

**A COMPARATIVE ANALYSIS OF GLOBAL-LOCAL PROCESSING  
IN CAPUCHIN MONKEYS (*SAPAJUS APELLA*) AND HUMANS**

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## **ABSTRACT**

Humans display a global advantage when presented with hierarchical visual patterns. Conversely, capuchin monkeys show a strong local advantage. In the present work, three studies have been carried out using a Matching-to-Sample procedure in order to clarify the conditions under which global or local advantage occurs in capuchin monkeys and humans.

The first study was addressed to understand the role played by stimulus redundancy on global-local processing. This study proved that both species can benefit from stimulus redundancy in processing hierarchical stimuli. Furthermore, it revealed that capuchins' local advantage persists when the grouping requirements occur also at local level.

The second study was addressed to understand whether or not inducing an attention bias towards either level of stimulus structure can affect global-local processing. Attentional bias was manipulated using tasks where the proportion of trials requiring global or local processing varied between conditions. Monkeys displayed a local advantage in the local-bias condition but a global advantage in the global-bias condition. Humans exhibited an effect of attentional bias on the processing speed of global-local trials across conditions.

The third study was addressed to understand the effect of spatial frequencies processing on global-local processing. The first experiment was addressed to clarify which spatial frequencies could be adopted. The second experiment was designed to assess whether attention allocation to different spatial frequencies (high or low) can affect global-local processing. Both species displayed an effect of spatial frequencies processing on global-local processing. However, this effect was confined to local trials only and occurred under different conditions in the two species.

Overall, the results of the present work indicate that attention plays a particularly important role in capuchin monkeys' visual cognition and are discussed in relation to the extent to which they can explain the observed differences between monkeys and humans in their global-local processing.

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## DECLARATIONS

The present research is based on my own work and has not been submitted for any other academic degree.

In order to carry out the first and second study of this research work (described in Chapter III and IV respectively), I was helped in the data collection with monkeys by Mr. Giuseppe Giustino. This formed part of Mr. Giustino's submission of an undergraduate dissertation at the University of Rome "La Sapienza", Italy.

Part of the experimental work carried out for Chapter III and IV has been published as part of the articles listed below:

De Lillo C., Palumbo M., Spinozzi G. & Giustino G. (2012). Effects of pattern redundancy and hierarchical grouping on global-local visual processing in monkeys (*Cebus apella*) and humans (*Homo sapiens*). *Behavioural Brain Research*, 226: 445-455.

De Lillo C., Spinozzi G., Palumbo M. & Giustino G. (2011). Attention allocation modulates the processing of hierarchical visual patterns: a comparative analysis of capuchin monkeys (*Cebus apella*) and humans. *Journal of Experimental Psychology: Animal Behavior Processes*. 37(3): 341-352.

The nature of my contribution includes carrying out the experiments with humans and monkeys, data analysis as well as contributing in designing the studies and drafting the articles.

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## LIST OF ABBREVIATIONS AND SYMBOLS

<b><math>\eta_p^2</math></b>	Partial eta-squared
<b>ASD</b>	Autism Spectrum Disorder
<b>ANOVA</b>	Analysis of Variance
<b>CNR</b>	<i>Consiglio Nazionale delle Ricerche</i> (National Research Council)
<b>cpd</b>	cycles per degree
<b>EQ</b>	Encephalization Quotient
<b>ERP</b>	Event Related Potential
<b>Exp</b>	Experiment
<b>fMRI</b>	functional Magnetic Resonance Imaging
<b>HSF</b>	High Spatial Frequencies
<b>ISTC</b>	<i>Istituto di Scienze e Tecnologie della Cognizione</i> (Institute of Cognitive Science and Technologies)
<b>LGN</b>	Lateral Geniculate Nucleus
<b>LSF</b>	Low Spatial Frequencies
<b>M</b>	Mean
<b>MRI</b>	Magnetic Resonance Imaging
<b>ms</b>	milliseconds
<b>MTS</b>	Matching-To-Sample
<b>mya</b>	million years ago
<b>NR-r</b>	Non Redundant (global level) – redundant (local level)
<b>NR-nr</b>	Non Redundant (global level) – non redundant (local level)

<b>ns</b>	non significant
<b>pp</b>	page(s)
<b>Par</b>	Paragraph
<b>PET</b>	Positron Emission Tomography
<b>PVC</b>	Polyvinyl Chloride
<b>R-nr</b>	Redundant (global level) – non redundant (local level)
<b>R-r</b>	Redundant (global level) – redundant (local level)
<b>RT</b>	Response Time
<b>SF</b>	Spatial Frequency
<b>SS</b>	Sample Stimulus
<b>S+</b>	Correct Comparison Stimulus
<b>S-</b>	Incorrect Comparison Stimulus
<b>va</b>	visual angle

## CHAPTER I

### INTRODUCTION

Animal behaviour and cognition have captivated human imagination from ancient times, and over the centuries many philosophers have speculated about the existence of the mind among the animal kingdom. After Charles Darwin positioned humans on a continuum with other animals in "*The descent of man*" (1871), the study of animal behaviour developed into a scientific topic, namely *ethology*, principally through the work of zoologists and ethologists Konrad Lorenz and Niko Tinbergen. Lorenz carried out his studies following an evolutionary perspective and developing the idea that behaviour has an important component which is genetically determined and therefore, is subject to evolution through natural selection (Lorenz, 1965).

In parallel to *ethology*, there was experimental psychology. The two schools differed in a few aspects, in particular, according to the ethologists, animal behaviour is a biological phenomenon and therefore, it is the results of natural selection and evolution. Lorenz's theory was that behaviour can be broken down into some innate and acquired components, whereas experimental psychologists emphasised mainly the importance of learning on behaviour.

Around the 30s of the last century, within experimental psychology, behaviourism arose. It had as promoters psychologists like Watson and Skinner, who considered psychological phenomena only like physical activities suggesting that it is impossible to make scientific assertions about mental processes (Watson, 1925). In response to behaviourism, cognitive psychology arose, trying to open the "*black box*" supposed inaccessible by behaviourists and suggesting that individuals, humans and possibly other animals, have

a mental life that can be examined in terms of cognitive mechanisms rather than stimulus-response associations.

Among comparative cognitive studies, investigations on behaviour and cognitive abilities of monkeys and apes are extremely significant given the position held by these species in evolution. Early studies of primate behaviour and cognition began with the work of Robert Yerkes known for his studies of primate intelligence and social behaviour of gorillas and chimpanzees (see Yerkes, 1925, 1943, Yerkes & Yerkes, 1929). His researches opened the way to a prolific century of studies culminating with the highly influential works of English anthropologist and primatologist Jane Goodall on social behaviour and tool use abilities displayed by the chimpanzees in the Democratic Republic of Congo (see, for instance, Goodall, 1964; Goodall, 1980 in Lehrman, Hinde, Shaw, pp 195-429). Throughout these years, many factors have led scientists to devote their attention towards primate behaviour and cognition: on one hand, the comprehension of the biology of other animals together with the search for animal models suitable for biomedical research. On the other hand, from an evolutionary standpoint, there are two reasons: the first is that, since non-human primates are phylogenetically related to humans, they all share a common ancestor who lived around 60 million years ago (mya). Therefore, comparative cognitive studies among primates can provide direct information about the origin of human cognitive system and its evolution. The second is directly related to a particular skill which seems to be a prerogative of human cognition: language. To our knowledge, only humans evolved a complex and articulated spoken language. In fact, whereas other animals can display complex communication systems, these do not rely on a symbolic system like the spoken language. Psychologists often claim that the lack of language determines a lack of cognitive codes useful to describe some non-spatial abstract relations, with a series of general cognitive consequences in the way they process

information (Premack, 1983). Therefore, the documentation of animal intelligence offers information about what the cognitive system could be in absence of language.

Comparative cognitive studies investigate and compare perceptual and cognitive processes across different species taking into consideration their biological and evolutionary relationships. In this way, they allow us to better understand the evolution of the brain under a morphological as well as a functional point of view. In fact, due to the lack of fossil records, the evolution of the brain is difficult to characterize in other ways. Thus, by studying the emergence of some cognitive features in living animals taxonomically related to us at different levels, it is possible to infer whether or not those features were held by previous common ancestors. In other words, if a trait is held by all the species that share a common ancestor, it is possible to conjecture that such feature was already present in that common ancestor and therefore, that it represents a homologous trait. This kind of analysis is particularly important for those traits that do not leave fossil records and may help us in understanding the origins, the evolution and the adaptive value of human cognitive processes. In this way, it allows us to understand how the human brain developed to such extent.

Early investigations of primate cognition were addressed mostly on understanding higher cognitive functions such as tool use, ability to solve complex tasks, concept formation and abstract reasoning (see for example Yerkes, 1916, or Premack & Woodruff's work about the theory of mind in chimpanzees, 1978). Yet, only relatively recently comparative psychologists began to focus their interest toward more fundamental issues like perception. Researches on primates' perception and cognition have been carried out to improve our understanding of brain functions in order to achieve knowledge suitable in medical research. Indeed, an extensive amount of neuro-physiological and electrophysiological research is performed on non-

human primates assuming that their cognitive system represents a good model of the human cognitive system. However, even though such assumption has worked well in several cases, it is not guaranteed that it will always be valid (Ghazanfar & Santos, 2004; Preuss, Qi, Kaas, 1999). Thereby, extremely important are also the findings coming from psychophysical studies, which revealed several differences among human and non-human cognitive functions. These differences are particularly evident in their visual processing even though the mechanisms underlying the visual processing are widely shared among primates. In fact, as the perception of the World does not depend only on anatomical structures, but it also depends on factors such as attention, personal history, expectation, memory and cognitive abilities, other animals may experience a different perceptual world (Fagot & Barbet, in: Wasserman & Zentall, 2009). Thus, at a higher level, there are several differences in the way in which primates process the visual information and understanding these differences could provide insights into the phylogeny and the evolution of the visual system and cognition. Furthermore, these studies may help us in understanding to what degree non-human primates can represent a good model in studies designed to better understand the human visual system.

The present work is a further attempt to clarify some relevant aspects of the human visual cognition in comparison to monkeys with particular regard to their perceptual organization. A total of 17 experiments, 8 in tufted capuchin monkeys (*Sapajus apella*) and 9 in humans have been carried out across three different studies which investigated three different factors that can be involved in perceptual organization. Before approaching important aspects of vision in human and non-human primates, an overview of the order *Primates* is presented below.

## 1.1 PRIMATES' BIOLOGY, ECOLOGY AND EVOLUTION

The order *Primates*, with approximately 65 genera including 365 species (Groves, 2001), is the third most diverse order of mammals. Although the oldest known primate fossil record date to the late Palaeocene (roughly 55 mya) with genera like *Altanius*, *Cantius*, *Donrussellia* and *Teilhardina* (Miller, Gunnell, Martin, 2005), molecular clock studies suggest that the primate lineage may date back at least 65 mya (Chatterjee, Ho, Barnes, Groves, 2009; Lee, 1999; Tavaré, Marshall, Will, Soligo, Martin, 2002; Williams, Kay, Kirk, 2010).

According to recent classifications (Groves 2001; 2005), the Primate order can be taxonomically divided as described in Figure 1.

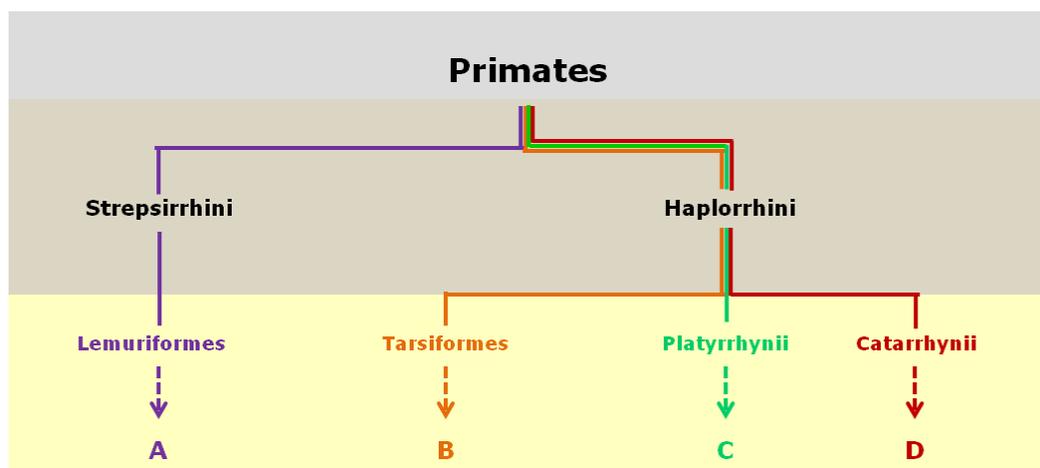


Figure 1. Diagram reporting the Primates' taxonomy. The diagram develops in sequence: Order, Suborder, Parvorder, Family, Subfamily and Genus. Common names for the most important species of each genus are also reported (the figure continues in the following pages).



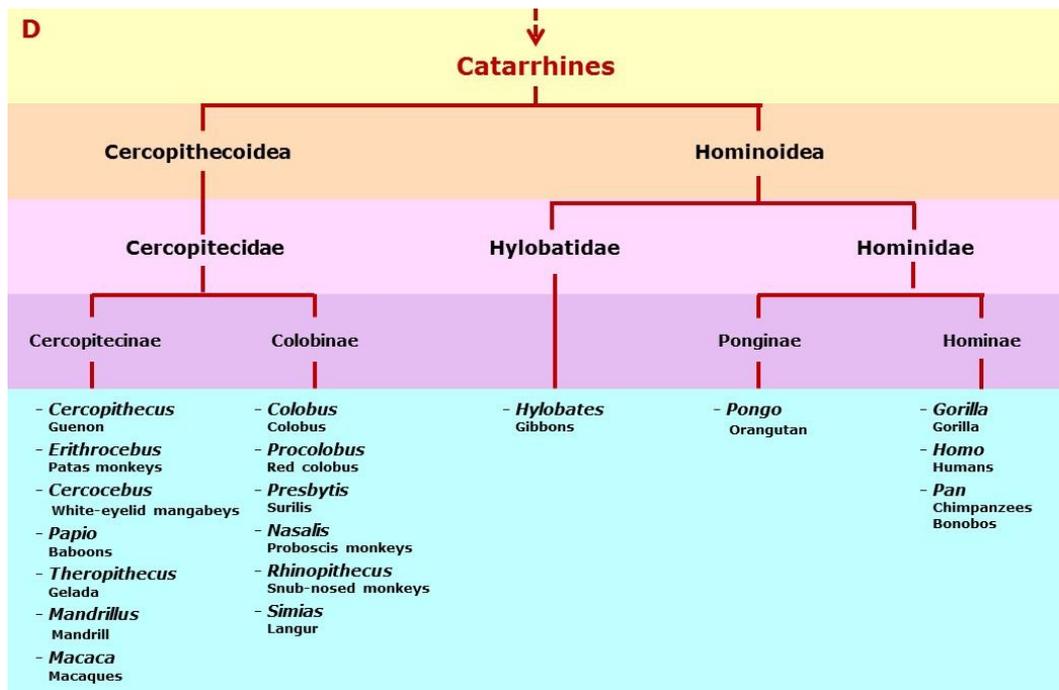
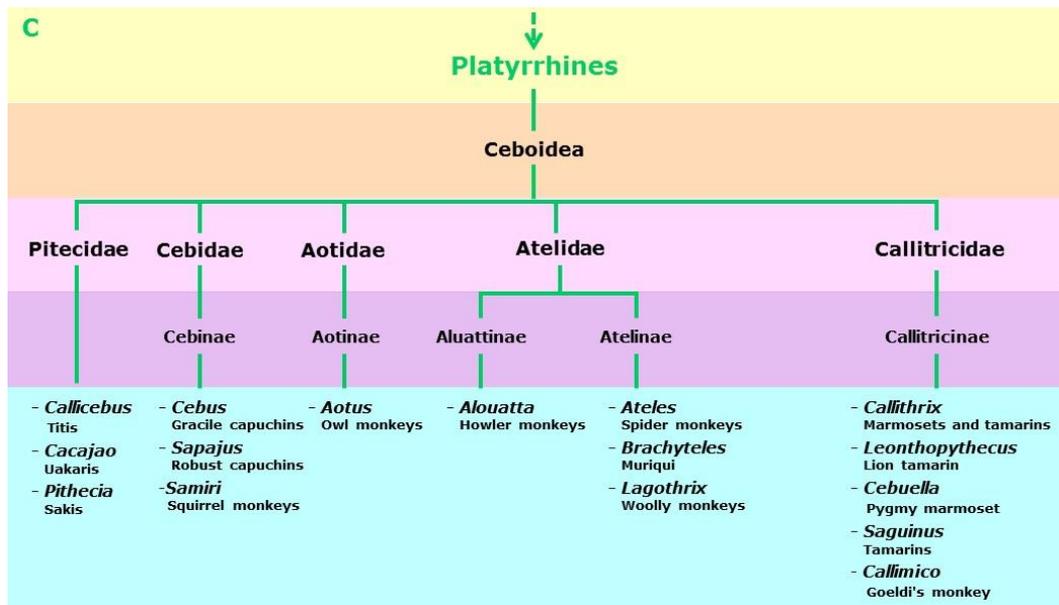


Figure 1. It continues from previous pages.

