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Research report

Effects of pattern redundancy and hierarchical grouping on global–local visual processing in monkeys (*Cebus apella*) and humans (*Homo sapiens*)Carlo De Lillo^{a,*}, Milena Palumbo^{a,b}, Giovanna Spinozzi^b, Giuseppe Giustino^b^a School of Psychology, University of Leicester, Henry Wellcome Building, Lancaster Road, Leicester LE1 9HN, UK^b Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche (CNR), Via Ullisse Aldrovandi 16/B, 00197 Rome, Italy

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ABSTRACT

Using a Matching-To-Sample (MTS) procedure we assessed the effects of stimulus redundancy, defined on the basis of the information–theory approach to shape goodness proposed by Garner (1974) [20], and grouping on the processing of hierarchical visual patterns in capuchin monkeys and humans. In a first experiment, the MTS performance of both capuchin monkeys and humans benefitted from stimulus redundancy. Moreover, a local advantage in capuchins was observed with visual patterns that required grouping at both global and local level. In a second experiment we eliminated the requirement to group at the local level. This was done to determine if the effects of redundancy would have been evident in condition more similar to those used in previous studies of global–local processing in a comparative context. The benefits of stimulus redundancy emerged again in both species but were confined to local processing in monkeys and to global processing in humans. A local advantage was observed in both species. In a third experiment, the reduction of the size of the stimuli and the increase of the quantity of the local elements produced a shift to global dominance in humans but the local dominance in monkeys was preserved. The implications of these results are discussed in relation to other similarities and differences in higher visual functions in humans and monkeys.

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1. Introduction

There is a substantial amount of visual neuro-scientific research on non-human primates [49] carried out assuming that it is possible to use data from humans and monkeys interchangeably. The assumed similarity of the visual system of primates has sometimes induced researchers to report electrophysiological data on monkeys alongside human behavioural data (see [35] for a recent review).

The assumption that non-human primates are a suitable model of human visual processes is justifiable on a number of grounds. In all diurnal primates, vision is the dominant sensory modality [19]. Moreover, the physiology of low level vision is similar in monkeys and humans [13,26] who also present similar contrast sensitivity functions to different spatial frequencies [12,36]. Moreover, given their close taxonomic distance, it could prove possible to map brain homologies in humans and monkeys. The mapping of homologies in humans and monkeys is particularly meaningful when carried out in relation to the neural bases of low level visual functions [34] but the homologies in the visual systems of humans and monkeys probably pertain to higher cortical visual pathways as well [49].

Notwithstanding these similarities, there is a growing body of literature indicating that there may be some differences between monkeys and humans in other aspects of visual cognition. For example, there is evidence that capuchin monkeys segment complex visual patterns differently from humans. Spinozzi et al. [44] compared performance of these two species in a Matching-To-Sample (MTS) task requiring the subjects to identify which among different stimulus parts presented as comparison stimuli, belonged to a whole pattern presented as the sample. The stimulus parts were formed by a number of elements that could be either connected on the basis of a variety of grouping principles (“grouped parts”) or unconnected (“ungrouped parts”). Humans showed a clear advantage for identifying the grouped parts. By contrast, monkeys showed a remarkable advantage for identifying the parts when they were ungrouped.

One possible explanation for the interspecies differences observed in the above study is that they may be due to a relative preponderance of different grouping processes in monkeys and humans. Evidence from the literature on human perception indicates that classic gestalt grouping principles [14] might vary in their attentional demands [3,4,23,24,29,32,41]. It is therefore possible that humans and non-human primates may derive different perceptual representations of the same patterns due a different bias towards the use of given grouping cues rather than others. The study by Spinozzi et al. [44] was not explicitly designed

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to evaluate this possibility. However, it featured either closed or open shapes in different stimulus conditions. Interestingly, closure proved an important factor in humans, who performed at a significantly higher level of accuracy in trials with closed shapes. By contrast, monkeys did not show this effect.

Another study addressed more specifically the issue of the relative weight of different organizational principles in humans and capuchin monkeys [47]. That study featured a comparative investigation of the relative use of proximity, shape similarity and orientation as perceptual grouping cues using a MTS task which required grouping and figure-ground segregation. Both monkeys and humans were sensitive to all these grouping cues. Nevertheless, the relative importance of each of these cues was different in the two species. Humans performed more efficiently in conditions requiring grouping by proximity than conditions requiring grouping by similarity of shape or element orientation. By contrast, capuchins processed equally well proximity and shape similarity groupings but made more errors when required to group on the basis of the orientation of figural elements (see Fig. 3 in [47]).

Grouping by proximity has been proposed as an explanation of cognitive differences in primates [2,16,18,42]. In a number of different contexts and cognitive domains it has been pointed out that baboons find it difficult, and attention demanding, to group spatially separated elements of a compound pattern into a coherent whole [11]. These findings suggest that humans may be less vulnerable than non-human primates to the spatial separation of elements of a visual scene and that this could explain, in an unsuspected way, a number of interspecies differences in cognition (see [17] for a discussion). Thus, a complex pattern of similarities and differences has been reported in the relative use of organizational principles in primates.

On the other hand, there is evidence from studies on pattern recognition that non-human primates are just as sensitive as humans are to the organizational properties of stimulus components. In a MTS study with different conditions where the arrangement of the component parts of the comparison stimuli was manipulated, De Lillo et al. [9] found striking similarities between the way in which capuchin monkeys and humans encoded the spatial relations between stimulus parts. The matching performance of both species was not affected by a global rotation of the whole stimulus, which preserved the internal relationship between the parts. By contrast, variations in the arrangement of local features of stimuli, obtained by scrambling their component parts, produced a dramatic decrement of performance in both humans and monkeys. The above study used jigsaw-like shapes as stimuli in order to minimise the possible use of verbal description by humans and to control for the level of familiarity in the two species.

Another study assessed spontaneous manipulations of stimulus cards with original or manipulated images of schematic faces and geometric patterns in capuchin monkeys [1]. It was found there that capuchins prefer stimuli where the regularity and symmetry of the original stimulus is preserved. A very low preference was expressed for cards where the regularity and symmetry of the patterns they depicted was compromised by scrambling their component parts.

Although this study [1] indicates a spontaneous preference for regular and/or symmetrical patterns in monkeys, it is not clear if this is because they find symmetrical patterns easier to process. In fact, Schrier et al. [43] tested stump-tailed monkeys (*Macaca arcoides*) on discrimination problems with different levels of figural symmetry as the experimental variable and found that discrimination performance was not facilitated by the symmetry of the patterns. In the study by Schrier et al. [43], the different levels of symmetry were obtained on the basis of Garner's [20] model of figural goodness that, given its importance for the present study, will be described in some detail below.

In an attempt to quantify pattern goodness within a gestalt tradition, Garner [20] gave a definition of goodness in terms of redundancy. According to Garner, the perceived goodness of a given pattern is inversely related to the size of the set of stimuli obtained by applying reflection and/or 90° rotation to that pattern. The reflection and rotation of good patterns generates small sets, making these patterns highly redundant. By contrast, poor patterns generate large sets and are characterised by a low level of redundancy. For example, a circle or a cross would be highly redundant shapes as their 90° rotation or reflection results in the same pattern. By contrast, a more irregular shape, such as a polygon containing several different angles, would be less redundant since it would produce different patterns following its rotation and/or reflection. Garner confirmed the relationship between redundancy and perceived goodness empirically by asking human participants to judge the relative goodness of dot patterns. Patterns from small equivalent sets (highly redundant) were rated as very good shapes, whereas patterns from large equivalent sets (less redundant) were rated as poorer shapes [22]. Follow up studies have shown that good patterns are encoded more efficiently [21], are easier to maintain in memory [6] and to sort into categories [7].

