring only one part of the stimuli, it was perhaps surprising to observe that conditions featuring two and three parts of the stimuli, did not produce intermediate levels of accuracy in Experiment 3. It would have been reasonable to expect that by adding rearranged parts one by one and therefore by gradually increasing the number of spatial relationships between the stimulus parts or portions of the contour of the stimulus affected by the transformation we would have gradually increased the difficulty of the task.

One possible interpretation of these results is that transformations involving all parts of the sample stimulus may have given rise to a completely new interpretation of the stimulus, which was perceived as a completely novel shape. This is consistent with the results of other studies conducted in adult humans where it has been indicated that attention shifts towards the configuration of elements in a visual array when the relationship between the parts creates emergent figures [22].

The pattern of results observed as a function of the number of parts of the comparison stimuli is also where the most dramatic differences between capuchin monkeys and humans emerge. In fact, in contrast with capuchins, in humans, conditions affecting the spatial relationships between stimulus parts produced a decrement in matching performance irrespective of the number of parts presented. This interspecies difference could be an expression of a different degree of reliance on the global properties of the stimuli, with humans emerging as the species most dependent on these properties rather than on local properties of stimulus parts irrespective of their interrelations. The ability to integrate local features in global wholes on the basis of the relationship of component parts in humans has been put in relation to higher functions of the occipital cortex [11] and of the right hemisphere in particular [1]. The behavioural differences observed here could therefore be mediated by functions

of these brain regions. Moreover, the integration of parts into wholes is an ability, which seems to be subject to cognitive development in children in preschool years [19]. As such, differences in the domain assessed here would be consistent with the results of other studies indicating cognitive differences between pre-school children and capuchin monkeys [5,6].

Nevertheless, interspecies differences in the present study need to be taken as a suggestion rather than a firm conclusion. Since humans could not receive the same extensive task exposure received by the monkeys, we cannot rule out that with more trials the performance of humans too could have improved in the conditions featuring less than four parts. The fact, however, that in other conditions featured in this study, humans showed a performance similar to that of capuchin monkeys, even if they received smaller number of trials than the monkeys, suggests that this possibility is unlikely. Further experiments may be needed to provide fully conclusive results on this issue. Also it is impossible to rule out that other spurious factors emerged from the use of a different apparatus with monkeys and humans. However, we find it difficult to explain in theoretical terms how the observed differences could have emerged by the use of a WGTA with the monkeys and a computerised version of the task in humans. Nevertheless, we are currently developing computerised testing stations to be used with monkeys which will make the testing conditions even more similar to those used with humans, in future comparative studies.

What, however, can be concluded without doubt on the basis of the results of this study is that capuchin monkeys and humans show a similar pattern of results in conditions where global properties of the stimuli and relational properties of stimulus parts are involved. This was important to assess considering results of previous comparative studies, which have cast doubt on the ability of non-human species [3] to process relational properties of stimulus parts.

We believe that the assessment of similarity and differences between visual processing in human and non-human primates is a very worthwhile enterprise considering, on the one hand, that research is often carried out on the visual system of non-human primates uncritically assuming that monkeys provide a good model of human perception, and on the other, that too cautious interpretations of the cognitive processes underpinning perception in non human organisms can lead us to underestimate the ability of non-human species to process complex properties of visual patterns.

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References

- [1] Banich MT. Cognitive neuroscience and neuropsychology. Boston: Houghton Mifflin; 2004. p. 189–92.