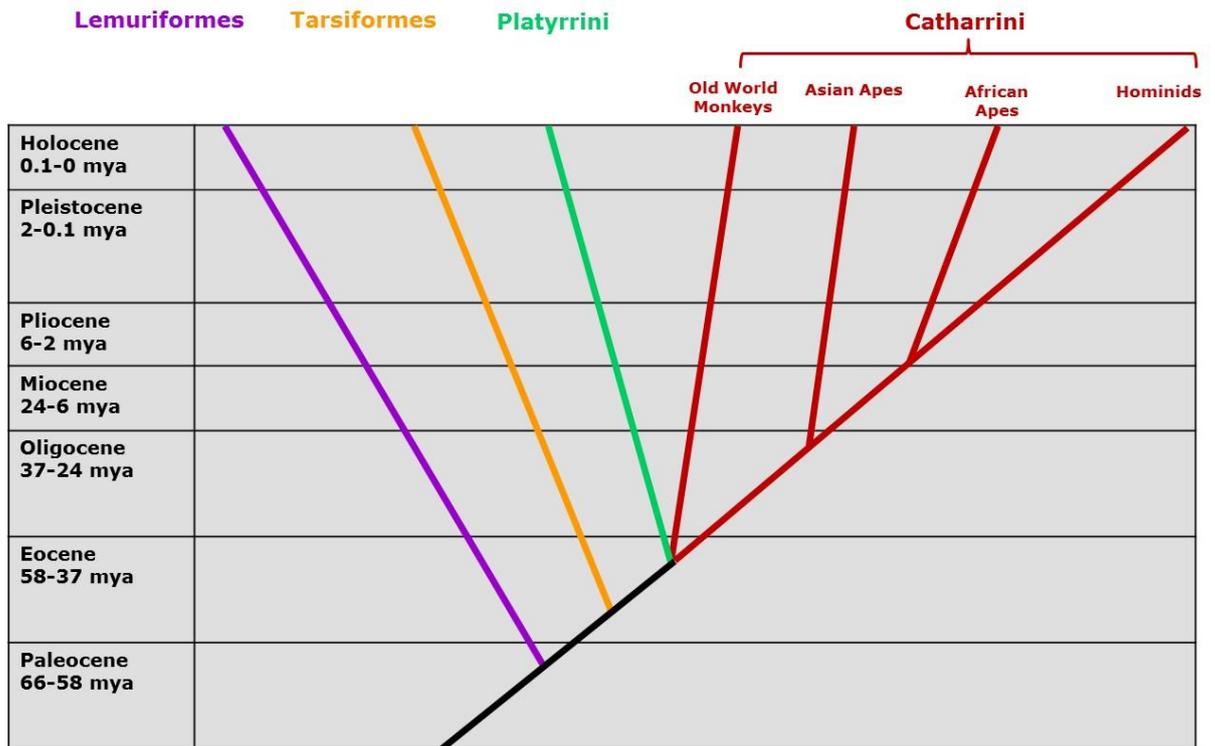


Figure 2. Evolutionary relationships among the major primates' taxa.

*Strepsirrhinii* includes mostly arboreal and often nocturnal species, such as lemurs and lorises, featuring some primitive characteristics. *Haplorhynii* includes many species, widely distributed, and is further divided into three major groups: *Tarsiformes*, *Platyrrhini* and *Catharrhini*. *Platyrrhini* are New World monkeys, also known as neo-tropical monkeys since they are found only in the tropical region of American continent. The taxon includes capuchin monkeys (*Cebus* and *Sapajus*), howler monkeys (*Alouatta*), marmosets (*Callithrix*), tamarinds (*Saguinus*), spider monkeys (*Ateles*), squirrel monkeys (*Saimiri*) and owl monkeys (*Aotus*). *Catharrhini* are Old World primates and include monkeys and apes of Africa and south-eastern Asia such as macaques (*Macaca*), baboons (*Papio*), guenons (*Cercopithecus*), colobi (*Colobus*), proboscis monkeys (*Nasalis*), langurs (*Simias*), gibbons (*Hylobates*), orang-

utans (*Pongo*), chimpanzees and bonobos (*Pan*), gorilla (*Gorilla*) and humans (*Homo*).

All primates evolved from a common ancestor that lived in trees. Therefore, the majority of the living species display adaptations to this kind of environment. As a result, they can walk on two or four limbs, knuckle-walk but also leap and swing (*brachiation*) from tree to tree (Napier & Napier, 1967).

The majority of non-human primates live in tropical or sub-tropical regions of Africa, Asia and Americas. Only two species live in temperate area like Japan (*Macaca fuscata*) and North-West Africa (*Macaca sylvanus*). Within their geographic range, non-human primates are found in several different environments, ranging from tropical rain forest to desert (Napier & Napier, 1967).

Many primates, although to different extent, display high level of encephalization, meaning that they have large brain size compared to the body size (Armstrong & Falk, 1982; Jerison, 1973).

In terms of morphology, primate brain can be roughly divided in three main parts: *brainstem*, *cerebellum* and *cerebrum*, each part having homologous functions among the group (Armstrong & Falk, 1982). Whereas to different extent, primates' brain displays convolutions that, amplifying the surface area relative to brain size, represent a good predictor of highly developed capabilities, cognitive skills and complex behaviours (Armstrong & Falk, 1982).

As New World monkeys separated by Old World monkeys in the late Palaeocene (around 55 mya), comparative studies involving them allow us to make assumptions about the evolution of some cognitive features up to an early common ancestor which lived in that period, almost at the early stages of primate evolution. This represents one of the reasons why tufted capuchin monkeys have been chosen to carry out this comparative study. Other reasons involve capuchins' high developed cognitive skills, comparable to those displayed by apes (see also below), which implies that they can be easily trained

to solve complex tasks, and their high degree of dexterity, which means that they can handle well the experimental set-up adopted in the present work.

## **1.2 TUFTED CAPUCHIN MONKEYS (*SAPAJUS SP.*)**

### **1.2.1 Taxonomy**

The species studied in the present work belongs to the family *Cebidae*, subfamily *Cebinae*. Prior to 2011, the subfamily contained only one genus: *Cebus*. However, in 2011 it was proposed to split the capuchin monkey group into two different groups: the gracile capuchins and the robust capuchins (Lynch-Alfaro, Boubli, Olson, Di Fiore, Wilson, Gutierrez-Espeleta, ... Alfaro, 2011). According to this new classification, gracile capuchins remain in the genus *Cebus*, whereas robust capuchin monkeys are considered as a new genus: *Sapajus*. Therefore, based on the classification proposed by Groves (2001, 2005) and Lynch-Alfaro *et al.* (2011), robust capuchin monkeys include the following species:

*Sapajus apella*

*Sapajus flavius*

*Sapajus nigritus*

*Sapajus xanthosternos*

This work is focused on the species formerly named *Cebus apella*, now called *Sapajus apella*. A few subspecies have also been identified, however, although the subjects tested in this study were all captive born, possible phenomena of inbreeding between different subspecies in their lineage cannot be ruled out and therefore, no information is known about the subspecies they belong to.

### **1.2.2 Basic anatomy**

Tufted capuchin monkeys display a characteristic black cap with two dark tufts. The lower limbs and tail are also black, whereas the rest of the body is brown. The thumbs of both limbs are pseudo-opposable helping them in grasping objects, therefore, they display high degree of dexterity and good precision grip (Costello & Fragaszy, 1988).

The brain size of capuchin monkeys is relatively big. Their "encephalization quotient" (EQ), defined as the ratio between actual and predicted brain mass for each species taking into consideration also its weight, ranges between 2.54 and 4.79 (average 2.63, Jerison, 1955, 1973). This number is bigger than a typical mammal brain (EQ = 1) and comparable with the EQ observed in apes (EQ = 2.63, Fragaszy, Visalberghi, Fedigan, 2004). They have also a neocortex ratio that is almost as large as the one of apes and their brain displays a relatively high level of convolution (Fragaszy *et al.*, 2004). The EQ has often been considered as predictor of cognitive abilities, in this regard the relatively high EQ and neocortex ratio observed in capuchins can explain the existence of the variety of complex social behaviours and cognitive skills as observed in this species.

### **1.2.3 Habitat and distribution**

Tufted capuchin monkeys can be found in many different kinds of environments such as tropical and sub-tropical forests. They prefer the main canopy level, but frequently they descend to the ground to travel and feed (Fragaszy *et al.*, 2004).

The capuchin monkeys' (*Cebus* and *Sapajus*) area of distribution includes Central and South America to northern Argentina. In

particular, the genus *Sapajus* is found mostly in the Amazon basin as depicted in Figure 3.

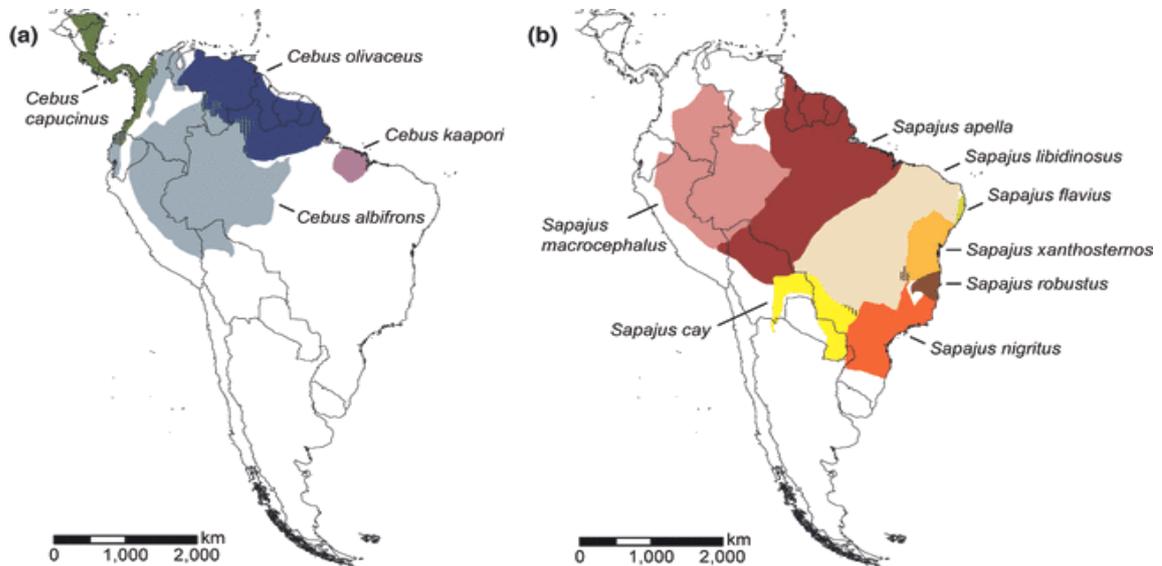


Figure 3. Capuchin monkey distribution. Approximate distributions of *Cebus* (a) and *Sapajus* (b) species in South America according to recent classifications (Lynch-Alfaro et al. 2011). (Image from Lynch-Alfaro et al. 2011, with permission).

#### 1.2.4 Tufted capuchin monkeys' ecology and behaviour

Tufted capuchin monkeys are omnivorous, feeding mostly on fruits, seeds and invertebrates or small vertebrates. Like other capuchins, they are social animals which form hierarchical groups of roughly 7-14 individuals ruled by dominant individuals (Freese & Oppenheimier, 1981).

As every primate, capuchins display a cleaning behaviour which consists in removing with the fingers small particles and parasites from the fur. This grooming behaviour can be directed to themselves or towards other components of the group, in this latter case it involves a large number of social implications such as affiliation and

alliance with other components of the group (see also Schino, Di Giuseppe, Visalberghi, 2009).

Tufted capuchin monkeys are very popular in the scientific environment thanks to their high developed ability in using tools (Visalberghi, 1990; Antinucci & Viaslberghi, 1986). They can use a huge variety of tools like stones as hammers and anvils to crack nuts, containers to hold water, sticks to reach different foods or sponges to absorb juice (Fragaszy, Izar, Visalberghi, Ottoni, De Oliveira, 2004; Fragaszy *et al.*, 2004; Ottoni & Izar, 2008; Ottoni, Dogo de Resende, Izar, 2005; Visalberghi, Addessi, Truppa, Spagnoletti, Ottoni, Izar, Fragaszy, 2009; Westergaard & Suomi, 1995).

### **1.3 VISION: THE DOMINANT SENSORY-MODALITY IN PRIMATES**

Visual perception depends on peripheral as well as central organs, therefore, a comparative analysis highlighting similarities and differences among primates for what concerns primates visual system is discussed as follows.

#### **1.3.1 Primates' eye anatomy and physiology**

In contrast with other mammals, primates' skull is characterized by the presence of a protective bony structure around the eyeballs which can be the postorbital bar like in *Strepsirrhines* or a full bony cup like in *Haplorrhines* (Campbell, Loy, 2000).

The position of the eyes is very consistent across the *taxon* as the majority of the species have their eyes positioned frontally. This orbital convergence determines a significant overlap among each eye visual field resulting in a three dimensional depth perception or stereopsis. This feature is extremely important for animals that evolved in the challenging three-dimensional habitat of the canopy

level (Ross, 1995). Another additional function of the orbital convergence is the binocular summation, namely, the increased sensitivity to faint visual stimuli allowed by a double input (Hughes, 1977; Heesy & Ross, 2001). However, this happens at the expense of the global visual field's size which is consequently reduced in almost every diurnal primate species.

The general organization of the primate eye is very consistent. Therefore, eyes always feature the same structures, such as *pupil*, *lens*, *sclera*, *choroid*, *retina*, with the same functions typical of a human eye. Minor differences may be observed mostly in terms of shape and colour of these parts and of the nature of the photoreceptive cells (see below).

Overall, diurnal primates share two kinds of photoreceptors: *cones* and *rods*. While rods are extremely sensitive and can fire at very low light intensity (Hecht, Shlar, Pirenne, 1942), cones require significantly more light intensity in order to produce a signal. The photo-transduction that takes place inside them features the same chemical processes across the *taxon* (see also Bruce, Green, Georgeson, 2003). Nevertheless, some differences may occur regarding the type of photo-pigments possessed, and therefore, about the type of colour perceived by different primate species. In fact, while all *Catarrhine* species, including humans, have three types of photo-pigments allowing trichromatic colour vision (De Valois, 1960; De Valois & Jacobs, 1968; Grether, 1940; Ibbotson, Hunt, Bowmaker, Mellon, 1992; Wyszecki & Stiles, 1982), most genera of neo-tropical monkeys have only one single, polymorphic gene locus on the X-chromosome, which means that each allele can exist only in one of the two alternative forms on the X-chromosome (Hunt, Williams, Bowmaker, Mollons, 1993; Jacobs, 1996). Therefore, heterozygous *Platyrrhine* females display trichromatic vision (one opsin is expressed by the autosome and two different opsins are expressed by the two heterozygous X alleles). By contrast,

homozygous females and males display necessary dichromatic vision (Lucas, Dominy, Riba-Hernandez, Stoner, Yamashita, Loría-Calderón, ... Darvell, 2003). As capuchin monkeys are *Platyrrhines*, due to the possibility that some subjects could not experience the trichromacy, in this work, only stimuli featuring black and white shapes were used.