The notion of redundancy has proved of extreme importance in human cognitive psychology [21,22,25,37–39] and it is possible to envisage the possible adaptive value, for example in terms of information management, of the ability to exploit the redundancy of stimuli that need to be processed and encoded. From a comparative standpoint it is thus intriguing that the results obtained by Schrier et al. [43] should indicate that monkeys who share with us a sophisticated visual and cognitive system may be less sensitive than humans to factors associated with stimulus redundancy. In fact, the stump-tailed monkeys used by Schrier et al. [43] were given a series of pattern discrimination problems using stimuli directly derived from Garner and Clement [22]. The stimuli consisted in dots arranged within a 3 × 3 matrix. Different discriminations featured stimuli of a given level of redundancy (or pattern goodness). The level of redundancy of the stimuli was defined according to Garner and Clement in terms of the size of rotation-and-reflection equivalence set they generated. The monkeys' learning and response latency were not faster for discriminations involving more redundant patterns (good patterns) compared to those with a lower level of redundancy (poor patterns). This contrasts with results obtained with humans using similar stimuli and paradigms [20]. A different sensitivity to redundancy between humans and other primates could therefore indicate an important peculiarity of the human cognitive systems in relation to its ability to efficiently manage information processing and storage.

Further assessments of the sensitivity of non-human primates to this factor would therefore be of value for this reason and for the other important reasons outlined below.

Navon [40] demonstrated that humans have a tendency to process the global form of hierarchical visual patterns, where a global shape is formed by the spatial arrangement of more local elements. Humans typically process global shapes faster and better than the shape of their local constituents and show an asymmetrical global-to-local interference. A number of studies carried out on non-human primates, by contrast, indicate that monkeys find it easier to process the shape of the local elements [8,10,16,46]. Although the extraction of the global shape of this type of stimuli is likely to require some form of grouping, it is possible that differences, albeit small, in the relative use of grouping cues as discussed above could explain at least some of the interspecies differences observed in this domain. Importantly, all the shapes used so far in studies where human and non-human primates have been compared, are highly redundant forms (circles, squares, diamonds, crosses etc.). One of the strengths of Navon's paradigm is that when using hierarchical stimuli it is possible to use the same

set of shapes at the local and global level making it unlikely that one level is easier to process than the other because of the specific shapes featured there. Nevertheless, it is possible that given that the global level may require grouping (see [31], for an early suggestion of this within the gestalt tradition), good shapes are those that are most likely to be perceived as wholes. Thus, if humans are sensitive to the goodness of shape, their grouping at global level could be facilitated. By contrast, if monkeys, as suggested by the study by Schrier et al. [43], do not exploit the redundancy of stimuli during the encoding of visual patterns, they would not benefit from this additional organizational factor.

The primary purpose of the present study is to assess the extent to which capuchin monkeys (*Cebus apella*) are sensitive to the redundancy of stimuli in a task that has elicited a reliable local advantage in this species [10,45,46]. The study of redundancy in relation to global–local processing would enable us to assess the possible role of this factor in determining the observed differences between monkeys and humans. A second aim of the study was to evaluate the importance of having to group stimuli at both levels of hierarchical stimuli. As comparative studies have typically used hierarchical stimuli requiring grouping at global level only, it is possible that a “global disadvantage” (as dubbed by Fagot and Barbet [15]) may derive exclusively from their relative difficulty to group elements rather than a local bias in perception. If that were the case, requiring capuchin monkeys to group at local level too could have eliminated the local advantage so far observed in this species. The use of stimuli that required grouping at local level too would have helped us to assess whether the presence of a requirement to group at global level was the exclusive reason for the local advantage so far observed in this species.

2. Experiment 1

In this experiment we evaluated the relative importance of stimulus redundancy in the global and local processing of humans and capuchin monkeys. We assembled hierarchical stimuli on the basis of Garner's [20] dot patterns. Each stimulus had a different shape at the global and local level but the degree of redundancy, either a high or a low, was always the same at both of levels of stimulus structure.

The use of Garner's dot patterns also presented us with the opportunity to evaluate another important issue related to the interspecies differences reported in the comparative literature on global–local processing. This is the possibility that a selective requirement to group at global level could be the only explanation for the local advantage observed so far in monkeys and the differences between their style of processing and that of humans. We now know that in monkeys the processing of the global level of hierarchical patterns is attention demanding [8,11] possibly because of the additional processing resources required by grouping operations at that level. Traditional hierarchical stimuli that feature solid forms at local level would not have this additional processing requirement, and, for this reason, may induce monkeys to preferentially attend that level.

Thus, in Experiment 1, we constructed hierarchical stimuli with dot patterns that would have required grouping at the local as well as at the global level of the stimuli. This approach has been taken before in the human literature (see [40], Exp 4) albeit for different theoretical reasons. We extended it to the comparative context in the present experiment. We reasoned that if a local advantage was observed in capuchin monkeys when grouping was also required at the local level, a stronger case could have been made for a local dominance in this species, not explained exclusively by the fact that the global level of the stimuli had unique qualitatively different demands from the processing of the local level in terms of grouping requirements.

2.1. Method

2.1.1. Participants

Five adult tufted capuchin monkeys (*Cebus apella*) and 12 humans participated in this experiment. The monkey sample included 4 males (Gal, Patè, Rubens, Vispo) and 1 female (Pippi) aged from 6 to 27 years old. All animals were captive born and housed at the Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche (C.N.R.), in Rome, Italy. Each monkey lived in a social group in an indoor–outdoor enclosure (indoor: 5 m² × 2.5 m high; outdoor: 40.0–130.0 m² × 3.0 m high). The monkeys were tested individually in an experimental cage (0.76 m long × 1.70 m wide × 0.73 m high) which they could access through a sliding door from the adjacent indoor enclosure. Each subject was separated from the group solely for the purpose of testing, just before each daily testing session. The animals had food pellets freely available before and after testing. Fresh fruit and vegetables were provided after testing. Water was available *ad libitum*. All the subjects were already familiar with the set-up because of their involvement in various perceptual and cognitive tasks. Three monkeys (Gal, Patè, Pippi) had been previously tested with tasks involving hierarchical stimuli [10,45]. The other two subjects had never been presented hierarchical visual patterns before, but they were tested in a MTS task used to assess the discrimination of non-hierarchical visual patterns [48].

The group of humans comprised 12 volunteers (6 males and 6 females ranging in age from 18 to 37 years) with normal or corrected to normal vision. They were recruited from the participant panel of the School of Psychology at the University of Leicester and were paid a small fee for taking part in the experiment.

2.1.2. Apparatus

A wooden apparatus was used with the capuchin monkeys (Fig. 1, left). It consisted of a vertical panel (45 cm long × 35 cm high × 2 cm thick) with two lateral walls (35 cm long × 35 cm high × 2 cm deep). The panel was fixed perpendicularly onto a board (45 cm × 35 cm), which could be moved forward and backward on a support, mounted on a metal trolley (50 cm long × 50 cm wide × 55 cm high).