- [2] Biederman I. Recognition-by-components: a theory of human image understanding. *Psychol Rev* 1987;94:115–47.
- [3] Cerella J. The pigeon's analysis of pictures. *Pattern Recognit* 1980;12:1–6.
- [4] D'Amato MR, Van Sant P. The person concept in monkeys (*Cebus apella*). *J Exp Psychol Anim Behav Process* 1988;14:43–55.
- [5] De Lillo C, McGonigle BO. The logic of searches in young children (*Homo sapiens*) and tufted capuchin monkeys (*Cebus apella*). *Int J Comp Psychol* 1997;10:1–24.
- [6] De Lillo C, Spinozzi G, Truppa V, Naylor DM. A comparative analysis of global and local processing of hierarchical visual stimuli in young children and monkeys (*Cebus apella*). *J Comp Psychol* 2005;119:155–65.
- [7] Deruelle C, Fagot J. Visual search for global/local stimulus features in humans and baboons. *Psychon Bull Rev* 1998;5:476–81.
- [8] Fagot J, Deruelle C. Processing of global and local visual information and hemispheric specialization in humans (*Homo sapiens*) and baboons (*Papio papio*). *J Exp Psychol Hum Percept Perform* 1997;23:429–42.
- [9] Fagot J, Tomonaga M. Global and local processing in humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*): use of a visual search task with compound stimuli. *J Comp Psychol* 1999;113:3–12.
- [10] Fagot J, Tomonaga M, Deruelle C. Processing of the global and local dimensions of visual hierarchical stimuli by humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), and baboons (*Papio papio*). In: Matsuzawa T, editor. Primate origins of human cognition and behavior. Tokyo: Springer-Verlag; 2001. p. 87–103.
- [11] Farah MJ. Visual agnosia: disorders of object recognition and what they tell us about vision. Cambridge, MA: MIT Press; 1990.
- [12] Fobes JL, King JE. Vision: the dominant primate modality. In: Fobes JL, King JE, editors. Primate behavior. New York: Academic Press; 1982. p. 219–43.
- [13] Haselgrove M, George DN, Pearce JM. The discrimination of structure. III. Representation of spatial relationships. *J Exp Psychol Anim Behav Process* 2005;31:433–48.
- [14] Hopkins WD, Washburn DA. Matching visual stimuli on the basis of global and local features by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). *Anim Cogn* 2002;5:27–31.
- [15] Kapadia MK, Ito M, Gilbert CD, Westheimer G. Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys. *Neuron* 1995;15:843–56.
- [16] Kirkpatrick-Steger K, Wasserman E, Biederman I. Effects of spatial rearrangement of object components on picture recognition in pigeons. *J Exp Anal Behav* 1996;65:465–75.
- [17] Kirkpatrick-Steger K, Wasserman EA, Biederman I. Effects of geon deletion, scrambling, and movement on picture recognition in pigeons. *J Exp Psychol Anim Behav Process* 1998;24:34–46.
- [18] Meinhardt G. Do part-whole relations facilitate recognition of scrambled objects? *Perception* 2002;31(suppl):75.
- [19] Mendoza Feeney S, Stiles J. Spatial analysis: an examination of preschoolers' perception and construction of geometric patterns. *Dev Psychol* 1996;32:933–41.
- [20] Navon D. Forest before the tree: the precedence of global features in visual perception. *Cognit Psychol* 1977;353–83.
- [21] Pierce J. Animal learning and cognition. Hove: Psychology Press; 1997. p. 333.
- [22] Pomerantz JR, Sager LC, Stoever RG. Perception of wholes and their component parts: some configural superiority effects. *J Exp Psychol Hum Percept Perform* 1977;3:422–35.
- [23] Spinozzi G, De Lillo C, Castelli S. Detection of grouped and ungrouped parts in visual patterns by tufted capuchin monkeys (*Cebus apella*) and humans (*Homo sapiens*). *J Comp Psychol* 2004;118:297–308.
- [24] Spinozzi G, De Lillo C, Salvi V. Local advantage in the visual processing of hierarchical stimuli following manipulations of stimulus size and element numerosity in monkeys (*Cebus apella*). *Behav Brain Res* 2006;166:45–54.
- [25] Spinozzi G, De Lillo C, Truppa V. Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). *J Comp Psychol* 2003;117:15–23.
- [26] Tinbergen N. The study of instinct. Oxford: Clarendon Press; 1951.
- [27] Vauclair J, Fagot J, Hopkins WD. Rotation of mental images in baboons when the visual input is directed to the left cerebral hemisphere. *Psychol Sci* 1993;4:99–103.
- [28] Ungerleider LG, Mishkin M. Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RJW, editors. Analysis of visual behaviour. Cambridge, MA: MIT Press; 1982. p. 549–86.
- [29] Walker S. Animal thought. London: Routledge & Kegan Paul; 1983. p. 437.