In all *Haplorrhini* species, but not in *Strhepsirrhines*, at the centre of the retina there is the *fovea centralis*, containing only cones (Kaas & Collins, 2003; Kremers, 2005), whereas across the rest of the retina, cones and rods are intermingled.

Diurnal primates rely mostly on vision and therefore, display a good visual acuity in comparison to other mammals. Measuring the smallest separation that can be perceived between high-contrast achromatic images is considered a good way to assess the visual acuity of animals. In this way, visual acuity of several non-human primate species has been determined, providing results very similar across the *taxon* (De Valois, 1971; Grether, 1940; Spence, 1937). For example, chimpanzees (*Pan troglodytes*) trained to distinguish alphabet letters of different size, using a Matching-To-Sample (MTS) procedure, demonstrated a visual acuity of  $1.5^\circ$  of visual angle (va) but separations of about  $0.67^\circ$  of va could still be detected (Matsuzawa, 1990). Analogously, rhesus monkeys (*Macaca mulatta*) and squirrel monkeys (*Saimiri sciureus*), trained to distinguish between high contrast grating patterns and uniform patterns, demonstrated a discrimination threshold extremely similar ( $0.65^\circ$  and  $0.74^\circ$  of va respectively) to that one displayed by humans with normal vision (Cowey & Ellis 1967; Weinstein & Grether, 1940). A similar pattern of results has also been demonstrated in capuchin monkeys (De Valois, 1971). The spatial resolution of several primate species has been assessed also by measuring the luminance contrast sensitivity to different spatial frequencies (SF). De Valois, Morgan and Snodderly (1974) compared the luminance contrast threshold of long-tailed monkeys (*Macaca fascicularis*), pig-tailed monkeys (*Macaca*

*nemestrina*) and humans, using SFs ranging from 0.6 and 33.0 cycle per degree (cpd). Their study proved attenuation of sensitivity for lower and higher SFs and a sensitivity peak for values ranging between 3 and 5 cpd in both humans and macaques. Similar results were recorded also with chimpanzees and humans tested with Gabor-type grating patterns (Matsuno & Tomonaga, 2006).

Finally, capuchin monkeys' temporal sensitivity (critical flicker fusion) is slightly superior to that recorded for humans. In fact, whereas capuchin monkeys see flickers as a continuous light at 58-60 Hz, humans do so at 55 Hz (De Valois, 1971).

### **1.3.2 Beyond the eye**

In primates the optic nerves project to the *superior colliculus*, involved in the control of eye and head movements (Wurts & Albano, 1980), and to the *Lateral Geniculate Nucleus* (LGN) where they synapses with the fibres directed to the visual cortex (De Valois, Abramov, Mead, 1967; see also Goodale & Milner, 2004). Primate LGN features six *laminae* of neuron bodies alternated with optic fibres. Optic fibres coming from the temporal side of each eye reaches the LGN on the same hemisphere, whereas optic fibres coming from the nasal side of each eye cross over to the opposite hemisphere to join the other LGN. Therefore, each side of the visual field is processed by the contra-lateral hemisphere (Polyak, 1957).

Primates' LGN feature layers of *magnocellular* and *parvocellular* cells interleaved with layers of *koniocellular* cells (see, for example, Hendry & Reid, 2000; Xu, Ichida, Allison, Boyd, Bonds, Casagrande, 2001). Each layer receives inputs only from one eye. The general organisation of LGN is considered consistent among primates and only few exceptions, involving mostly tarsiers, have been reported (Rosa, Pettigrew, Cooper, 1996).

From the LGN neurons project their axons to the striate visual cortex (Cudeiro & Sillito, 2006).

### **1.3.3 Organisation of primate visual cortex**

Pioneering experiments to map the visual cortex were made in cats (Hubel & Wiesel, 1959; 1962) and afterward repeated in monkeys (Hubel & Wiesel, 1968). Nowadays, thanks to the developing of new technologies (e.g., fMRI, PET) our understanding of human visual cortex have been widely increased. Nevertheless, due to some experimental procedures that cannot be replicated with humans, monkeys still represent the species in which the majority of the experiments in this field have been carried out. Therefore, a lot is known about their visual cortex revealing a high degree of similarities, and therefore possible homologies, with human visual cortex (De Yoe & Van Essen, 1988; Kapadia, Ito, Gilbert, Westheimer, 1995; Livigstone & Hubel, 1987; Ungerleider & Mishkin, 1982).

The striate cortex (V1) is the main receiving area for signals coming from the LGN. The primate striate cortex features six different layers (De Valois, Abramov, Mead, 1967). Layer 1 is on the surface, while layer 6 is deep inside the visual cortex. Layer 4 can be further divided into three separate sub-layers (4A, 4B, 4C). The axons projected from the LGN synapse with cells in most layers. Nevertheless, they have more connection with layer 4C, where *magnocellular* and *parvocellular* cells end in individual sub-layers, and in layer 1 and 3, where the *koniocellular* cells end.

In almost every primate, visual information proceeds from the striate cortex to the extra-striate cortex, a cortical area surrounding V1 and featuring a complex network of connections (De Yoe & Van Essen, 1988). From here, in many species it moves to V2 and then it segregates into two main pathways: the "dorsal stream" and the

"ventral stream". The dorsal stream passes through V3, then, runs through the middle and medial temporal areas, up to the parietal lobe in the area 7A. Whereas the ventral stream passes through V4, up to the posterior and anterior infero-temporal areas located in the temporal lobe (Baizer, Ungerleider, Desimone, 1991; Milner & Goodale, 1995; Young, 1992). Despite the majority of the connections seem to segregate after V2 (Maunsell & Newsome, 1987), the internal structure of V1 and V2 indicates that the division starts earlier in V1 (De Yoe & Van Essen, 1985; Livingstone & Hubel, 1983). The two pathways are anatomically distinguishable and functionally specialised. In humans, lesions in the MT area, which falls into the dorsal pathway, determine deficits in the motion perception (*akinetopsia*) whereas pattern discrimination is not affected (Newsome & Parè, 1988). Other visual disorders like *hemispatial neglect*, *simultanagnosia*, *apraxia* and *optic ataxia* are thought to be related to lesions in specific areas in the dorsal pathway (Stasheff & Barton, 2001; Kim, Na, Kim, Adair, Lee, Heilman, 1999; Zeki, 1991). Conversely, the ventral stream, which is connected with the medial temporal lobe, the limbic system and the dorsal stream, allows object recognition. Lesions in V4, where the ventral stream runs, affect colour discrimination (Heywood & Cowey, 1987). Yet, V4 seems involved also in controlling attentional strategies (Shiller & Lee, 1991; Baizer, Ungerleider, Desimone, 1991).

Although the above mentioned features are shared by the majority of primates (see, for example, De Valois & De Valois, 1988; De Valois, 1971; De Valois, Morgan, Snodderly, 1974), few minor independent characteristics have also been observed. For example, capuchin monkeys seem to display a few independent features in their visual cortex. They do not have the strongly monocular organisation into columns across the depth of the visual cortex as observed in other monkeys. In particular, in layer 4 of the striate cortex, capuchin and squirrel monkeys show areas where inputs from

each eye overlap (see Armstrong & Shea, 1997 for a discussion). Yet, the reason of such functional difference is unknown. Capuchin monkeys display a changed proportion in the limbic area compared to other species suggesting that, in this region, integrations of sensory inputs could be more than in other primate species (Armstrong & Shea, 1997). Despite these minor differences, the cortex representation of the visual field observed in capuchins and other monkey species is the same (Rosa, Piñon, Gattass, Sousa, 2000).

#### **1.4 CROSS-SPECIES DIFFERENCES IN PRIMATE VISUAL COGNITION**

Visual cognition refers to the way in which animals acquire and process visual information. In the past century, *Gestalt* psychologists like Kurt Koffka, Wolfgang Köhler and Max Wertheimer put forward some theories based on the idea that the human mind is capable of achieving a global representation of the visual scene where "*The whole is other than the sum of its parts*" (Koffka, 1935). Processes like perceptual grouping, figure-ground segregation, perception of goodness of shape, amodal completion and visual illusions are some aspects, among others, of visual cognition which have been widely studied in humans and in a variety of other animals. This was done to allow interspecies comparisons and therefore, to possibly shed some light on the evolution of the human visual system and cognition.

Perceptual grouping describes the way in which single elements are grouped into a coherent whole (Wertheimer, 1912a, 1912b, 1922, 1923). It is based on well-known grouping principles such as similarity, proximity, good continuation, common fate, symmetry, closure and *prägnanz* or "law of salience" (Wertheimer, 1912a, 1912b, 1922, 1923). In contrast, figure-ground segregation describes the way by which a shape is perceived as more salient and therefore appears in front of the remaining parts of the visual scene which

assumes a 'back-ground' character. It is based on rules such as "surroundedness", size, orientation, symmetry, contrast, parallelism and convexity (Rubin, 1921). A specific aspect of perceptual grouping is the global-local processing, therefore, the act of processing a complex visual stimulus like a coherent whole. The present work is a comparative analysis of global-local processing in humans and capuchin monkeys, therefore this aspect will be discussed in detail later in the discussion (see Section 1.5).

Another idea arisen within *Gestalt* psychology is the perceived "goodness" of a shape. According to Garner (1974), there is a relationship between the perceived goodness and shape redundancy. The redundancy of a stimulus is directly related to its symmetry: highly symmetrical shapes are therefore considered highly redundant, whereas less symmetrical shapes are considered less redundant (see also below for a discussion on redundancy). In order to evaluate the relationship between pattern redundancy and perceived goodness, Garner asked human subjects to judge the relative goodness of dot-patterns arranged following several degrees of redundancy. According to Garner (1974) the redundancy or goodness of a pattern is directly related to its symmetry and inversely related to the number of equivalent patterns that could be obtained by a 90° rotation and/or reflection of a single pattern (see also Chapter III for a detailed discussion of redundancy). While redundant patterns were judged as very good shapes, less redundant patterns were considered as less good shapes (Garner & Clement, 1963). Several studies established that the perceived goodness of a pattern is effective in improving visual encoding and memory retention (Checkosky & Whitlock, 1973; Garner, 1970).

Another remarkable cognitive skill typical of human visual cognition is the ability to identify objects partly hidden by other objects. This means that objects can be perceived as wholes although some of their parts are not visible (Kanizsa, 1979) operating a form

of perceptual completion also known as 'amodal completion' (Michotte, 1963; Michotte, Thinès, Crabbé, 1964). Several comparative studies have demonstrated that a range of species, including chimpanzees (*Pan troglodytes*; Sato, Kanazawa, Fujita, 1997), baboons (*Papio papio*; Deruelle, Barbet, Dépy, Fagot, 2000; Fagot, Barbet, Parron, Deruelle, 2006; Nagasaka, Brooks, Edward, Wasserman, 2010), Japanese macaques (*Macaca fuscata*; Sugita, 1999), mice (*Mus sp.*; Kanizsa, Renzi, Conte, Compostela, Guerani, 1993) hens and domestic chicks (*Gallus sp.*; Forkman, 1998; Forkman & Vallortigara, 1999; Lea, Slater, Ryan 1996; Regolin & Vallortigara, 1995) display this ability. With pigeons results are controversial, as some report that they display this ability but others report the opposite (Sekuler, Lee, Shettleworth, 1996; Wasserman, Di Pietro, Young, 2001; Watanabe & Furuya, 1997). Nevertheless, the experimental demonstration of amodal completion in such a wide variety of species suggests that it has a high adaptive value. For example, amodal completion allows animals to spot predators or prey partly occluded in an environmental background which certainly increases the chances of survival. However, while the presence of amodal completion seems to be unquestionable in animals, the factors influencing it have not been clarified yet and would deserve further investigations.

Another important aspect concerning visual cognition is the perception of visual illusions. Visual illusions refer to conditions in which subjective perception greatly contradicts the physical reality of the stimuli. When a visual illusion occurs, the visual information is processed by the brain in such way that some features like size, position, brightness etc., do not match with the physical measurement of the visual stimulus. Many visual illusions, involving the appreciation of the whole scene and the relationships among its elemental parts, require a good global processing. Therefore, understanding if other animals can experience some visual illusions is

very important in order to better understand their global-local processing.

Overall, animals like mice (Kanizsa, Renzi, Conte, Compostela, Guerani, 1993), cats (Bravo, Blake, Morrison, 1988), pigeons (Fujita, Blough, Blough, 1991), domestic chicks (Regolin & Vallortigara, 1995; Rosa-Salva, Rugani, Cavazzana, Regolin, Vallortigara, 2013) and at least a species of fish (e.g., goldfish: Agrillo, Miletto-Petrazzini, Dadda, 2013) showed behavioural responses to visual illusions suggesting that they may experience a human-like perception of different illusory patterns.

In particular, non-human primates seem to perceive a wide range of visual illusions, for example chimpanzees are sensitive to the *Delboeuf illusion* as well as the *Ponzo illusion* (Parrish & Beran, 2014; Fujita, 1997). Along with chimpanzees, rhesus monkeys have proven sensitive to the *Ponzo illusion* (Fujita, 1996) as well as the *Zöllner illusion* (Agrillo, Parrish, Beran, 2014a) whereas the *Corridor illusion* has been proved in baboons (Barbet & Fagot, 2002). Furthermore, there is evidence that the *Müller-Lyer illusion* can be perceived by capuchin monkeys (*Sapajus apella*, Suganuma, Pessoa, Monge-Fuentes, Castro, Tavares, 2007). However, mixed results have also been reported. For example, baboons do not seem to perceive the *Ebbinghaus illusion* (Parron & Fagot, 2007). Furthermore, a comparative study on the perception of the *Solitaire illusion* in humans, chimpanzees, rhesus monkeys and capuchin monkeys, revealed that, unlike humans, chimpanzees do not appear to perceive this type of illusion. However, the performance of rhesus and capuchin monkeys suggested that there could be a potential effect of the *Solitaire illusion* in these species (Agrillo, Parrish, Beran, 2014b). In fact, in this comparative study chimpanzees consistently did not display any tendency to perceive the *Solitaire illusion*. Conversely, one rhesus monkey displayed a clear and consistent bias indicating a strong sensitivity to this illusion, while other subjects sometimes

showed a bias, sometimes did not show any bias. Therefore, as group, monkeys' performance was not comparable to humans' performance (see also Frith & Frith, 1972). However, some individual results indicate that there could be a potential effect of the *Solitaire* illusion in these species (Agrillo et al., 2014b).

This pattern of results may be related to the perception of other *Gestalt* features which may vary across primates. In fact, many illusions require the appreciation of the whole scene and the relationship between its composing parts. Therefore, failure in perceiving some visual illusions by certain species may indicate a difficulty in appreciating the relationships between stimulus parts. This can ultimately relate with a different way to process the local elements or the global information of a visual stimulus. For example, the focal attention typical of species that display a local bias should affect the perception of the *Ebbinghaus* illusion. In fact, such focal attention should decrease the interference of the surrounding patterns on the central pattern. Therefore, it will be expected that the effect of the illusion in these species is much less pronounced in comparison to humans (Parron & Fagot, 2007). Therefore, assessing if non-human primate species are prone to perceive visual illusions may be informative in clarifying some factors involved in their global-local processing.

### **1.5 GLOBAL-LOCAL PROCESSING IN HUMAN AND NON-HUMAN PRIMATES**

Identification of the factors involved in the processing of the relationships between wholes and their constituent parts represents a fundamental issue of the study of perceptual organisation. As emphasised also by the *Gestalt* psychologists, in the real world objects have hierarchical structures as they are composed of parts and subparts. As a forest is composed by many trees and each tree is

then composed of branches and leaves, every visual scene involves many levels of organisation, each one requiring grouping or segregation. Therefore, the analysis of the visual scene involves the analysis of each level.