The vertical panel had two symmetrical rectangular openings (5 cm long × 9 cm high), each located at 10 cm from the centre. Three polyvinyl chloride lids (6 cm long × 11 cm high × 0.3 cm deep) were used for stimulus presentation (Fig. 1, right). Two lids were placed in front of the rectangular openings of the vertical panel. They could be slid laterally in both directions along two parallel metal tracks (45 cm long × 1 cm high), which were mounted horizontally on the panel, 1 cm above and below the openings. The two comparison stimuli were placed on these two sliding panels.

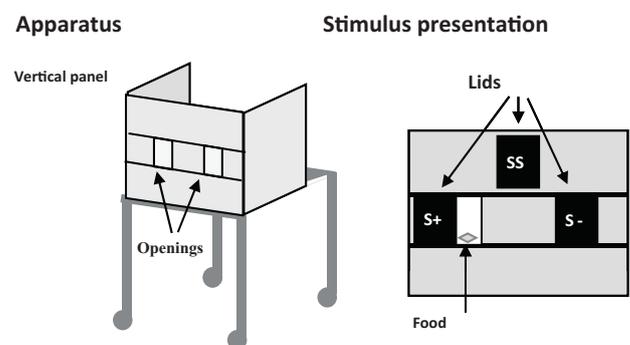


Fig. 1. Schematic representation of the apparatus used to test the monkeys. (Left) The apparatus mounted on the trolley; (right) the front panel of the apparatus used for stimulus presentation and for dispensing the reward. See text for further explanation.

The third lid, holding the sample stimulus, was fixed in the centre of the vertical panel, 1 cm above the two openings and equidistant from them.

The apparatus was placed in front of the experimental box, behind a transparent Plexiglas panel (45 cm long × 40 cm high) mounted on the front wall of the experimental box. The Plexiglas panel had two symmetrical lateral armholes (15 cm long × 5.5 cm high) at the level of the rectangular openings of the apparatus. The monkey had to insert an arm through one of the two holes and move one of the sliding lids covering the rectangular openings in order to retrieve a peanut. The rectangular openings of the apparatus were positioned at the subjects' eye level.

The experimental set-up used with humans consisted of a Pentium PCs and a 17 in. SVGA monitors with a resolution of 1024 × 768 pixels. A response box was allowed the subject 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.). Thus, with human subjects it was possible to collect RT (1 ms accuracy) data as well as response accuracy.

2.1.3. Stimuli

The set of hierarchical stimuli comprised 24 compound patterns (Fig. 2), each consisting of 25 dots grouped in five clusters of five dots each. In each pattern, the dots within the clusters were

spatially arranged to form five small identical configurations (i.e., the local level of the hierarchical stimulus) whereas the five clusters were spatially arranged to create a large configuration (i.e., the global level of the hierarchical stimulus). The local configurations were created placing five dots in the cells of an imaginary 3 × 3 matrix, with at least one dot in each column and each row. The shapes used to construct the global and the local levels of the stimuli were derived from four redundant (R3, R4, R5 and R6) and four with a lower degree of redundancy that are referred to as Non-Redundant (NR3, NR4, NR5 and NR6) dot patterns, as defined by Garner [20]. These patterns are shown in Fig. 2a. Two subsets of hierarchical dot-stimuli were created: (1) the redundant subset, which included 12 stimuli featuring redundant shapes at both the global and the local level (i.e., the R-r subset); and (2) the non-redundant subset, which comprised 12 stimuli featuring non-redundant shapes at both levels (i.e., the NR-nr subset). In each stimulus, the identity of the global shape was always different from the identity of the local shape. Fig. 2b shows the two sets of hierarchical stimuli generated with these particular combinations. For each stimulus, the capital letter denotes the shape used at the global level and the lower-case letter indicates the shape used at the local level (e.g., NR3-nr4 refers to a global non-redundant "NR3" shape made up of five local non-redundant "nr4" shapes).

All the stimuli measured 5.7 cm × 5.7 cm at global level (i.e., the global configuration) and 1.38 cm × 1.38 cm at local level (i.e., the local configurations), with each dot element measuring 0.22 cm × 0.22 cm. At a distance of about 30 cm (see below) the

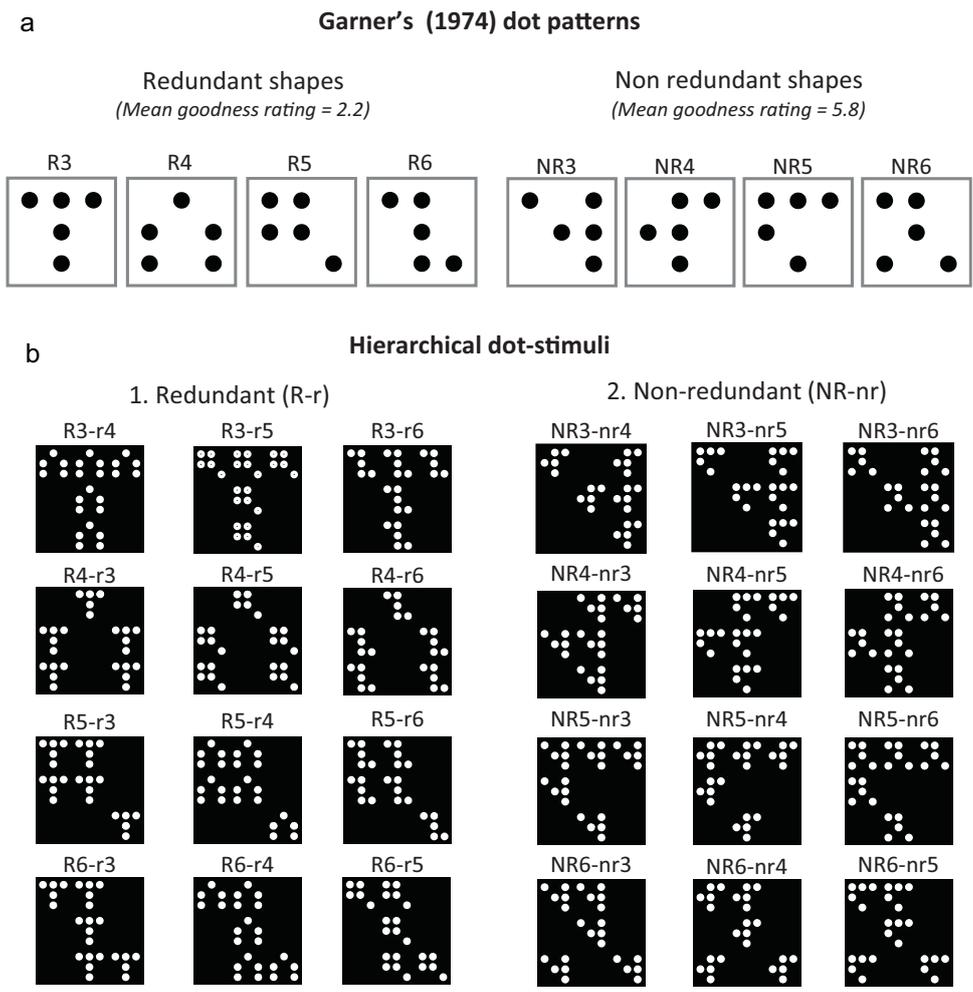


Fig. 2. Garner's dot patterns with different degrees of redundancy (a) used to build the hierarchical stimuli (b) used in Experiment 1. The figure reports the mean goodness rating of the patterns reported by Garner and Clements [22], which was obtained by asking participants to rate the perceived goodness of a pattern on a likert scale.

visual angles of the global and local configurations were about 11° and 2.6°, respectively. Stimuli appeared as white shapes on a black background.