In 1977, Navon reported that humans process the global aspect of a visual scene faster and better than the local details. On the basis of this finding he formulated the *global precedence hypothesis*. He carried out four experiments using hierarchical stimuli which are stimuli organised in two levels of hierarchy, e.g., big letters formed by small letters. Stimuli could be consistent or inconsistent. Consistent stimuli featured the same letter at both levels of processing. Conversely, inconsistent stimuli featured different letters at each level of processing. In the first two experiments subjects were asked to identify an auditory stimulus, which consisted of a letter pronounced by a native English recorded in a file, while watching a hierarchical stimulus which could or could not conflict with the auditory stimulus either at the global or at the local level. Results showed that, overall, the auditory discriminations were affected only by the global configurations and not by the shape of the local elements. In another experiment, inconsistent stimuli were used and subjects had to respond only to the level of processing each time. The results showed that, whereas the identity of local level did not affect the global recognition, global letters which conflicted with local ones did affect the responses at local levels, showing that people cannot skip the global level even when asked to attend to the local level only. In the fourth experiment, subjects had to compare two hierarchical shapes that could differ at either the global or the local level. Also this experiment proved that humans identify global differences more often than local ones. Following these experiments, Navon formulated the well-known *global precedence hypothesis* (1977). According to this hypothesis, healthy adult human subjects presented with hierarchically organized stimuli show a *global*

*advantage* and a *global-to-local interference*. The *global advantage* describes the process by which the global aspect of hierarchical stimuli is processed faster than their component parts. Navon (1977) described this phenomenon using the well-known metaphor “*The forest before the trees*” (Navon, 1977). The *global-to-local interference* refers to the fact that in humans, when presented with inconsistent hierarchical stimuli, the identity of the global level affects the recognition at the local level. Therefore, when subjects are asked to recognise hierarchical stimuli and to focus at the local level only, the global recognition still affects local recognition. However, this does not happen when they are asked to process the global level. This interference demonstrates that people cannot skip the global level even when asked to attend to the local level only.

A huge amount of literature followed Navon’s work reporting that in humans the global-advantage can be affected by several stimulus features. For example, when the visual angle (i.e., the perceived stimulus size) increases, the global advantage decreases (Kinchla & Wolfe, 1979). Furthermore, manipulations in the size of the local elements or the global configurations and the position where they can fall in the visual field, i.e., the stimulus eccentricity, can also affect the global-local processing (Amirkhiabani & Lovegrove, 1996).

LaGasse (1993) investigated whether some Gestalt features like the numerosity of local elements can affect global-local processing in humans. She ran several experiments using stimuli in which the global shape was made up by many local elements, in comparison to stimuli where the global shape was made up of a few and sparse local elements. Her experiments demonstrated that the global advantage is dramatically affected by the reduction of the number of local elements (LaGasse, 1993).

The global advantage is affected also by manipulations of the strength of perceptual grouping clues, described by orientation,

closure and connectedness of local elements (Han, Humphreys, Chen, 1999a; 1999b; Han & Humphreys, 1999).

It has been found that some health conditions can affect the global precedence. For example, children diagnosed with Autism Spectrum Disorder (ASD) show typically a local advantage (Happè, 1999) although this seems to be valid only under some conditions. In fact, in 1999, Plaisted, Swettenham and Rees carried out a study in which the global-local processing performance of children affected by the ASD and typically developing children was compared. The test featured two different attentional conditions. In the divided attention task, children did not have to attend to a specific level of hierarchical stimuli. Conversely, in the selective attention task, children were instructed to attend to each level of processing. The study proved that global-local performance in autistic children is a function of the attentional condition. In fact, in the divided attention task, children affected by ASD made more errors when they had to process the global level of the stimuli, revealing the local bias typically reported in literature (Happè, 1999). Conversely, in the selective attention task, the performance between the two groups of children did not differ, revealing a normal global processing in both groups of children. Furthermore, in conditions featuring inconsistent stimuli, in parallel to a change in dominance, also a change in the type of interference was observed. In fact, autistic children displayed local-to-global interference in the divided attention task but a global-to-local interference in the selective attention task (Plaisted *et al.*, 1999). According to the authors, two different hypotheses could explain this pattern of results. One hypothesis suggests that these children may lack some mechanisms that inhibit local information when obvious priming is not provided. Conversely, the other hypothesis suggests that, in the same situation, they may voluntarily attend to local information (Plaisted *et al.*, 1999). This latter hypothesis would be consistent with the “weak central coherence theory” which suggests

that the local advantage in autistic children represent a different style of cognitive processing and not an actual deficit in processing the global aspect of visual stimuli (Frith, 1989; Happé, 1999; Happé & Frith, 2006).

Diffuse neuro-cognitive dysfunctions including deficits in the perception of *Gestalt* features as well as deficits in the global processing have been reported in patients diagnosed with schizophrenia (Ferman, Smith, Boeve, Graff-Radford, Lucas, Knopman, Petersen, Ivnik, Wszolek, Uitti, Dickson, 2006; Goodarzi, Wykes, Hemsley, 2000; Spencer, Nestor, Niznikiewicz, Salisbury, Shenton, McCarley, 2003). Subjects affected by this disease, often display a relative preference for local as opposed to global aspects of hierarchical stimuli (Butler, Schechter, Zemon, Schwartz, Greenstein, Gordon, Schroeder, Javitt, 2001; Coleman, Cestnick, Korostishevsky, Krause, Huang, Mendell, Levy, 2009). However, the reason underlying this pattern is still the object of debate. Physiological and behavioural data revealed that these deficits can occur at an early stage in visual processing and might be related to physiological disorders in areas V3/V3a of the extra-striate cortex (Johnson, Lowery, Kohler, Turetsky, 2005). These deficits may include the magnocellular pathway which seems involved in global processing (Coleman, Cestnick, Korostishevsky, Krause, Huang, Mendell, Levy, 2009).

The global-local processing depends also on age development. According to a few research studies, new born babies show a global advantage (Macchi-Cassia, Simion, Milani, Umiltà, 2002). Authors proved that, even though newborns could detect both levels of visual information, they preferred the processing of the global level over the local one. An additional experiment in the same study demonstrated that the global bias was associated with the content in low spatial frequencies of the stimuli and it disappeared after selective removal of low spatial frequencies. By contrast, young preschool children (aged between 35 and 55 months), tested with the Matching-To-

Sample task, did not show neither local nor global advantage (De Lillo, Spinozzi, Truppa, Naylor, 2005). This result differs from the local advantage typically found in adult people. In this study, three experiments were carried out on preschool children and compared to those previously collected on tufted capuchin monkeys. In the first two experiments, monkeys displayed a local advantage whereas children processed equally well both levels of hierarchical stimuli. In the last experiment, the density of local elements was manipulated. In this experiment, while children's performance remained stable across conditions, monkeys' performance in the global processing was dramatically affected in conditions featuring a few and sparse local elements. Therefore, the density of local elements within hierarchical stimuli is an important factor for monkeys' visual processing. Interestingly, Neiwirth, Gleichman, Olinick and Lamp (2006) ran a similar experiment comparing adult tamarins (*Saguinus oedipus*) to young children (5 years old) and adult humans using hierarchical stimuli featuring dense or sparse stimuli. In agreement with previous literature, adult humans showed a global bias in every condition. By contrast, children (5 years old) revealed a global bias with dense stimuli but did not show any advantage with sparse displays. The results obtained from both monkey species will be further discussed later. The discontinuous pattern observed during the human development in the studies reported here could possibly be explained by the evidence that the newborn visual system is not fully developed. Therefore, an underdeveloped visual system may not allow a good processing of local elements possibly yielding to the global advantage found in newborns. Moreover, these findings taken together suggest that the human global advantage could start to emerge gradually around the age of five. In fact, another study carried out on children ranging in age from 4 to 9 years found a local advantage with children aging about 4 years and suggested a pattern correlated with development from local preference to a full global

preference around the age of 9 years (Poirel, Mellet, Houdè, Pineau, 2008). Authors also reported that in younger children the interference exists in both directions (i.e., global-to-local and vice versa), as opposed to elder children in which only the typical adult-like global-to-local interference was reported. Therefore, based on these results, authors suggested that both the global-local processing and the strategy used to perform the discrimination task can change with the age (Poirel *et al.*, 2008). Another study assessed children's recognition of animals on the basis of their parts over their whole structures, following manipulations of parts of the animal or of the entire figure (Davidoff & Roberson, 2002). This study demonstrated that children (in particular those aging from 6 to 10 years) are better in recognising animals on the basis of their parts rather than on their whole shapes. Conversely, around the age of 15-16 equal performance in the recognition of whole shapes and their parts emerged (Davidoff & Roberson, 2002).

Interestingly, it has been found that even the cultural background can affect the global precedence, in fact, the *Himba*, a remote population living in north Namibia, when tested with hierarchical stimuli display a local bias which contrasts what has been observed with any other non-clinical adult human population (Davidoff, Fonteneau, Fagot, 2008).

The global advantage can be considered as an adaptive value since it has some important functions such as the utilization of low resolution with a resulting reduction of the processing resources and the disambiguation of unclear details of information (Navon, 1977). In fact, since visual information is mostly dynamic, usually there is no time for a complete analysis of the constantly changing input. Consequently, having a rough idea of the general structure of the visual scene is often more valuable than spotting a few isolated details (Navon, 1977). Given the remarkable value of the global advantage, it is interesting to clarify whether or not this cognitive

feature is represented also in the rest of the animal kingdom, in particular in animals taxonomically related with us and by doing so to attempt to trace back the evolution of this aspect of human visual cognition.

Pioneering work in the comparative study of the global-local processing has been carried out by Fagot and Deruelle (1997). They carried out six experiments on eight baboons and compared the results with those obtained from fourteen human subjects. A Matching-To-Sample procedure (see Chapter II) was adopted, using hierarchical stimuli. The six experiments were carried out using a similar procedure but adopting small changes in order to avoid confounds and to disentangle the role played by different factors independently. Coherently with Navon's findings, humans displayed a global advantage and a global-to-local interference, by contrast, baboons showed a local advantage and no interference effects.

The local advantage seems to be a distinctive feature of many monkey species, since it has been found also in other *Catarrhine* specie like rhesus macaques (Hopkins & Washburn, 2002). Conversely, studies carried on chimpanzees did not demonstrate any clear global/local bias in this species. Fagot & Tomonaga (1999), across three experiments, assessed the global-local processing of two adult chimpanzees in comparison to that of the two humans. In the first experiment, subjects were tested with hierarchical stimuli using a visual search task. In contrast to humans, who displayed a global advantage, chimpanzees did not show any advantage. In the second experiment, a few manipulations were made in order to obtain three kinds of stimuli: two types featured always many and dense local elements but could be either big or small at the global level. Conversely, the third type of stimuli featured always big global configurations but a few and sparse local elements. Humans showed a general global advantage in every condition, whereas chimpanzees showed a local advantage with stimuli featuring sparse local elements

but no advantage with dense stimuli, regardless for the dimension of the global configurations. In the last experiment there were two conditions: both conditions featured stimuli with a few and distant local elements, like those used in experiment 2, but in one condition the local elements were connected by a line. Overall, chimpanzees showed a global advantage with stimuli featuring local elements connected by lines, but a local advantage in absence of lines connecting the local elements.

Another research (Hopkins & Washburn, 2002) examined whether chimpanzees and rhesus monkeys, tested with hierarchical stimuli, exhibit any advantage or interference between the two levels of processing of hierarchical stimuli. They tested five young chimpanzees and five rhesus monkeys using a Matching-To-Sample task. Chimpanzees and macaques demonstrated a good ability in discriminating both levels of processing. However, chimpanzees displayed a global-to-local processing strategy whereas rhesus monkeys exhibited a local-to-global processing strategy (Hopkins & Washburn, 2002).

Overall, these studies taken together do not indicate any strong bias towards global or local processing in species taxonomically closer to humans like chimpanzees.

In 2003, Spinozzi, De Lillo and Truppa extended this kind of research to a New World primate species: the tufted capuchin monkeys. They tested monkeys with hierarchical patterns using a simultaneous Matching-To-Sample procedure. A general local advantage was found in the first two experiments, which featured different types of hierarchical stimuli. Interestingly, this local bias did not depend by the fact that capuchins were not able to process the global configurations. In fact, global shapes were always matched above chance level by every subject. Nevertheless, a significant higher performance was observed in trials requiring processing of local configurations (Spinozzi *et al.* 2003). In a third experiment the

same kind of hierarchical stimuli were used, however manipulations on the density of local elements occurred. Thus, there were two new conditions: one featuring a few and relatively sparse local elements, the other featuring many and relatively dense local elements. Monkeys did not exhibit any global or local advantage in the condition featuring stimuli with many and dense local elements. In fact, their performance was very high in both levels of processing. Conversely, their performance on the global trials was significantly affected when stimuli featuring a few and sparse local elements were used, and a clear local bias emerged again (Spinozzi *et al.* 2003).

As mentioned above, Neiworth *et al.* (2006) compared the global-local processing of adult humans, young children, and adult tamarins (*Saguinus oedipus*) with Navon-like stimuli under conditions featuring either dense or sparse local elements. In agreement with the previous literature, adult humans showed a global bias regardless to the density of the local elements. By contrast, children and adult tamarins showed a global advantage with dense stimuli but no advantage with sparse stimuli.

Therefore, with few exceptions, confined to the condition with dense local elements, the local advantage seems to be a common feature in monkeys' visual cognition. Furthermore, the uncertain pattern exhibited so far by chimpanzees suggests a possible evolutionary trend in the emerging of human global precedence. The difference in the way in which human and non-human primates process hierarchically organised stimuli has raised a significant interest among investigators in comparative cognition. However, the reason for this local advantage is still poorly understood (Fagot & Deruelle, 1997). It is possible to argue that in capuchins the local advantage could be an adaptation to their particular ecological niche, where they are specialised to search for small seeds or insects. According to this hypothesis, the local advantage should be affected by reducing the stimulus visual angle and so the actual perceived size

of stimuli. To test this suggestion, Spinozzi, De Lillo and Salvi (2005) ran two experiments with the aim to evaluate the role played by the stimulus size and the amount of local elements respectively. In the first experiment they used two types of hierarchical stimuli, respectively larger and smaller than those used in their previous study (Spinozzi *et al.* 2003). Remarkably, in the smaller stimuli the global level sustained the same visual angle of the local level of the larger ones. However, the local advantage persisted in both conditions (Spinozzi *et al.*, 2005). Another hypothesis to explain the local advantage in monkeys suggests that this species may use different grouping principles from humans. To test this hypothesis, Spinozzi, De Lillo and Castelli (2004) carried out another study based on four experiments each one specifically aimed at evaluating monkeys ability to recognise grouped and ungrouped patterns. In the first experiment, monkeys were presented with complex visual patterns (e.g., three circles partly overlapping) and they had to identify the comparison stimulus featuring some of the parts of these shapes as opposed to the non-comparison stimulus featuring a similar whole shape but not related to the sample stimulus. There were two conditions: the grouped and ungrouped condition. In the grouped-condition, the comparison stimuli featured grouped shapes of the sample stimulus (e.g., a whole circle out of three circles featured in the sample stimulus). In the ungrouped-condition, the comparison stimuli featured ungrouped parts of the sample stimulus (e.g., parts of the three circles presented as relatively disconnected elements). Interestingly, monkeys' performance was better when stimuli featured ungrouped parts than grouped parts. In the second experiment the paradigm was inverted and therefore, the parts of the figures, either grouped or ungrouped, appeared as sample stimulus, whereas the whole figures appeared as comparison stimuli. In this experiment, monkeys' performance across conditions was equal. In a third experiment, new stimuli were used but similar results were

observed. A fourth experiment allowed interspecies comparison by testing humans with the same paradigm used with monkeys. In contrast to monkeys, humans performed better in grouped condition. That study revealed that monkeys' performance is negatively affected by the use of grouping principles that humans find beneficial and it is not affected by cues, such as closure, to which humans are sensitive. Therefore, this suggested that capuchins may use different grouping cues in comparison to humans. For this reason, a new study specifically aimed at assessing the use of different grouping cues in humans and capuchins was carried out (Spinozzi, De Lillo, Truppa, Castorina, 2009). This study analysed the role played by *Gestalt* grouping cues such as proximity, shape similarity and orientation of local elements. The test involved matching hierarchical stimuli with filled shapes which resembled the hierarchical stimuli at global level. The hierarchical stimuli could present as grouping cue either the proximity or the shape similarity or the orientation of local elements. The study revealed performances above the chance level in every condition, demonstrating that they are sensitive to these grouping clues. However, performances were better when the discrimination process involved the use of the proximity and the shape similarity as grouping clues compared to when it involved the orientation.

By contrast, humans' accuracy was significantly higher when the grouping cue to use was the proximity of elements rather than when it was the shape similarity or the orientation. Even though the relative importance of each cue has been proved to play a different weight in the two species, it seems that the ability of following these *Gestalt* features to group local elements into a coherent whole is an important trait of capuchins' visual cognition (Spinozzi *et al.*, 2009). However, capuchins as well as humans seem to be highly sensitive to the spatial relationships between stimulus parts as showed by a further experiment in which the matching performance of both species was measured after producing different manipulations of

stimulus structure. The results of the experiment demonstrated that the global rotation of the whole stimulus did not impair stimulus recognition. By contrast, when the spatial relationships between each part of the same stimulus were disrupted, for example by dividing the stimulus in four parts and then arranging them in a different order, it significantly affected performances of both humans and monkeys (De Lillo, Spinozzi, Truppa, 2007).

In conclusion, after several years of research in this domain, it has been proved difficult to find a specific factor that can fully account for the monkeys' typical local advantage. Therefore, in the present work, other cognitive processes which could be involved in capuchin monkey global-local processing will be assessed and are introduced below.

### **1.5.1 The role of stimulus redundancy on global-local processing**

A factor well acknowledged to play a key role in human visual processing is the sensitivity to symmetry of the stimulus, also described as the "redundancy" of the stimulus (Garner, 1974). According to Garner (1974) the redundancy or goodness of a pattern is directly related to its symmetry and inversely related to the number of equivalent patterns that could be obtained by a 90° rotation and/or reflection of a single pattern. As reflection, Garner considered a 180° rotation on the medial vertical of the stimulus, which generates a mirror like image of such pattern. In other words, good patterns, following a 90° rotation or a complete reflection, generate small sets, and therefore, are considered highly redundant. For example, a circle and a cross are considered highly redundant shapes as their reflection or 90° rotation results always in the same pattern. However, non-redundant patterns following these manipulations generate a large number of different shapes. For

instance, irregular forms like polygons featuring many sides and different angles, or open irregular shapes made up of different segments, are considered less redundant, as following each reflection or 90° rotation they can produce a set featuring up to 8 different new patterns (a visual description of Garner dot patterns is presented in Chapter III).

The concept of redundancy has been considered very important in human visual cognition (Garner, 1970; Garner & Clement, 1963; Jamieson & Mewhort, 2005; Miller, 1958; Mohr & Pulvermüller 2002; Murdock, 1968). As described above, there is a direct relationship between perceived goodness and stimulus redundancy (Garner & Clement, 1963). Further studies have demonstrated also that good patterns are detected more efficiently (Garner, 1970) and are easier to remember (Checkosky & Whitlock, 1973). In other words, the low structural information load associated with good patterns can be detected to allow an easier and faster encoding by humans (Garner & Sutliff, 1974). Nevertheless, the role of this stimulus property in the global-local processing has not been well documented and this gap in the literature becomes even wider if other animals are taken into account.

To my knowledge, the only study which tested the ability of a monkey species to detect stimulus redundancy was carried out by Schrier, Povar and Schrier (1979). They tested stump tailed monkeys with stimuli featuring different level of symmetry according to Garner patterns. However, their study demonstrated that redundant and non-redundant patterns were processed equally well by this species. Another study carried out on capuchin monkeys was aimed at assessing if capuchins prefer symmetrical over non-symmetrical or irregular patterns (Anderson, Kuroshima, Hattori, Fujita, 2005). The task consisted of assessing the difference in spontaneous manipulations between cards featuring regular and symmetrical shapes and cards featuring non-symmetrical shapes or

shapes where the image was compromised by scrambling their component parts. Capuchin monkeys expressed a clear preference for cards in which the symmetry and regularity of the original stimulus was preserved. However, they did not evaluate if this happened because they find symmetrical images easier to process. Therefore, understanding whether or not New World species such as capuchin monkeys can benefit of stimulus redundancy to allow a faster encoding of the visual information represents an extremely interesting research field which can help us in clarifying if they use similar cognitive process to those used by humans.

### **1.5.2 The role of attentional biases toward different levels of hierarchical stimuli on global-local processing**

Another important process that plays a remarkable role in human and non-human perceptual organisation is visual attention. Several findings suggest that grouping by proximity in humans requires attentional resources (Ben-Av, Sagi, Braun, 1992; Mack, Tang, Tuma, Kahn, Rock, 1992). In fact, attentional biases are widely acknowledged to be effective in modulating the speed of processing of each level of hierarchical stimuli (Kinchla, Solis-Macias, Hoffman, 1983; Lamb & Robertson, 1987, 1988; Miller, 1981; Robertson, Egly, Lamb, Kerth, 1993; Ward, 1982). Such priming effects have been tested either by presenting a cue indicating the level of processing that was more likely to occur at a particular level of stimulus structure (Robertson *et al.*, 1993) or by changing the proportion of trials requiring attention to a specific level of stimulus structure within trial sessions (Kinchla *et al.*, 1983; Lamb & Robertson, 1987). However, to our knowledge, there are no studies which have evaluated the role played by attention allocation to one level of processing of stimulus structure in capuchin monkeys. In fact, whereas many factors which could possibly explain monkey local bias

have been already ruled out, nothing has been done to test the role played by visual attention in monkey global-local processing.

In humans, selective attention to a particular level of hierarchical stimuli and its effect to enhance and/or hinder the processing at that level has been interpreted as being due to a mechanism based on a spatial allocation of attention. Using the 'spotlight' metaphor of attention, some researchers suggested that the efficiency of responding to either level of a compound pattern can be affected by variations in the diameter of the 'spotlight' (Lamb & Robertson, 1988; Robertson, Egly, Lamb, Kerth 1993; Ward, 1982). According to this hypothesis, the processing of local elements is facilitated when the attended visual area is small like the size of local shapes, whereas the processing of global configurations is facilitated when the attended visual area is large like the size of a global structure.

Some studies have attempted to modulate the visual attention of animals towards a particular level of stimulus structure using priming procedures. For instance, Fremouw, Herbranson and Shimp (1998) tested pigeons with Navon-type stimuli demonstrating that biasing attention toward a particular level of hierarchical patterns is effective in facilitating the processing of that level. Further experiments (Fremouw, Herbranson, Shimp, 2002) using a priming cue based on colour presented before each trial, demonstrated that pigeons can easily switch their visual attention towards either level of hierarchical stimuli. Overall, these studies show that pigeons, like humans, can selectively shift attention between different levels of hierarchical stimuli. Therefore, these studies indicate that attention can play a potentially underestimated role in pattern recognition displayed by animals. If this is the case, such a role should be taken into account when running studies on monkeys assuming that they represent a good model of the human brain.

### **1.5.3 The role of Spatial Frequencies processing on global-local processing**

A factor widely acknowledged to be involved in human global-local processing is the spatial frequency of the stimulus. Spatial frequency (SF) refers to the number of light intensity changes over space in an image (e.g., produced by presenting a dark grating on a light background) and is measured by cycles per degree (cpd) of visual angle. Global perception typically requires low spatial frequency (LSF) processing and local perception requires high spatial frequency (HSF) processing (Shulman, Sullivan, Gish, Sakoda, 1986; Shulman & Wilson 1987; Robertson, 1996). Lamb & Yund (1993) found that filtering out the LSF content of hierarchical stimuli, impaired RTs in the global trial but not in the local ones, indicating that the LSFs are involved in the global advantage typically observed with humans. Further studies have shown that after removing the LSFs from hierarchical stimuli, the global precedence is reduced (Badcock, Whitworth, Badcock, Lovegrove, 1990; Boeschoten, Kemner, Kenemans, Van Engeland, 2005; Hughes, Fendrich, Reuter-Lorenz, 1990).

Several studies displayed that, in humans, the global-local processing is related to hemispheric specialization. Therefore, the left hemisphere is predisposed towards local processing whereas the right hemisphere towards global processing (Fink, Halligan, Marshall, Frith, Frackowiak, Dolan, 1996; Han, Weaver, Murray, Kang, Yund, Woods, 2002; Hübner, 1997; Hübner & Volberg, 2005; Robertson & Lamb, 1991). The human brain seems to be asymmetrical specialised also for the processing of HSFs and LSFs, with HSFs processed more by the left hemisphere and LSFs processed more by the right hemisphere (Christman, Kitterle, Hellige, 1991; Kitterle, Christman, Hellige, 1990). Furthermore, results from studies which involved functional Magnetic Resonance Imaging (fMRI), Event Related

Potential (ERP) and Positron Emission Tomography (PET) techniques demonstrated that there is an overlap between brain localizations for global and local processing and for low and high spatial frequencies processing respectively (Boeschoten *et al.*, 2005; Evans, Shedden, Hevenor, Hahn, 2000; Fink *et al.*, 1996; Heinze, Hinrichs, Scholz, Burchert, Mangun, 1998; Malinowski, Hübner, Keil, Gruber, 2002; Martinez, Moses, Frank, Buxton, Wong, Stiles, 1997; Proverbio, Minniti, Zani, 1998; Van Kleeck, 1989). However, a few studies do not support these findings (e.g., Grabowska, Nowicka, 1996; Grabowska, Nowicka, Szatkowska, 1992).

In human visual channels, LSF are transmitted faster than HSFs (Breitmeyer 1975; Lupp, Hauske, Wolf, 1976). Therefore, since the global level of patterns contains mostly lower spatial frequencies, whereas the local elements contain mostly higher ones, it has been hypothesised that the information contained at the global level is transmitted faster than the information contained at the local level. According to Sergent (1982), the global level of compound stimuli can be identified even with very short exposure to the stimulus. By contrast, under the same conditions the recognition of local shape is strongly impaired. At very short exposure, only the LSFs are available (see also Breitmeyer & Ganz, 1977) thereby, this may account for the global precedence. Global precedence could depend also on the asymmetric inhibition between transient and sustained channels. While transient channels are activated mostly during exposition to LSFs, signalling the presence of the stimulus, sustained channels respond gradually to medium and high SFs along with the exposition to the stimulus (Felipe, Bueades, Artigas, 1993; Tolhurst, 1975). In humans transient channels can inhibit sustained channels but not *vice versa* (Breitmeyer, 1984). Therefore, this inhibitory interaction between SF channels may be responsible for the global advantage.

The interaction between global-local processing and SFs processing can also be seen in relation to the distribution of attention.

As suggested by Shulman and Wilson (1987), in humans sensitivity to particular spatial frequencies might be controlled by the areal spread of attention to local or global information. Shulman and colleague carried out four experiments to determine if the allocation of attention to either global or local level of hierarchical stimuli affects the detectability of different spatial frequencies. A relative shift in the detectability of low and high frequencies was observed. LSF processing was facilitated during global processing whereas HSF processing was facilitated during local processing. One possible interpretation suggested by the authors featured the 'zoom-lens' model previously proposed by Eriksen & Yeh (1985). According to this paradigm, the efficiency of processing at any location decreases as attention becomes more spread out. Therefore, when attention is spread more widely there is a loss of sensitivity to high frequencies, while the sensitivity to low frequencies increases. By contrast, when the spotlight of attention becomes narrower, there is a loss of sensitivity to lower spatial frequencies together with an increase of sensitivity to higher ones. In 2011 Flevaris, Bentin and Robertson replicated the experiment using compound grating patterns. They used sine-wave grating patterns including both relatively high and relatively low SFs integrated in the same stimulus, with each SF perpendicular to the other ones. The compound SF patterns were presented so that the two SF gratings resulted tilted left and right of 45° compared to the vertical. The task consisted in a same-different judgment of hierarchical stimuli followed by a tilted left-or-right judgement of the compound gratings. They demonstrated that attention allocation to each level of hierarchical stimuli influenced the selection of LSFs and HSFs. In particular, using compound grating patterns allowed them to investigate the nature of the process involved in the SF selection. In fact, if the SF selection was based merely on their absolute values, probably a lower level mechanism would be responsible for this outcome. Conversely, if the SF selection

is based on a selective process that considers a certain SF value high or low depending on the context in which it is presented, then the selection is probably guided by a higher cognitive mechanism. The results from the study provided evidence for this latter hypothesis since attention allocation to each level of stimulus structure affected subsequent selection of LSFs or HSFs. Moreover, the bias was determined by the role of each SF (either high or low) in the compound grating, rather than by its absolute value in cpd. In fact, the same frequency elicited diverse responses depending on its *relative* role, either high or low, in the compound stimulus, not depending on its absolute value. The findings suggest that attention to hierarchical level modulates attention selection of SFs, supporting the idea that a flexible top-down mechanism is involved in the link between the SF processing and the global-local processing.

## **1.6 THE PRESENT WORK**

Within a comparative framework, given the high degree of similarities, and therefore possible homologies, shared by human and non-human primates in their visual system, studies designed to disentangle alternative explanations of the observed differences in their global–local processing could help in clarifying the emergence and the evolution of the human cognitive system. Therefore, the aim of this work is to clarify the role played by three different factors in capuchin monkeys' global-local processing and thus to suggest possible explanations for their typical local advantage.

In the present work, three different studies featuring a total of 17 experiments (8 in monkeys and 9 in humans) are presented as part of three different chapters.

The principal aim of the first study was to assess whether or not the stimulus redundancy can affect global-local processing. As discussed

above, humans can benefit from stimulus redundancy in their visual processing (Garner, 1974, 1970). Conversely, the results of similar studies carried out in other non-human primates are extremely scarce. In fact, the only study that attempted to address this issue in macaques did not provide any evidence for a benefit of stimulus redundancy in such species (Schrier *et al.*, 1979) despite the fact that non-human primates share with us a very similar visual system and cognition. It should be emphasized that all the comparative studies on global-local processing carried out among primates usually employed highly redundant shapes (e.g., circles, crosses, squares). Given that hierarchical stimuli often feature the same shapes at both levels of processing, they usually share the same degree of difficulty. Notwithstanding this, since processing the global level requires grouping (see Kofka, 1935) and good shapes are more likely to be perceived as wholes, human sensitivity to stimulus redundancy could facilitate their grouping at the global level and therefore, promote the global advantage. Hence, if other non-human primates are not able to detect stimulus redundancy, this would imply they are not able to take advantage of this additional organizational factor, and this could already represent a possible explanation for the local advantage typically observed in monkeys. Therefore, assessing the role of stimulus redundancy in comparative studies on the global-local processing allows us to evaluate the possible role of this factor in determining the observed differences between humans and monkeys in their global-local processing.

This was done by administering a discrimination task (for further details on the general procedure, see Chapter II) where subjects had to identify hierarchical dot patterns, redundant and non-redundant, derived from those described by Garner (1974). If humans and monkeys display a different sensitivity to redundancy, this could pinpoint an important distinctive feature of human cognition in relation to its ability to efficiently manage, process and store visual information.

By contrast, finding out that other non-human species can detect the stimulus redundancy would indicate that such high cognitive skill is not an exclusive trait of human cognitive system and therefore, may open the way to further studies in other species in the same domain.

Normally, comparative studies on the global-local processing have been carried out using hierarchical stimuli featuring grouping at global level only (e.g., Fagot & Deruelle, 1997; Spinozzi *et al.* 2003). Therefore, some investigators suggested that the local advantage, or the “global disadvantage” as proposed by Fagot and Barbet (2006), may be related to a certain difficulty, displayed by monkeys, to group elements into a coherent whole rather than to a local bias in perception. If this idea is true, monkeys should not display a local advantage in conditions featuring stimuli where the requirement to group elements was present also at the local level. Therefore, a second aim of the first study is to assess the effect of the requirement of double grouping at the local level on capuchin global-local processing. If the presence of a requirement to group also at the local level does not affect monkey local advantage, this would ultimately rule out the idea that capuchin monkey local advantage depends on a supposed inability, displayed by this species, in connecting elements into a whole. To test this hypothesis, as part of this study, two experiments featuring stimuli which required grouping at both levels of processing, global and local, were carried out.