For monkeys, the stimuli were created using Microsoft PowerPoint. Each stimulus was printed on paper and was glued onto the PVC lids of the apparatus. For humans, bitmaps of these stimuli were used for 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 about twice the distance used with the monkeys (see below) so that the visual angle subtended by the stimuli was kept approximately the same as that used with the monkeys (about 11°).

2.1.4. Procedure

A simultaneous MTS task was used for the experiment. For the testing of monkeys, the apparatus was placed in front of the experimental box, at a distance of about 30 cm. At the beginning of each trial the experimenter stood behind the trolley in a central position and placed the sample stimulus (SS) at the centre of the panel and the two comparison stimuli, the matching stimulus (S+) and the non-matching stimulus (S−), on the sliding lids covering the rectangular openings of the panel. Then, 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. In order 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. The monkey could obtain the reward only if it moved the lid featuring the matching stimulus (S+). After the monkey had moved one of the two lids with either hand, the panel was moved away from the box. Trials were separated by an interval of about 30 s, during which the experimenter recorded the animal's choice and selected the stimuli for the next trial.

For the testing of humans, each participant sat in front of a computer at a distance of approximately 60 cm from the screen. Each trial started with the sample stimulus displayed centrally at the top of the screen and with the two comparison stimuli appearing at the bottom left and right corners of the screen, respectively. The subject's task was to indicate, by pressing the "1" or the "5" key, respectively located on the left and right of the computer keyboard, which of the two laterally presented comparative stimuli (S+ and S−) was identical to the centrally presented sample stimulus (SS). Before starting each experimental session the subjects were instructed to respond as fast as possible. All the three stimuli remained present on the screen until a response was made.

Two identity-matching conditions were presented to both monkeys and humans. In the *global matching condition*, S+ was identical to the sample and S− differed from the sample only at the global level. For instance, if the sample was the "R3–r4" stimulus, S+ featured the same stimulus as the sample (R3–r4), whereas S− could be a large "R5" configuration made up of small "r4" configurations (R5–r4). In the *local matching condition*, S+ was identical to the sample, but S− differed from the sample only at local level. For example, when the sample was the "R3–r4" stimulus, S+ also featured the same stimulus as the sample (i.e., R3–r4), and S− consisted of a large "R3" configuration made up, for example, of small "r5" configurations (i.e., R3–r5).

Each monkey performed 8 sessions of 24 trials each, one session a day, for a total of 192 trials. Each session included all the 24 hierarchical stimuli shown in Fig. 2b, with each stimulus being presented once as the sample. Within each session, there were 12 "redundant" and 12 "non-redundant" trials, in which the sample stimulus involved either redundant (e.g., R3–r4) or non-redundant

(e.g., NR4–nr3) shapes at both global and local levels. Only the local or the global matching condition was presented within each session, with trials including redundant and non-redundant sample stimuli randomly intermixed. All daily sessions were preceded by 9 MTS practice trials, using different stimuli from those used in the test (e.g., simple filled shapes such as arrow, heart, hour-glass and round arch shapes). These trials were used to assess the MTS performance level of each animal before each task. The criterion to be reached before the administration of the testing session was of 8 correct responses out of 9. No physical restriction was imposed on the animals during testing.

Each human participant performed a session of 192 trials, which included 96 global trials and 96 local trials. Within the global and local matching trials, 48 trials featured redundant sample stimuli and 48 trials featured non-redundant sample stimuli, randomly intermixed.

2.2. Results

2.2.1. Accuracy

The results of Experiment 1 are presented as percentages of correct responses in Fig. 3.

A 2 (Level of Processing) × 2 (Redundancy) × 2 (Species) mixed model ANOVA revealed a significant main effect for species, $F(1, 15) = 122.24$, $p < .001$, $\eta_p^2 = .89$, with humans ($M = 96.0\%$) performing better than monkeys ($M = 77.2\%$) overall. The effect of level of processing was also significant, $F(1, 15) = 21.31$, $p < .001$, $\eta_p^2 = .59$, with a higher level of accuracy recorded in the local trials ($M = 88.8\%$) compared to the global trials ($M = 84.4\%$). More importantly, a significant effect of stimulus redundancy emerged, $F(1, 15) = 15.15$, $p < .01$, $\eta_p^2 = .50$, with redundant stimuli ($M = 88.1\%$) being processed with a higher level of accuracy than non-redundant ones ($M = 85.1\%$).

The effect of redundancy did not interact with species ($p > .1$), showing that both species were more accurate when processing redundant stimuli (humans, $M = 97.0\%$; monkeys, $M = 79.2\%$) than non-redundant stimuli (humans, $M = 95.0\%$; monkeys, $M = 75.2\%$). On the other hand, there was a significant interaction between level of processing and species, $F(1, 15) = 23.03$, $p < .001$, $\eta_p^2 = .61$. Post-hoc comparisons (Duncan test) showed that, in monkeys, a significantly higher level of accuracy was obtained for the local trials ($M = 81.7\%$) compared to the global ($M = 72.7\%$) trials ($p < .01$). In humans, no significant differences emerged between the accuracy scores registered in the global ($M = 96.1\%$) and the local ($M = 95.9\%$) trials. The interaction redundancy by level of processing was also not significant ($p > .1$), indicating, in this experiment, a lack of relationship between redundancy and the level of processing where it is present.

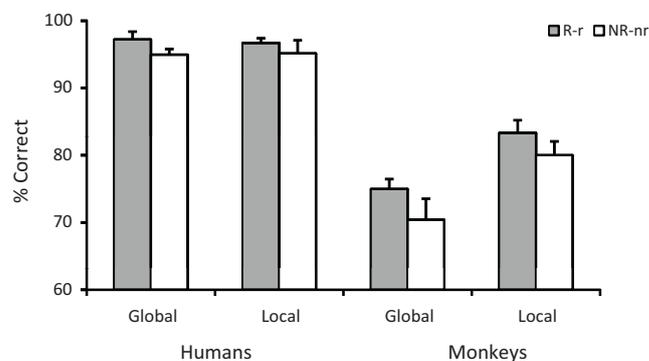


Fig. 3. Experiment 1: Mean percentage of correct responses observed in the different conditions of Experiment 1. Error bars represent the Standard Error of the Mean.

2.2.2. RT

In this and the following experiments, RTs were analysed in humans only as it was not possible to record RTs with the apparatus used with monkeys.

A 2 (Level of Processing) × 2 (Redundancy) ANOVA performed on the mean RTs recorded for humans revealed a significant main effect of Redundancy, $F(1, 11) = 39.83, p < .001, \eta_p^2 = .78$, with redundant stimuli (R-r $M = 1586.7$ ms, $SE = 84.1$ ms) being processed faster than non-redundant ones (NR-nr $M = 1874.8$ ms, $SE = 99.7$ ms). By contrast, consistently with the accuracy results, no significant main effect emerged for level of processing (global trials $M = 1757.4$ ms, $SE = 99.5$ ms; local trials $M = 1703.7$ ms, $SE = 88.6$ ms n.s.). Finally, a significant interaction between level of processing and redundancy was found, $F(1, 11) = 8.33, p < .05, \eta_p^2 = .43$.

Planned comparisons revealed that redundant stimuli were processed faster than non-redundant in both the global [R-r $M = 1656.2$ ms, $SE = 106.4$ ms; NR-nr $M = 1858.6$ ms, $SE = 100.1$; $t(11) = 3.651, p < .01$] and the local condition [R-r $M = 1517.2$ ms, $SE = 66.1$; NR-nr $M = 1890.2$ ms, $SE = 101.7$ ms, $t(11) = 7.013, p < .001$]. Nevertheless, the difference was sharper in this latter condition and this could explain the significant interaction.