The second study was aimed at assessing whether or not biasing the visual attention toward different level of hierarchical stimuli can affect the global-local recognition in tufted capuchin monkeys as it was reported not just in studies carried out on humans but also in other animals like pigeons (Fremouw *et al.*, 1998; Kinchla *et al.*, 1983 Lamb & Robertson, 1987). In order to bias the attention to each level of processing, each experimental session featured a majority of trials which required the recognition of only one level of processing and was intermixed with a minority of trials which required the recognition of the

other level of processing (see Chapter IV for further details). This procedure proved effective in biasing the attention toward each level of processing in previous studies on humans (Kinchla *et al.*, 1983).

A growing body of literature demonstrated that spatial frequencies processing and global-local processing are strongly interconnected and there is evidence that this relationship can be interpreted in terms of attentional processes (see for example Flevaris *et al.*, 2011; Shulman & Wilson, 1987). Therefore, the aim of the last study is to assess whether or not biasing attention to different spatial frequencies (high or low) can affect subsequent global-local recognition in both capuchins and humans. To do so, a similar paradigm used in the second study and in previous literature (Kinchla *et al.*, 1983) was used but transferred to non-hierarchical stimuli.

If attention proves effective in modulating monkey global-local processing in both studies, this would suggest that visual attention can play an extremely important role in monkey visual cognition. This may potentially imply that the capuchin monkey typical local advantage, should not be considered a “disadvantage” in perceiving the global representation of the visual scene (Fagot & Barbet, 2006), instead it could be considered like a proper “cognitive style”. Such cognitive style, coherently with the theory of evolution proposed by Darwin (1871) for phenotypic traits, should be sensitive to natural selection (see also Lorenz, 1965) and therefore may have evolved because it could represent a benefit for monkey survival. Such finding may shed a new light on what is our understanding about the evolution of human global-local processing.

The general cognitive and behavioural consequences of such hypothesis are further discussed in Chapter VI.

## CHAPTER II

### GENERAL METHOD AND PROCEDURE

#### 2.1 THE MATCHING-TO-SAMPLE PROCEDURE IN STUDIES ON ANIMAL COGNITION

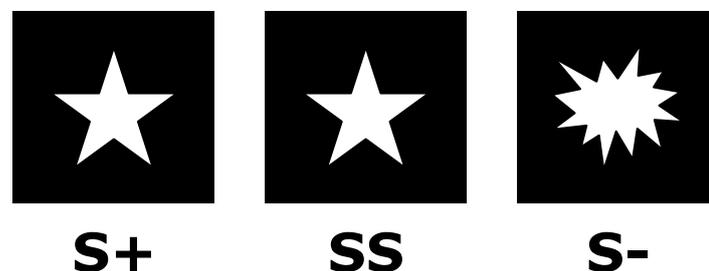
The Matching-To-Sample, developed during the behaviourism period, is a procedure used to instruct an animal about a task to solve. In the Matching-To-Sample procedure, the animal has to choose between different stimuli to establish which one matches, in several different ways, a sample stimulus. The correct choice is followed by reinforcement, usually food. The task can involve a match in which one of the comparison stimuli is identical or similar (see also below) to the sample stimulus, whereas the others are different at least in some aspects. Alternatively, it can involve an association, where, for example, a colour corresponds to a particular key (Skinner, 1950; Blough, 1959; Ferster, 1960).

There are many variations of the MTS procedure. In the *Identity MTS* task, the correct comparison stimulus (S+) is identical to the sample stimulus (SS), whereas in the *Similarity MTS* task, S+ is similar but not identical to SS. In both cases, the non-correct comparison stimulus (S-) is always different from SS. Alternatively, the task can be reversed and therefore, it can consist in a non-MTS task, in which the non-matching stimulus has to be chosen. The matching can be done through an association. Therefore, through the experience the animal learns that a particular stimulus is associated with a particular key to press. In any case the animal learns the association, and therefore the task to solve, thanks to reinforcement (typically food) provided after the correct choice has been made.

Each variation of the MTS task can be used as *simultaneous* or *delayed MTS task*. In the first one, the comparison stimuli can be viewed simultaneously with the sample stimulus, this procedure is adopted for instance in studies in visual processing and cognition. On the other side, in the *delayed MTS task* there is a delay in the presentation of the comparison stimuli. The length of this delay can be different so that it can be determined how long the subject can keep information. This kind of procedure is suitable in particular in studies focused on working memory.

The amount of information that subjects can hold varies across species and depends also on the duration of the delay. For instance, pigeons' ability to accurately choose the comparison stimuli decreases as the delay between stimuli presentations increases (Grant, 1975, 1976). On average, when stimuli are presented with a delay of ten seconds, pigeons' performance is around 66% of correct responses. By contrast, capuchin monkeys are able to do the correct matching with much longer delays (D'Amato, 1973).

Whether it is identity or similarity, simultaneous or delayed MTS task, to reach the criterion and therefore, to consider that the animal has learnt the task, the subject has to make choices significantly above the chance level of 50% of correct answers.



*Figure 4. Example of Identity-MTS task with simple white shapes on a black background.*

## **2.2 GENERAL METHOD AND PROCEDURE USED WITH MONKEYS**

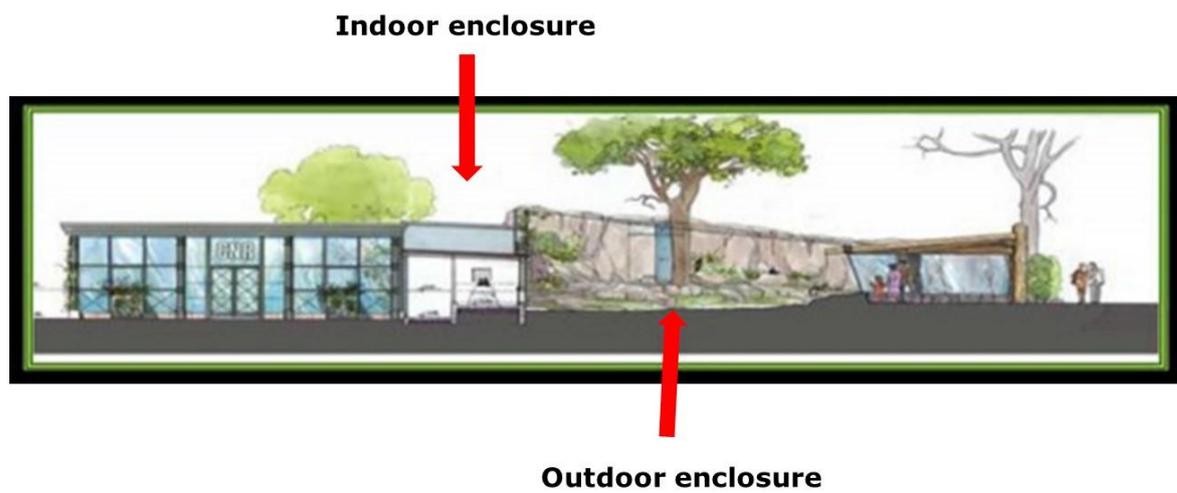
In this section some shared aspect about the general method used in this work will be described. Due to the differences between each study, further information, particularly related to the stimuli, will be provided in a dedicated session of each study.

### **2.2.1 Participants**

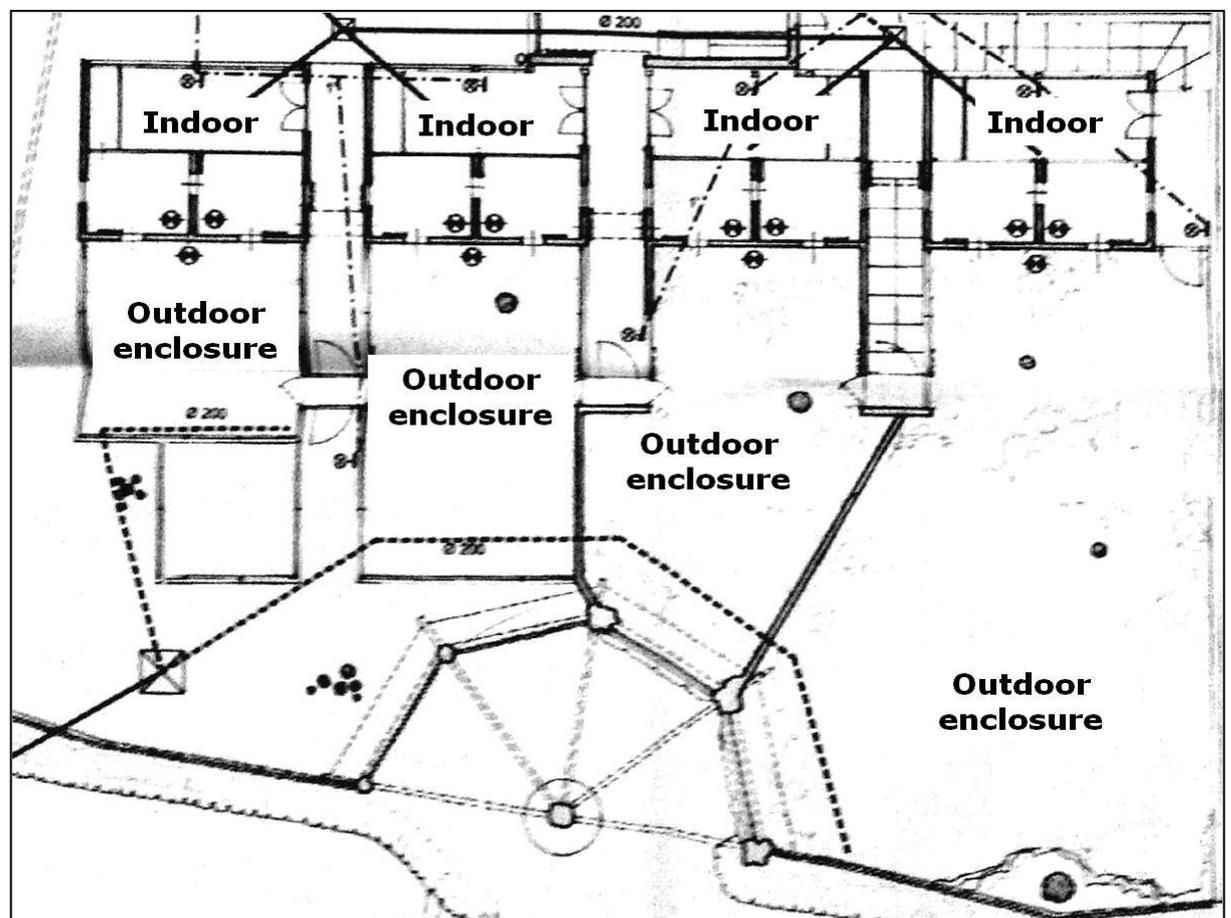
In the following studies, five adult tufted capuchin monkeys were tested. The whole monkey sample included 1 female (Pippi) and 4 males (Patè, Gal, Vispo and Rubens), all aged between 6 and 27 years old at the time when the first study began. Pippi, Gal and Rubens participated in all the three studies, whereas Patè and Vispo did not participate in the third study due to their failure in processing the stimuli required in that study above the chance level.

All monkeys were born in captivity and lived in social groups hosted in 4 different indoor–outdoor enclosures at Primate Centre of the *Istituto di Scienze e Tecnologie della Cognizione (ISTC), Consiglio Nazionale delle Ricerche (CNR)*, in Rome, Italy. Each indoor enclosure measured: 5.0 m<sup>2</sup> x 2.5 m high. The outdoor enclosures measured from 40.0 m<sup>2</sup> to 130.0 m<sup>2</sup> (x 3.0 m high). Tests were carried out on each monkey taken individually, in an experimental cage (1.70 m long x 0.76 m wide x 0.73 m high) which they spontaneously could access from the adjacent enclosure. An overview of the facilities is reported in Figure 5 and 6.

a)



b)



*Figure 5. Overview of the Primate Centre (ISTC-CNR) in Rome, Italy. a) Drawing of a side view of the Centre; b) Map of the Centre. (All figures with permission of the Primate Centre).*

Subjects were free to move around the indoor-outdoor facilities all the time and they were separated by the group only during the experimental sessions which would last, on average, no more than 20 minutes. Animals spontaneously took part in the experiments as, by doing so, they could receive a reward, usually food. Importantly, during the tests, they were never physically constrained.

Water was always available and animals were fed regularly with a variety of fresh fruit and vegetables together with some proteinaceous food (e.g., cottage cheese, boiled eggs). At the beginning of the project, three subjects (Pippi, Patè, Gal) had already participated in previous experiments involving hierarchical stimuli. Yet, all subjects were previously trained with the MTS procedure using non-hierarchical visual stimuli.

All the three studies were approved by the Italian Health Department.



*Figure 6. Photograph of one of the 4 outdoor enclosures (All figures with permission from the Primate Centre).*

## 2.2.2 Apparatus

Figure 7 depicts the apparatus used with monkeys. It consisted of a vertical panel (35 cm high x 45 cm long) with two lateral walls (35 cm high x 35 cm long) fixed onto a board (45 cm x 35 cm). This could slide back and forth on a support placed on a trolley (55 cm high x 50 cm long x 50 cm wide). At equal distance from the centre the vertical panel featured two rectangular openings (9 cm high x 5 cm large) used for stimulus presentation and reward collection.

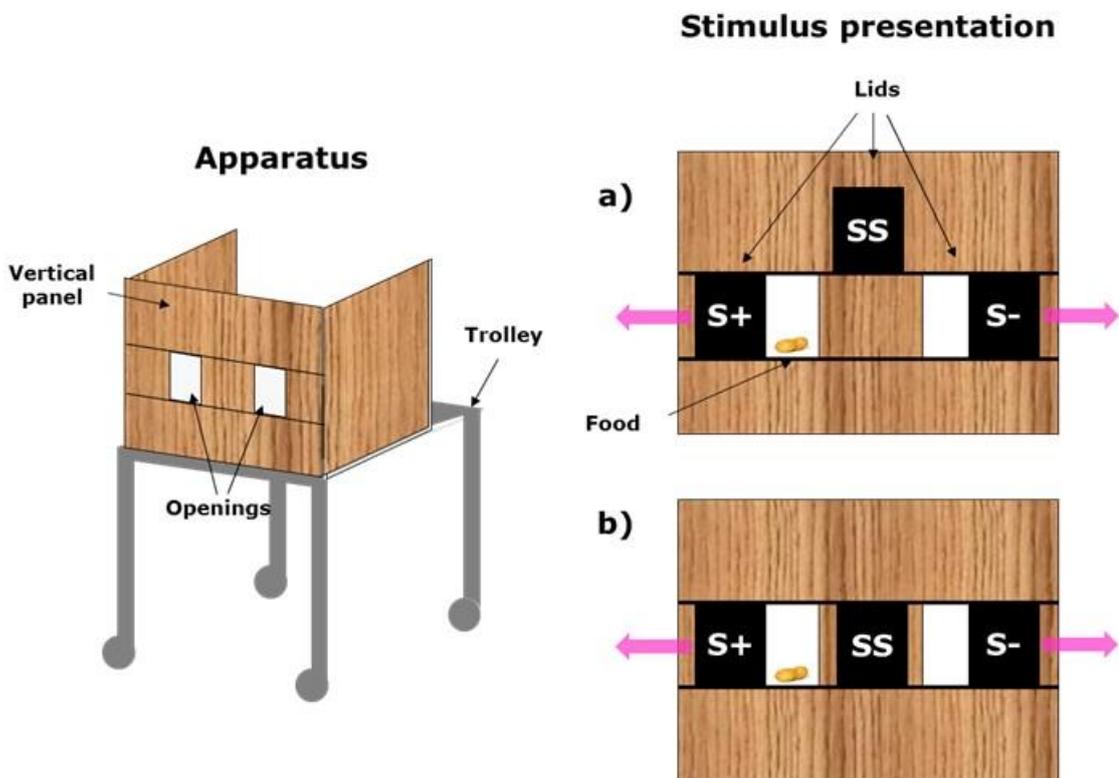


Figure 7. Apparatus used with monkeys in the three studies. Due to some experimental conditions, the position of the central stimulus varied across the three studies as described in (a) and (b).

During the test, three PVC lids (11 cm high x 6 cm large) reporting the visual stimuli were placed on the panel. The lid featuring the sample stimulus (SS) was placed in a central slot, either in line with the comparison stimuli or above them (see Figure 7)

depending on the study (see each study for a description). The lids featuring the two comparison stimuli (S+ and S-) were placed in front of the two openings and could be moved, along two metal tracks, in both directions.

The experimental box which hosted the monkey during the test featured a side wall (40 cm high x 45 cm large) made of transparent Plexiglas which allowed the monkey to view the presented stimuli. The Plexiglas wall featured two symmetrical armholes (5.5 cm high x 15 cm large) positioned roughly at the same level of the rectangular openings of the apparatus. In this way, when the apparatus was placed in front of the experimental box, the monkey, after viewing the presented stimuli, could insert an arm through one of the two holes and move one of the lids covering the openings reporting the stimuli. Only behind the lid reporting the correct comparison stimulus, monkeys could find a small piece of peanut as reward.



*Figure 8. Photograph of a monkey in the process of solving a Matching-To-Sample task with the apparatus described above (Picture of the author).*

### **2.2.3 Stimuli**

Stimuli were different for each study. For this reason, they will be described in the appropriate section of each study.

In general, stimuli were printed on paper and were glued onto PVC lids in order to be presented with the apparatus. They were laminated to prevent damaging and eventually replaced with an identical stimulus at the first sign of deterioration.

### **2.2.4 Procedure**

An identity simultaneous Matching-To-Sample procedure was used across the three studies as described above. During the tests, the apparatus was positioned frontally, 30 cm away from the experimental box. The experimenter, behind the apparatus, would position the lid featuring the sample stimulus in the centre and the lids featuring the two comparison stimuli in front of the two openings. Then, a piece of peanut (half half of one peanut seed) was placed behind the lid reporting the correct comparison stimulus (S+). The experimenter had to move both hands simultaneously while doing this procedure. Furthermore, she was instructed to stay still and do not look directly at the monkey or at the apparatus all time. This procedure was done in order to avoid that the experimenter could accidentally give to the monkey some clues about the location of the reward. By moving the correct stimulus, the monkey could access to the reward. Only one lid at time could be moved, then, after the choice was made, the apparatus was moved away from the animal to prevent them from attempting to move the other lid. 30-40 seconds would pass between the previous and the following trials, during this time the experimenter recorded the data.

#### 2.2.4.1 Training

Before starting the proper experiments, subjects were trained to the Identity-MTS task with different stimuli. The training stimuli were simple white shapes (roughly 3 cm x 3 cm) in a black background like those described in Figure 5 (e.g., hour-glasses, arrows, stars and explosions). The training, which lasted several months and was carried out also between an experiment and the following, consisted of one daily session featuring 24 trials, administered for at least 5 days a week. In the first stage of the training, only two kinds of stimuli were used. The two stimuli could be presented as sample or comparison stimulus an equal number of times within a session. Similarly, each comparison stimulus appeared on each side of the panel an equal amount of times. If the monkey did not make the right matching, the trial was repeated until 12 correct responses were made. When each subject reached the acquisition criterion of 90% or more correct responses on 4 consecutive sessions (excluding the correction sessions), it would be transferred to the next step of the training (*transfer test*). Two transfer tests, featuring 8 sessions of 24 trials each, were administered to each subject. In order to assess if the original matching performance was maintained and if the monkey was performing the transfer with the new stimuli, every session featured an equal number of old and new stimuli.

#### 2.2.4.2 Testing

Once the animal successfully passed the training phase, it took part in the experiments. The procedure of each experiment is further explained in the appropriate section of each chapter. Between each experiment, subjects continued the training with simple shapes in order to maintain acquired skills.

The position of the sample stimulus in the apparatus changed across the three studies. It was always positioned in the centre at the same distance between the two comparison stimuli. However, in

Study 1 and Study 2 it was above the comparison stimuli (see Figure 7a), whereas in Study 3 it was on the same level as described in Figure 7b. This latter change was made as an attempt to ease the monkeys' task as they demonstrated some difficulties in solving it.

## **2.3 GENERAL METHOD AND PROCEDURE USED WITH HUMANS**

### **2.3.1 Participants**

The human participants were chosen from the participant panel of the University of Leicester, UK, which consisted of students (undergraduates and postgraduates) and members of staff of the same university. The conditions to be enrolled in the experiments were to feature normal or corrected-to-normal vision, not being diagnosed with dyslexia and having a normal motility of both arms. Subjects were always naïve about the experimental hypotheses of all studies. As subjects changed across the three studies, further details about their gender and age will be given in the method section of each experiment. A small payment was given to each participant as compensation for the time spent to take part in the experiments.

### **2.3.2 Apparatus**

The apparatus used with humans featured a Pentium computer and a 17-inch SVGA monitor (1024 × 768 pixels resolution) connected with a response-box which allowed the subject to make a choice by pressing two buttons positioned on the left and right side respectively of an array of buttons. Stimuli were presented on the computer screen using *E-prime* software (*Psychology Software Tools Inc.*) allowing to collect accuracy data as well as response times (1ms accuracy).

Minor changes in the stimuli presentation occurred across the three different studies in order to maintain the similarity with monkeys tests (i.e., the alignment between stimuli varied from the first two studies and the third as was done with monkeys, see figure 7a and 7b) and are further discussed in the method section of each study. In every experiment reported in this work, only the RTs for correct answers were included in the data analysis.

### **2.3.3 Stimuli**

The stimuli, converted in bitmaps, were presented using the experimental set-up described in Chapter II. The size of the stimuli was controlled so that stimuli presented to humans featured the same visual angle as with monkeys. The eye-screen distance was maintained constant throughout the whole experiments using a chin-rest.

### **2.3.4 Procedure**

An identity simultaneous MTS procedure was used across the three studies as described above. In every study subjects had to indicate, by pressing the left or the right key of a response box, which of the two patterns was identical to the centrally presented pattern. The three stimuli were displayed until a response was made, then a blank screen would appear. To move to the next trial, the subject had to press a different button among the other three keys present on the response box. Further details of the MTS task with each kind of stimuli are provided in the methods section of each study.

## **CHAPTER III**

### **STUDY ON STIMULUS REDUNDANCY**

#### **EFFECT OF STIMULUS REDUNDANCY ON GLOBAL-LOCAL PROCESSING**

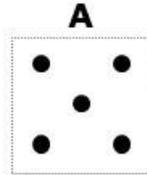
##### **3.1 INTRODUCTION**

Stimulus redundancy is an important factor that plays a key role in human visual processing (Garner, 1974). According to Garner (1974) the redundancy or goodness of a pattern is directly related to its symmetry and inversely related to the number of equivalent patterns that could be obtained by a 90° rotation and/or reflection of a single pattern (see also Chapter I for a discussion). Figure 9 depicts a redundant and a non-redundant pattern. The redundant pattern, an X formed by 5 dots, after 90° rotation and/or reflection generates always the same pattern. By contrast, the non-redundant pattern, an irregular shape still formed by 5 dots, following the same manipulations, can generate up to 8 different new patterns.

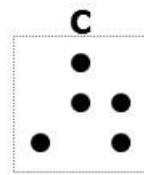
Albeit the ability to detect the stimulus redundancy represents an extremely important aspect of human visual cognition (Garner, 1970; Garner & Clement, 1963; Jamieson & Mewhort, 2005; Miller, 1958; Mohr & Pulvermüller 2002; Murdock, 1968), comparative studies aimed at assessing the role of this stimulus property in other animals are very scarce (see Schirer *et al.*, 1979; Anderson *et al.*, 2005). Furthermore, none of them were aimed at assessing the role of stimulus redundancy in relation to the global-local processing.

a)

**Redundant shapes**  
(mean goodness  
rating = 1.0)



**Non redundant shapes**  
(mean goodness  
rating = 5.8)



b)

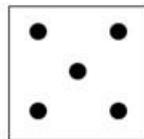
**Garner's (1974) set of alternative dot patterns**

**Redundant (R)**

**R1 (A)**

**Reflections**

**90° Rotations**



**Non redundant (NR)**

**NR2 (C)**

**Reflections**

**90° Rotations**

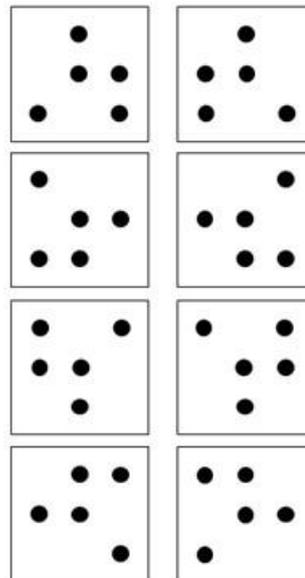


Figure 9. Garner's (1974) dot-patterns. a) Example of Redundant (R) and non-redundant (NR) patterns. b) Number of possible alternative patterns that can be produced by rotating or reflecting the same pattern.

The principal aim of this study is to assess whether or not capuchin monkeys are sensitive to the stimulus redundancy in a task that has been previously demonstrated to elicit a local advantage in

this species (De Lillo *et al.*, 2005; Spinozzi *et al.*, 2003; 2006). Studying if the global-local processing can be related to the perception of redundancy can allow us to assess if monkeys use similar cognitive processes to those used by humans. This can help to pinpoint whether or not this factor can account for some of the observed differences between monkeys and humans. Therefore, the aim of this study is to address the question of whether or not redundant hierarchical stimuli can facilitate the global-local processing in comparison with non-redundant ones in both capuchins and humans.

A second aim of this study is also analysing the effect of the requirement of double grouping at the local level on capuchin global-local processing. In fact, comparative studies in this domain have generally used hierarchical stimuli involving grouping at global level only (e.g., Fagot and Deruelle 1997; Spinozzi *et al.* 2003). The local advantage in monkeys has been put in relation to deficits in grouping (Fagot & Barbet, 2006), if this hypothesis is correct, the requirement to group also at the local level should eliminate it. To test this hypothesis, as part of this study, two experiments featuring stimuli where the requirement of grouping was present at both levels of processing, global and local, were carried out. In this way, it was possible to assess whether or not the requirement to group elements at global level represents the main reason for the local advantage typically displayed with capuchin monkeys.

In this study, five experiments (in both species) were carried out in order to evaluate the relative importance of stimulus redundancy in the processing of hierarchically organised stimuli of humans and capuchin monkeys. Therefore, a set of redundant and non-redundant stimuli based on Garner's patterns (1974) was produced (see Figure 9). Moreover, across the five experiments, few manipulations occurred in the stimuli sets in order to evaluate, along with the effect of redundancy on global-local processing, also the effect played by

other factors like the requirement of a grouping also at local level, the visual angle, the density and numerosity of local elements. The rationale of all these manipulations will be explained in a dedicated session before each experiment.

### **3.2 EXPERIMENT 1**

In this experiment, hierarchical stimuli on the basis of Garner's dot-patterns (1974) were assembled. At each level of processing, stimuli featured a different shape; however, the degree of redundancy, either high or low, was kept constant across levels. The use of Garner's dot-patterns also allowed us to address another important issue in relation to monkeys' visual cognition. It is possible that a selective requirement to group at the global level can be the main explanation of monkey local bias because they may differ from humans in their ability to group (Fagot & Deruelle 1997; Spinozzi *et al.* 2003). Therefore, in this experiment, hierarchical stimuli with dot-patterns that required grouping at both global and local level of the stimuli were constructed. A similar procedure was used before in human literature albeit for different theoretical reasons. In fact, Navon (1977) in his influential work he ran an experiment based on a same-different discrimination task where stimuli featured clusters of geometrical shapes arranged to form a geometrical global shape. Therefore, each stimulus featured three levels: geometrical shapes (first level) grouped in clusters to form local configurations (second level) and a global configuration (third level) formed by the arrangement of the local clusters. So, in the present experiment, this paradigm was extended to the comparative context. The experiment rested on the rationale that if a local advantage is observed in capuchin monkeys even in conditions featuring grouping also at the local level, then monkey local advantage cannot be explained by

deficient grouping skills in monkeys. In fact, traditional hierarchical stimuli characterised by solid forms at the local level do not have this additional grouping requirement. Therefore, they may induce monkeys to preferentially attend that level. In fact, as discussed in the introduction, if monkey local bias depends on a lack, displayed by this species, to group elements into a coherent whole, the requirement to group also at the local level should significantly affect their typical local bias.

### **3.2.1 Method**

#### ***3.2.1.1 Participants***

Five adult tufted capuchin monkeys and 12 humans were tested in this experiment. The monkey sample included 1 female (Pippi) and 4 males (Gal, Patè, Rubens and Vispo). At the time of the beginning of this experiment, three monkeys (Pippi, Gal and Patè) had been previously tested with tasks involving hierarchical stimuli. The other two subjects (Rubens and Vispo) had never been presented with hierarchical visual patterns before. However, they were previously trained with the MTS procedure using non-hierarchical visual stimuli.

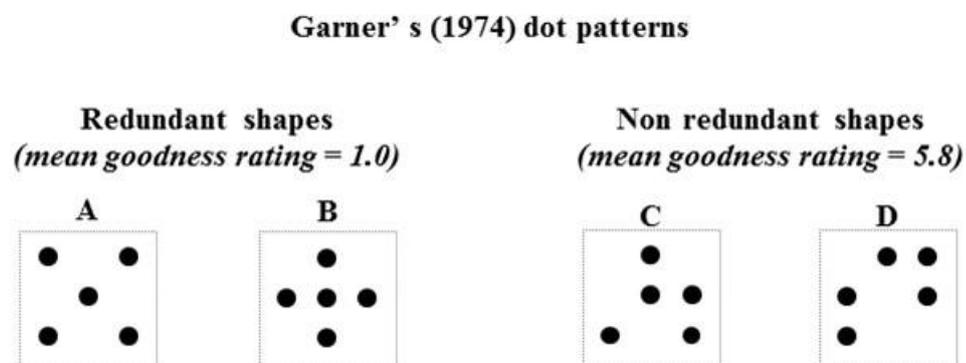
The human sample included 12 volunteers (6 males and 6 females ranging in age from 18 to 37 years). The requirements to take part in the experiment are described in Chapter II.