2.3. Discussion

The results of Experiment 1 indicate that, in both capuchin monkeys and humans, visual processing benefits from stimulus redundancy in a MTS task with hierarchical stimuli that required local or global processing in different trials. The lack of interaction between the level of redundancy in the stimuli and the species tested indicates that the benefits in MTS performance induced by the presence of redundancy in the stimuli are similar in monkeys and in humans. On the other hand, the lack of interaction between redundancy and level of processing suggests the absence of a functional relationship between these factors.

This experiment also shows, for the first time in the literature, that a local advantage can be observed in capuchin monkeys when they process hierarchical stimuli that require grouping also at the local level and not at the global level only as in previous studies

[10,45,46]. These latter results suggest that the local advantage in capuchin monkeys cannot be accounted for exclusively by their alleged relative difficulty of grouping elements at the global level.

The extent to which the local advantage so frequently observed in monkey species also emerges in conditions where grouping is required at the local level of hierarchical stimuli has never been investigated before and was an important issue to assess. However, since the hierarchical stimuli used in Experiment 1 had never been used before, it was important to verify the presence of the beneficial effects of redundancy with the type of stimuli, which have more traditionally been employed in studies of local and global processing. It was also interesting to verify if with traditional hierarchical patterns a clearer relationship between redundancy and level of processing would have emerged. We did so in Experiment 2.

3. Experiment 2

The aim of Experiment 2 was to assess the effect of redundancy on the global/local processing of humans and capuchin monkeys in conditions featuring the same shapes of Experiment 1 but with local elements depicted as solid lines rather than collections of dots, in analogy with the hierarchical stimuli typically used in previous studies of local–global processing.

3.1. Method

3.1.1. Participants and apparatus

The same five monkeys and the same 12 human participants used in Experiment 1 took part in Experiment 2. For the present experiment we employed the same apparatus used in Experiment 1 with humans and monkeys, respectively.

3.1.2. Stimuli and procedure

The stimuli were 24 hierarchical patterns of the type used by Navon [40], each made up of the spatial arrangement of five local elements (see Fig. 4). The shapes of the global and the local level of the hierarchical stimuli were the same as those used in Experiment 1 with the only exception that now the dots at the local level were

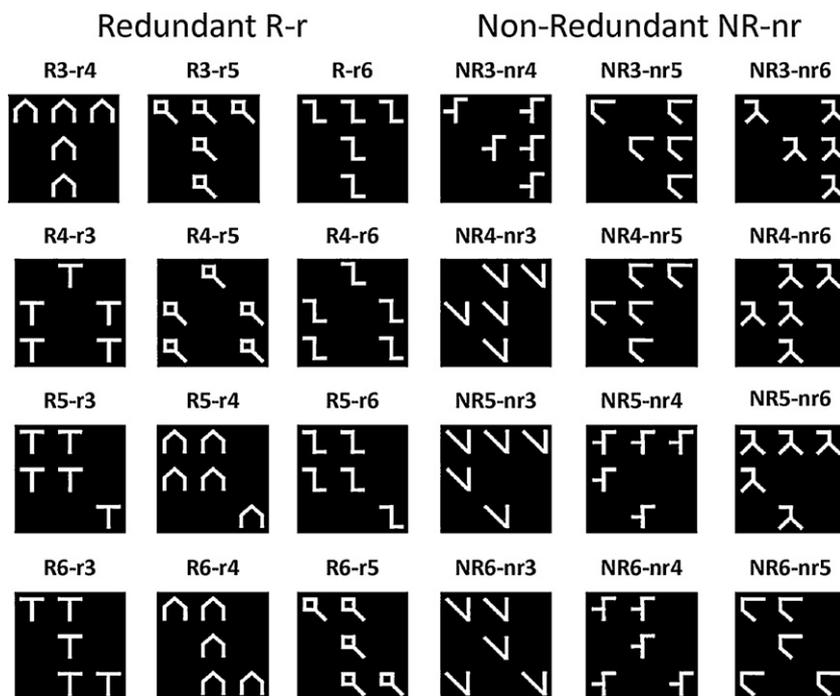


Fig. 4. Set of stimuli used for Experiment 2.

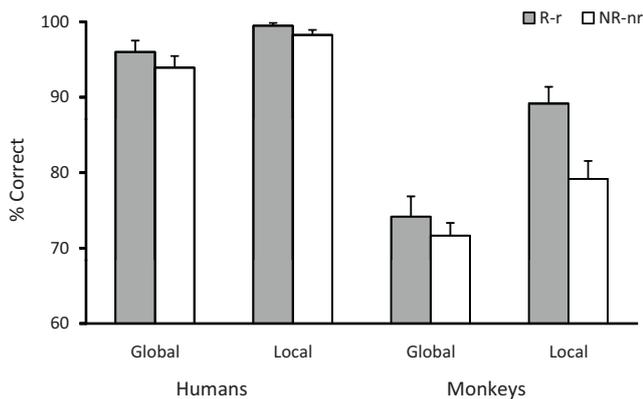


Fig. 5. Experiment 2: Mean percentage of correct responses observed for the two species in the different conditions of the task. Error bars represent the Standard Error of the Mean.

connected by solid lines. Experimental design, task and procedure were all the same as in Experiment 1.

3.2. Results

3.2.1. Accuracy

Fig. 5 reports the accuracy scores obtained by humans and monkeys for both redundant and non-redundant Navon-like stimuli, in the local and the global condition.

A 2 (Level of Processing) \times 2 (Redundancy) \times 2 (Species) mixed model ANOVA revealed a highly significant main effect for species, $F(1, 15) = 151.82, p < .001, \eta_p^2 = .91$, with humans ($M = 96.9\%$) performing better than monkeys ($M = 78.5\%$) overall. The effect of level of processing was also significant, $F(1, 15) = 34.86, p < .001, \eta_p^2 = .70$, with local trials (91.5%) being responded with a higher level of accuracy than global trials (83.9%). Moreover, a significant effect of stimulus redundancy was found, $F(1, 15) = 16.59, p = .001, \eta_p^2 = .53$, with redundant stimuli ($M = 89.7\%$) being processed with a higher level of accuracy than non-redundant ($M = 85.8\%$) ones. Furthermore, all the 2-way interactions were significant: Species by Level of processing, $F(1, 15) = 8.19, p < .05, \eta_p^2 = .35$, Redundancy by Species, $F(1, 15) = 5.63, p < .05, \eta_p^2 = .27$, Level of Processing by Redundancy, $F(1, 15) = 6.47, p < .05, \eta_p^2 = .30$. Finally, the third order interaction Level of Processing by Redundancy by Species was also significant $F(1, 15) = 10.32, p < .01, \eta_p^2 = .41$.

In order to explain this complex pattern of interactions, separate post hoc comparisons were performed on the data of each species. In capuchins, performance differences between redundant and non-redundant stimuli were significant in the local trials (R-r $M = 89.2\%$; NR-nr $M = 79.2\%$, $p < .05$) but not in the global trials (R-r $M = 74.2\%$; NR-nr $M = 71.7\%$, $p > .1$). These differences seem to explain most of the interactions since the monkeys' local advantage emerged whether or not the stimuli were redundant.

In humans, the accuracy level for redundant stimuli was higher than that observed for non-redundant stimuli in the global trials (R-r $M = 96.0\%$; NR-nr $M = 93.9\%$, $p < .01$). However, the difference between redundant and non-redundant stimuli only approached to significance in the local trials (R-r $M = 99.5\%$; NR-nr $M = 98.3\%$, $p = .06$; see Fig. 5).

3.2.2. RT

In humans, a 2 (Level of Processing) \times 2 (Redundancy) ANOVA revealed a highly significant main effect for level of processing, $F(1, 11) = 47.12, p < .001, \eta_p^2 = .811$, with local trials ($M = 1220.8$ ms, $SE = 100.4$ ms) being processed faster than global trials ($M = 1416.6$ ms, $SE = 108.9$ ms). There was also a significant effect of redundancy, $F(1, 11) = 54.83, p < .001, \eta_p^2 = .833$, with

redundant stimuli ($M = 1225.2$ ms, $SE = 94.8$ ms) being processed significantly faster than non-redundant stimuli ($M = 1412.2$ ms, $SE = 113.5$ ms). The interaction between the two factors was not significant.

3.3. Discussion

The results of Experiment 2 confirmed the presence of an effect of redundancy in both monkeys and humans using stimuli which, in contrast with those of Experiment 1, did not require grouping at the local level.

However, the pattern of interactions observed in this experiment indicates an asymmetry in the effects of redundancy in monkeys and humans. Whereas monkeys displayed a positive effect of redundancy in the local trials but not in the global trials, humans showed a significant effect of redundancy in the global trials but not in the local trials. Nevertheless, the lack of interaction between redundancy and level of processing in the RT data suggests a similar increase in the speed of responding for redundant stimuli in both the local and the global trials. It is therefore likely that the absence of an effect of redundancy in the accuracy scores for the local trials in humans is explained by a ceiling effect due to the very high level of performance of humans in this task.

Apart from the effects of redundancy discussed above, Experiment 2 revealed once again a generally better performance in humans, and a higher level of accuracy in the local trials in both species. The local bias observed in humans, although less pronounced than that of monkeys, contrasts with the results of Experiment 1, where no local or global advantage emerged in humans in conditions featuring patterns that entailed grouping at the local level of the stimuli (i.e., hierarchical dot-patterns). This seems to be at odds with previously published result as a local advantage does not normally emerge in humans unless specific factors are manipulated (see [28] for a review). Experiment 3 aimed to clarify the reasons for the local advantage in humans that we observed in Experiment 2.

4. Experiment 3

Evidence from the human literature suggests that the global–local processing of hierarchical patterns may be affected by some properties of the stimuli, such as the visual angle or the number and the relative size of the local elements [27,30]. For example, stimuli subtending a large visual angle can preclude a global precedence effect in humans; likewise, patterns composed of a few, relatively large elements can reverse or reduce the global advantage typically observed in our species. In Experiment 2 we used relatively large stimuli compared to those often used in the literature. Thus, the local advantage that we observed in humans there could have been explained by factors related to the visual angle subtended by the stimuli [30].

Experiment 3 aimed at verifying whether this was the case by manipulating stimulus size. In this experiment we also manipulated the number and the relative size of the local elements forming the stimuli since this variable has also been shown to affect the processing of different levels of hierarchical stimuli in humans [27].

4.1. Method

4.1.1. Participants and apparatus

The same five monkeys and the same 12 human participants took part in Experiment 3. The apparatus were the same used with humans and monkeys in the previous experiments.

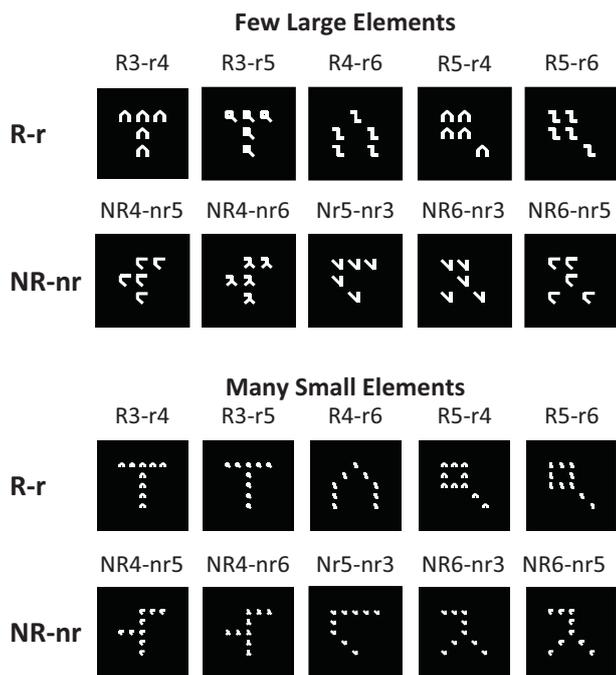


Fig. 6. Set of stimuli used for Experiment 3.

4.1.2. Stimuli and procedure

For this experiment, the stimuli were created using a subset of 10 shapes from the 24 used in Experiment 2. However, the shapes were reduced in size, so that each subtended a visual angle of about 7° at the global level. Moreover, on the basis of these shapes two subsets of hierarchical patterns were created, which differed in the number and the relative size of their elements. The *few-element* subset consisted of 10 stimuli composed of five relatively large elements. These stimuli were obtained by a proportional reduction of dimensions of the corresponding patterns used in the Experiment 2. The *many-element* subset consisted of 10 stimuli formed by nine relatively small elements. For each subset there were five redundant (R-r) and five non-redundant (NR-nr) shapes at both levels of processing. As in Experiment 2, in each stimulus, the global shape was always different from the local shapes. Each individual element measured about 0.9 cm × 0.9 cm (i.e., 1.7°) in the few-element patterns and about 0.37 cm × 0.37 cm (i.e., 0.7°) in the many-element patterns. The set of redundant and non-redundant patterns for each stimulus subset used in the present experiment are reported in Fig. 6. Task and procedure were as in the previous experiments.

4.2. Results

4.2.1. Accuracy

Fig. 7 illustrates the percentage of correct responses recorded for humans and monkeys in the few/large- (a), and in the many/small-element (b) conditions.

A 2 (Species) × 2 (Numerosity) × 2 (Level of Processing) × 2 (Redundancy) mixed ANOVA revealed main effects for the factors species, $F(1, 15) = 138.14, p < .001$, with humans performing at a higher level of accuracy than monkeys, and level of processing, $F(1, 15) = 44.67, p < .001$, with a higher level of accuracy in the local trials than in the global trials. The factor redundancy was also significant, $F(1, 15) = 12.91, p < .01$, with redundant stimuli producing a higher level of accuracy than non-redundant stimuli. Significant interactions emerged between the factors Species and Level of processing, $F(1, 15) = 63.97, p < .001$, and Numerosity and Redundancy, $F(1, 15) = 12.84, p < .01$. The third order interactions

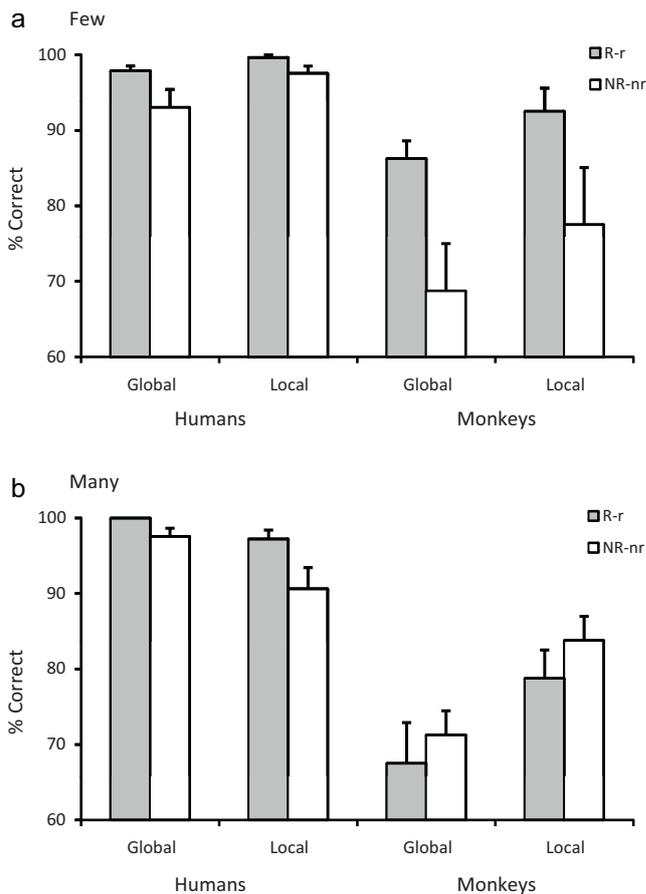


Fig. 7. Experiment 3: Mean percentage of correct responses observed for the two species in the different conditions of the experiment, presented in separate graphs for the few (a) and many (b) conditions. Error bars represent the Standard Error of the Mean.

Species × Numerosity × Level of processing, $F(1, 15) = 6.87, p < .05$, and Species × Numerosity × Redundancy, $F(1, 15) = 15.71, p < .01$, were also significant.

Planned comparisons carried out to explain the third order interactions revealed that humans had a global advantage when processing the stimuli with many small elements, $t(11) = 3.02, p < .05$, and a local advantage when processing the stimuli with few large elements, $t(11) = 2.57, p < .05$. Monkeys showed a different pattern of results since they had a local advantage with both stimuli with many small elements, $t(4) = 4.40, p < .05$, and stimuli with few large elements, $t(4) = 3.54, p < .05$. These results explain the significant species by numerosity by level of processing interaction. The interaction species by numerosity by redundancy is explained by the fact that whereas humans showed a benefit when processing redundant compared to non-redundant stimuli in both many-small, $t(11) = 2.86, p < .05$, and few-large, $t(11) = 2.50, p < .05$, stimuli; monkeys showed a significant effect of redundancy in trials with few-large stimuli, $t(4) = 3.03, p < .05$.

4.2.2. RT

In humans, a 2 (Numerosity) × 2 (Level of Processing) × 2 (Redundancy) ANOVA revealed a significant main effect of redundancy, $F(1,11) = 21.57, p = .001, \eta_p^2 = .662$. Redundant stimuli ($M = 1009.8$ ms, $SE = 99.2$ ms) were processed faster than non-redundant ones ($M = 1230.7$ ms, $SE = 140.4$ ms). A significant interaction emerged also between numerosity and level of processing, $F(1,11) = 25.76, p < .001, \eta_p^2 = .701$, and between level of

processing and redundancy, $F(1,11)=5.75$, $p<.05$, $\eta_p^2 = .343$. No other main effects or interactions were significant.

Paired sample t -test carried out to explain the interaction numerosity by level of processing showed that, in the few condition, the local trials ($M=1051.2$ ms, $SE=110.7$ ms) were processed significantly faster than the global ($M=1158.1$ ms, $SE=129.0$ ms; $t(11)=4.49$, $p<.001$). By contrast, in the many condition, the global trials ($M=1095.1$ ms, $SE=116.5$) were processed significantly faster than the local trials ($M=1176.6$ ms; $SE=124.3$, $t(11)=4.26$, $p<.001$). This last result is consistent with the results of the accuracy analysis reported above.

The interaction level of processing by redundancy was explained by the fact that redundant stimuli were processed faster than non-redundant stimuli, irrespectively of the numerosity of their elements in both the global ($R-r M=1004.6$ ms, $SE=103.2$ ms; $NR-nr M=1248.5$ ms, $SE=143.1$ ms; $t(11)=4.90$, $p<.001$) and the local trials ($R-r M=1014.9$ ms, $SE=95.5$ ms, $NR-nr M=1212.9$ ms, $SE=138.1$; $t(11)=4.19$, $p<.01$).

4.3. Discussion

The results of Experiment 3 support the notion that the emergence of a local advantage in humans observed in Experiment 2 could be explained mainly by the use of patterns composed of few relatively large elements. In fact, consistently with the results of previous studies [27,28], the global advantage typical of humans was restored when participants were presented with patterns composed of many relatively smaller elements. Therefore, in line with previous literature, the size and quantity of the stimulus constituents was shown to influence the preferred level of processing in humans. The robustness of the local advantage in capuchin monkeys was confirmed by the fact that it was not affected by these stimulus manipulations. In relation to the factor redundancy, this third experiment also confirmed that monkeys can detect and benefit from this stimulus property as their performance improved with redundant stimuli. Nevertheless, this positive effect of redundancy in monkeys was present only in the trials featuring stimuli with few sparse local elements. It is difficult to provide at this stage a clear explanation for this selective effect of redundancy in monkeys in trials with sparse stimuli. It is however worth noticing that albeit larger overall, the stimuli in the sparse condition of Experiment 3 preserved the same proportion between the size and relative distance of local elements as the stimuli used in Experiment 2. Since we obtained similar effect of redundancy in Experiment 2, it seems that the relative distance of the elements could be critical for the emergence of the effect. However, in the present experiment the beneficial effect of redundancy emerged in monkeys in the global trials as well as in the local trials. This contrast with the results of Experiment 2 where there was a clear relationship between the level of processing and benefits of redundancy. The reasons for this difference in the results of the two experiments are unclear at this stage and further investigations would be needed to clarify them.

5. General discussion

5.1. Redundancy

The results of this study indicate that capuchin monkeys can benefit from the redundancy of hierarchical visual stimuli in a MTS task. To our knowledge this is the first report of a beneficial effect of redundancy in the visual processing of a monkey species. In fact, it contrasts with previous results [43], which suggested that stump-tailed monkeys are not sensitive to stimulus redundancy. In the experiments reported here and in those carried out by Schrier et al.

[43], redundancy was defined according to Garner [20] and this makes the two studies to some extent similar. However, Schrier et al. [43] used a binary discrimination task rather than MTS and the dot patterns in their stimuli were not arranged to form hierarchical shapes. As such, it cannot be excluded that macaques or other non-human primate species may show positive effects of stimulus redundancy if tested with the paradigm featured here and it would be important to assess the generality of our finding with other species of monkeys and apes.

Garner's work [20,21] showed a close interlink between the degree of redundancy in the stimulus, the perceived goodness of stimulus shape and the ease of processing of visual patterns. Thus, our results with capuchin monkeys would suggest that non-human primates might also perceive shape "goodness" in a similar way to humans. The sensitivity to stimulus redundancy and its beneficial effects is well established in studies of human perception [20,25,37–39] and our results confirmed that the benefits of redundancy were clearly displayed by humans in the paradigm featured in our study.

The relationship between redundancy and level processing is less clear considering the varied pattern of results obtained in the three experiments.

In Experiment 2, there was an asymmetrical pattern of accuracy results in humans and capuchin monkeys as shown by the interaction of redundancy and level of processing in the two species. In fact, in humans redundancy failed to have a beneficial effect in the local trials. Conversely, in monkeys its presence was beneficial in the local trials only.

In a recent study [8], we provided results suggesting that the typical local advantage of monkeys could be explained by their preferential allocation of attention at the local level of the stimuli. In fact, the local advantage of monkeys can be reversed when experimental manipulations induce the animals to switch their spontaneous allocation of attention from the local to the global level of the stimuli. Given this demonstration that monkey do shift attention from different levels of stimulus structure, it is possible that the sensitivity of monkeys to redundancy is particularly strong when their attention spontaneously converges on the level of stimulus structure where it is present, such as the local level. For the same reason, humans may be more sensitive to redundancy when it is present at the global level of the stimuli.

However, it should also be noted that in humans in Experiment 2 the factor redundancy also approached significance in the local trials and this could indicate a general overall higher sensitivity to this factor in humans. In fact, the RT analysis indicated that redundant stimuli were matched faster than non-redundant stimuli by humans at both levels of stimulus processing. Evidence for an overall higher sensitivity to redundancy in humans also emerged in the results of Experiment 3. In that experiment, a positive effect of redundancy on accuracy was observed again in both species but was particularly robust in humans. In fact, whereas monkeys benefitted from stimulus redundancy only in the conditions featuring stimuli with few large elements, in humans they were observed in both conditions featuring stimuli with few large elements and in those with many small elements. The same results were confirmed by the RT analysis that showed that humans were faster when processing redundant stimuli in all conditions.

Thus, if the results of Experiment 2 may suggest a functional relationship between level of processing and the degree of redundancy of the stimuli, the results of both Experiments 1 and 3 seem to indicate otherwise. The lack of interaction between the two factors in Experiment 1 indicates that redundant stimuli were easier to process than non-redundant stimuli, regardless of the level of processing required by the matching task. Similarly in Experiment 3 humans processed redundant stimuli at a higher level of accuracy

in all conditions. Monkeys showed a facilitatory effect of redundancy in the few large stimuli only but this effect was evident in both the local and the global trials.

Further experiments specifically aimed at clarifying the relationship between attention and redundancy in monkeys would be of extreme interest. It would also be important to clarify the extent to which there is a functional relationship between redundancy and level of processing or whether the results observed in our Experiment 2 are more likely to be just due to fluctuations caused by other still unspecified reasons.

5.2. Hierarchical grouping

Apart from providing a first demonstration of a positive effect of redundancy in monkey's visual processing, a second important result of our study was the demonstration that local advantage in monkeys emerges in conditions where some grouping is required at that level of processing. This is a key finding since global–local processing in monkeys has so far been studied using Navon stimuli with solid shapes as local elements. With this type of hierarchical stimuli grouping processes are only required to derive global shapes. The robust local advantage observed in monkeys in previous studies could therefore be attributed entirely to a relative difficulty of monkeys with grouping processes. Indeed, a relative difficulty with grouping has been suggested as the main explanation for the presence of a local advantage in monkeys [15]. It cannot be denied that the resources necessary to group by proximity could be responsible in monkeys for a number of differences in visual processing compared to humans. These include the lack of an effect of flankers in the Ebbinghaus illusion in baboons [42] and the fact that the distance between visual elements can dramatically affect the ability of monkeys to process them conjointly, with a series of more general cognitive consequences [17]. Our results, however, indicate that the lack versus presence of the need to use grouping processes at the local and global level of the stimuli cannot on its own explain all occurrences of the local advantage of monkeys. It could be argued that in Experiment 1, even if grouping was required at both levels, the local advantage in monkeys could be explained by the fact that the global level required them to deploy grouping processes twice. This in itself could explain their local advantage, purely in terms of a relative difficulty with grouping. In order to assess this possibility we carried out a paired sample *t*-test comparing the performance of the monkeys in the global trials of Experiments 1 and 2. It did not reveal a significant difference [$t(4) = .10$, n.s.]. In fact, the means were extremely similar [global trials Exp 1 $M = 72.7\%$, $SE = 1.5\%$; global trials Exp 2 $M = 72.9\%$, $SE = 1.5\%$]. This indicates that, even if present, the requirement of grouping twice when processing the global level does not produce additional difficulties in monkeys and cannot on its own explain their local advantage when processing these stimuli. Similarly, a comparison of the performance of the monkeys in the local trials of Experiment 1 (that required grouping at that level) and of Experiment 2 (that did not), did not reveal a significant difference [$t(4) = 2.69$, n.s., local trials Exp 1 $M = 81.7\%$, $SE = 1.0\%$; local trials Exp 2 $M = 84.2\%$, $SE = 1.6\%$]. We can therefore conclude that, although important, grouping requirements in general cannot fully account for the local advantage in monkeys on the present study.

It is also of interest to compare the pattern of results obtained with humans in relation to the issue of global–local processing in the different experiments of this study. The pattern that we obtained seems to indicate that there may be different contributing factors in the processing of gestalts. Humans did not show a local or global advantage in Experiment 1, where there was an attention demanding need to group elements at both the local and the global level. At the same time there might have been an

increased level of salience at the local level due to the size of the stimuli at that level. Thus, a trade-off between these two factors may have caused the absence of an effect of level of processing and could have reduced the typical global advantage observed in humans.

In Experiment 2, we reduced the need to use attentional resources in order to process the local level of the stimuli as the requirement to group elements by proximity at that level was removed. This, paired with the fact that the stimuli used in our first two experiments featured few relatively large local constituents may have caused the emergence of the uncharacteristic local advantage we observed in our human participants. We tested the hypothesis that the size of the stimuli and/or the number and relative size of elements was responsible for this effect in Experiment 3 by directly manipulating these structural properties of hierarchical patterns in conditions similar to those of Experiment 2 (no need to group by proximity at local level) and similar to those of previous experiments. Here emerged a global advantage when the salience of the local level is reduced by decreasing the size of the local elements and increasing their density (i.e., many-element patterns). This latter result confirmed that the explanation of the pattern of results obtained in Experiment 2 is plausible and consistent with other reports in the literature on human cognition which have suggested that the number and relative size of the local elements present in hierarchical stimuli can affect the quality of processing of different level of stimulus structure and that the global advantage in humans can be reversed by increasing the size and sparsity of the local elements (see [28] for a review).

In sum, our study provides a first demonstration that monkeys are sensitive to stimulus redundancy and that a local advantage in monkeys emerges also in conditions where grouping is required to process lower and higher hierarchical levels of structure of visual stimuli. These are important findings for the characterisation of the extent to which visual processing in non-human primates resemble that of humans. The overall pattern of results obtained here indicates that the explanation of the dominance of global and local processing in monkeys cannot rest on trivial factors. Together with other evidence that global–local processing in monkeys and humans is influenced by top-down attentional processes [8], the present results suggest that interspecies differences in this domain are likely to tap onto relatively high cortical functions.

Within a comparative framework it has often proved difficult to pinpoint to cognitive abilities that allow the detection of non-peripheral interspecies' differences and, at the same time, meaningful comparisons of closely related species, likely to share homologies in the brain functions that underpin them. Differences in the style of processing of visual patterns such as those emerged in this study seem to offer us the opportunity to do so. Thus, studies aimed at disentangling alternative explanations of the differences observed in the global–local processing of humans and other primate species could help the formulation of informed hypotheses regarding the emergence of human cognitive sophistication and help the assessment of the strengths and limitations of the use of primate models of human visual cognition.

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