#### ***3.2.1.2 Stimuli and Procedure***

The set of hierarchical stimuli included 8 compound dot-patterns. The stimuli were created using Microsoft PowerPoint and appeared as white shapes on a black background. Each compound pattern consisted of 25 dots arranged in five clusters of five dots each. The five dots of each cluster were arranged to form a pattern like those described by Garner (1974), which featured the local level of the stimulus. Then, these five clusters were spatially arranged, again on

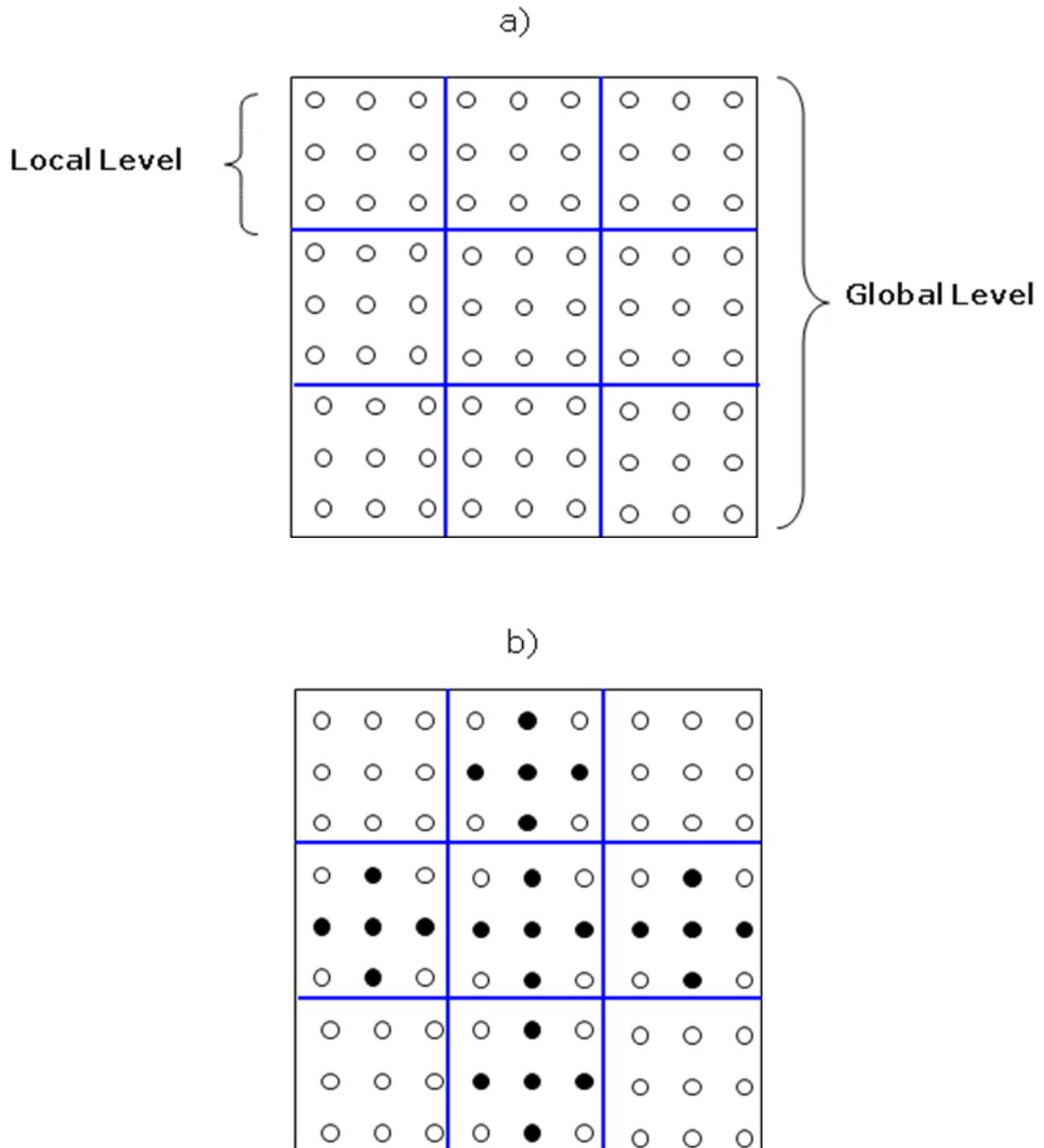
the basis of Garner dot-patterns (1974), to create a large configuration which featured the global level of the hierarchical stimulus.

The configurations used for the global and the local levels of the stimuli were derived from two highly redundant (A and B) and two Non-Redundant (C and D) dot-patterns from the stimulus set proposed by Garner (1974). Garner's stimulus set is presented in Figure 10.



*Figure 10. Redundant and non-redundant dot-patterns according to Garner (1974) utilized to produce the redundant and non-redundant dot-stimuli used in Experiment 1.*

The local dot configurations were created by using a 3 x 3 dot matrix, in which each column and each row had at least one dot involved in representing the local shape (see Figure 11). Then, the matrix was repeated 3 times in the two orthogonal directions in order to obtain a new matrix featuring 9 x 9 dots. Therefore, the global configuration was made up by inserting at least one local cluster, obtained by the small matrix, in one of the three rows and columns.



*Figure 11. Example of stimulus creation. a) Matrix adopted to create the stimuli employed in Experiments 1 and 2. b) Example of the stimulus creation.*

The global configuration always measured 5.7 cm x 5.7 cm whereas the local clusters measured 1.38 cm x 1.38 cm. Each dot measured 0.22 cm of diameter. At a distance of about 30 cm, these stimuli featured about 11° of visual angle at global level and 2.6° of visual angle at the local level.

The stimuli, converted in bitmaps, were presented using the experimental set-up described in Chapter II.

Figure 12 depicts the two sets of hierarchical stimuli used in this experiment. In the stimulus label, the capital and lower-case letters indicate the forms used at the global and local levels respectively.

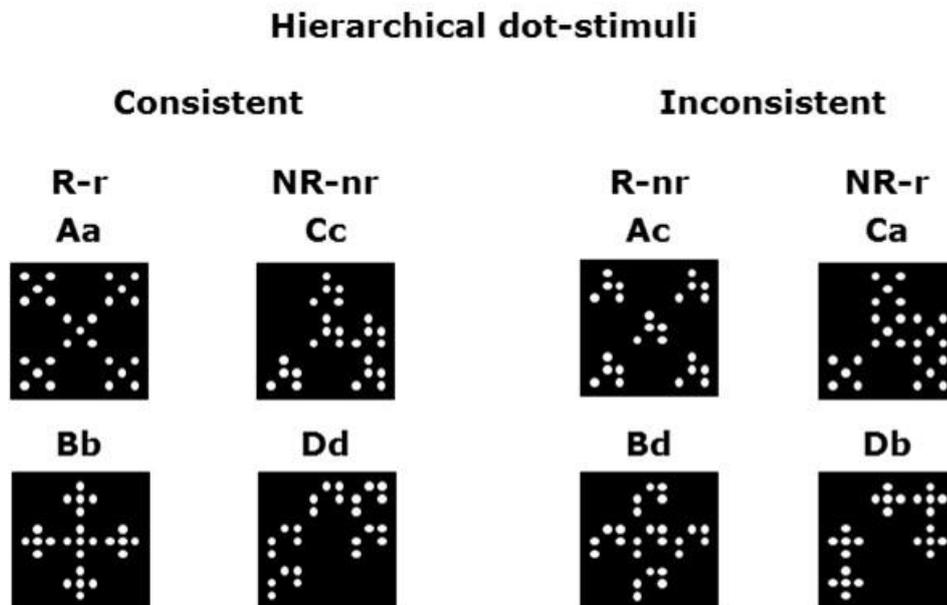


Figure 12. Stimulus set adopted in Experiment 1.

The stimuli were either consistent or inconsistent in shape and redundancy.

(a) The *Consistent sub-set* featured stimuli in which the shape at the local level was the same of the shape at the global level, therefore the level of redundancy was identical across levels (i.e., R-r and NR-nr). It included 4 compound dot-patterns divided in two subsets of hierarchical dot-stimuli: the *redundant subset*, which included 2 stimuli featuring redundant (R-r) shapes at both levels of processing; and the *non-redundant subset*, which consisted of 2 stimuli featuring non-redundant (NR-nr) shapes at both levels of processing. The identity of the global shape was always the same of the identity of the local shape.

(b) The *Inconsistent sub-set* featured stimuli in which the shape at the local level was always different from the shape at the global one. Therefore, stimuli could be either redundant at the local level but non-redundant at the global one (R-nr), or vice versa (NR-r). It included 4 compound dot-patterns of which 2 were redundant at global level and non-redundant at the local one (R-nr) and 2 were non redundant at global level but redundant at the local one (NR-r).

An identity Matching-To-Sample procedure was used for all the five experiments. Full details about the MTS procedure are discussed in the dedicated session in Chapter II.

Figure 13 depicts an example of global and local trials with hierarchical dot-patterns.

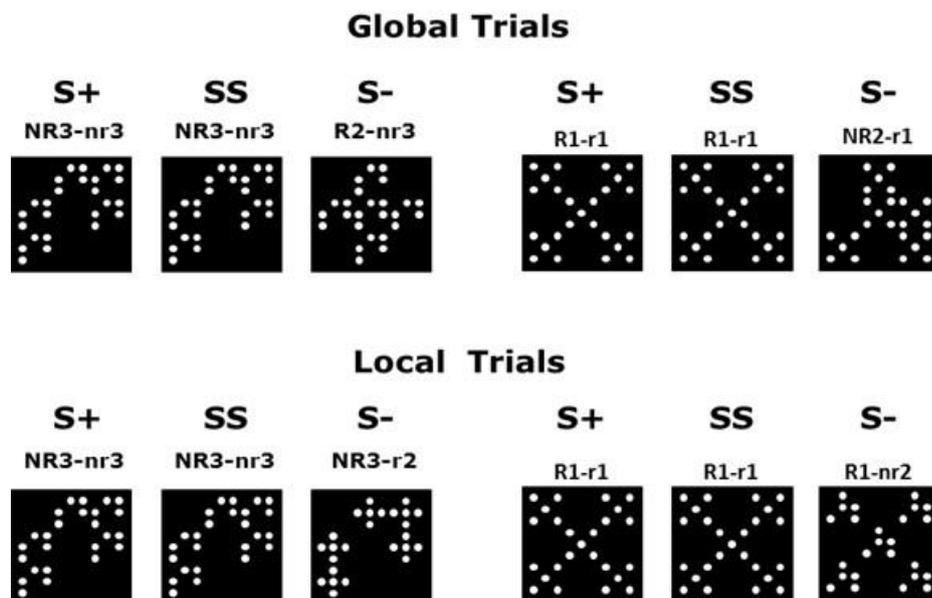


Figure 13. Examples of global and local trials using the MTS task with hierarchical dot-patterns. The figure depicts matching trials between non-redundant (left) and redundant (right) stimuli.

There were two identity-matching conditions: in the global-matching condition, the correct comparison stimulus was identical to the sample stimulus whereas the non-correct comparison stimulus

differed from the sample only at the global level. In the local-matching condition, the situation was reversed (i.e., S+ was identical to the sample; S- differed from the sample only at the local level).

Each monkey performed 8 sessions, one session per day for a total of 192 trials. Each session featured 24 testing trials divided as follows: 6 redundant consistent (R-r), 6 non-redundant consistent (NR-nr), 6 redundant at the global level but non-redundant at local (R-nr) and 6 non-redundant at the global level and redundant at local one (NR-r). In this and in the following experiments, before each experimental session, 9 practice identity-MTS trials were administered using non-hierarchical stimuli (e.g., simple white forms on a black background). These trials were important to determine the MTS performance of the subject before the task. The criterion to be reached before administering the testing session was of at least 8 correct responses out of 9.

Each human participant performed all 192 trials in one session featuring all stimuli randomly intermixed. The session featured 96 consistent (R-r and NR-nr), and 96 inconsistent (R-nr and NR-r) stimuli. The trials involving inconsistent stimuli featured 48 matches between redundant and 48 matches between non-redundant patterns. Whereas the trials involving inconsistent stimuli featured 96 matches where the redundancy occurred only at one level of processing (i.e., 48 R-nr and 48 NR-r). Within each sub-set, there were 48 global trials and 48 local trials.

### 3.2.2 Results Experiment 1

Results are reported for consistent and inconsistent stimuli separately.

#### 3.2.2.1 Consistent Stimuli

##### 3.2.2.1.1 Accuracy

Figure 14 displays the percentages of correct responses observed in the different trials with the two species. Moreover, individual percentages of correct responses recorded for each monkey are presented in Table 1.

*Table 1. Mean individual percentages of correct responses recorded for each animal with Consistent stimuli of Experiment 1*

Subjects	Local		Global	
	NR-nr	R-r	NR-nr	R-r
<b>Gal</b>	91.7	95.8	83.3	79.2
<b>Patè</b>	91.7	91.7	66.7	70.8
<b>Pippi</b>	87.5	87.5	87.5	79.2
<b>Rubens</b>	75.0	79.2	79.2	58.3
<b>Vispo</b>	79.2	79.2	79.2	79.2

A 2 (Level of Processing)  $\times$  2 (Redundancy)  $\times$  2 (Species) mixed model ANOVA was carried out on the mean percentage of correct responses recorded for the two species with consistent stimuli. The ANOVA revealed significant main effects for Species,  $F(1, 15) = 66.61$ ,  $p < .001$ ,  $\eta_p^2 = .998$ , and Level of Processing,  $F(1, 15) = 12.905$ ,  $p < .01$ ,  $\eta_p^2 = .462$ . Therefore it suggests that, overall, humans performed at a higher level of accuracy ( $M = 96.3\%$ ) than monkeys ( $M = 81.1\%$ ) and that, overall, local trials ( $M = 91.4\%$ ) were performed better than global trials ( $M = 86.0\%$ ). Furthermore,

the analysis highlighted the following significant interactions: Species x Level of Processing,  $F(1, 15) = 7.752, p < .05, \eta_p^2 = 0.341$ , Species by Redundancy,  $F(1, 15) = 5.817, p < .05, \eta_p^2 = 0.279$ , and Species x Level of Processing by Redundancy,  $F(1, 15) = 5.597, p < .05, \eta_p^2 = .272$ .

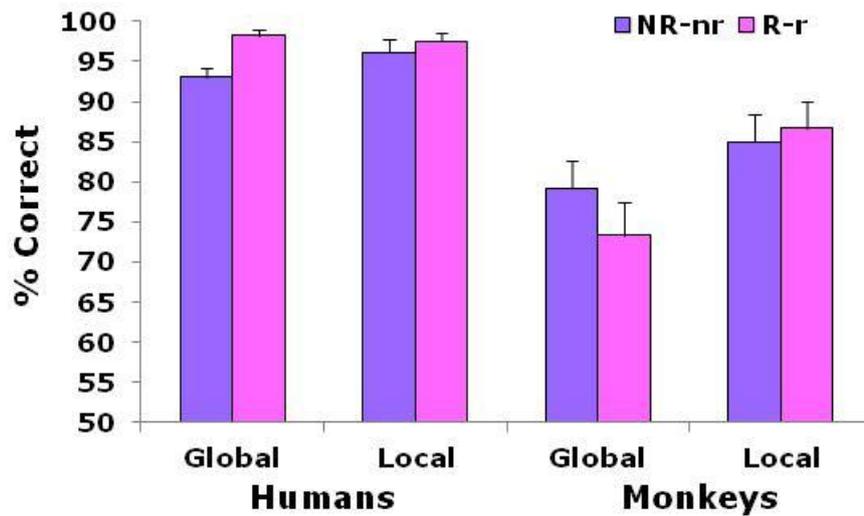


Figure 14. Mean percentages of correct responses recorded for both species in the different trials of Experiment 1 with Consistent stimuli. Error bars represent one Standard Error.

Pair-wise comparisons ( $t$ -tests, with Bonferroni correction) revealed that human subjects, in the global trials, matched redundant stimuli with a higher level of accuracy than non-redundant ones, R-r,  $M = 98.3%$ , NR-nr,  $M = 93.1%$ ;  $t(11) = 3.804, p < .01$ . Pair-wise comparisons between the percentage of correct responses registered for the redundant and non-redundant stimuli across local and global trials revealed that monkeys showed a significant local advantage with the redundant stimuli, *Redundant stimuli*: local trials,  $M = 86.7%$ ; global trials,  $M = 73.3%$ ;  $t(4) = 3.29, p = .03$ . However, after applying the Bonferroni correction for 4 comparisons ( $\alpha = 0.0125$ ) this result does not remain significant. No further significant

results were found. Although with Bonferroni correction this last results does not remain significant, it suggests that monkeys could potentially benefit from stimulus redundancy and that this benefit could be evident in particular in the local trials. The possible reasons underlying these results are further discussed below taking into consideration the whole study (see Par. 3.7).

### 3.2.2.1.2 Response Times

A 2 (Level of Processing) x 2 (Redundancy) repeated measures ANOVA conducted on the latency registered with consistent stimuli, filtered per correct answers only, revealed a significant interaction Level of Processing by Redundancy,  $F(1, 11) = 5.916, p < .05, \eta_p^2 = .350$ . As it was observed in the accuracy data, post-hoc comparisons revealed that, in the global trials, humans processed redundant stimuli faster than non-redundant ones, R-r,  $M = 1326.1$  ms; NR-nr,  $M = 1616.3$  ms;  $t(11) = 2.342, p < .05$ .

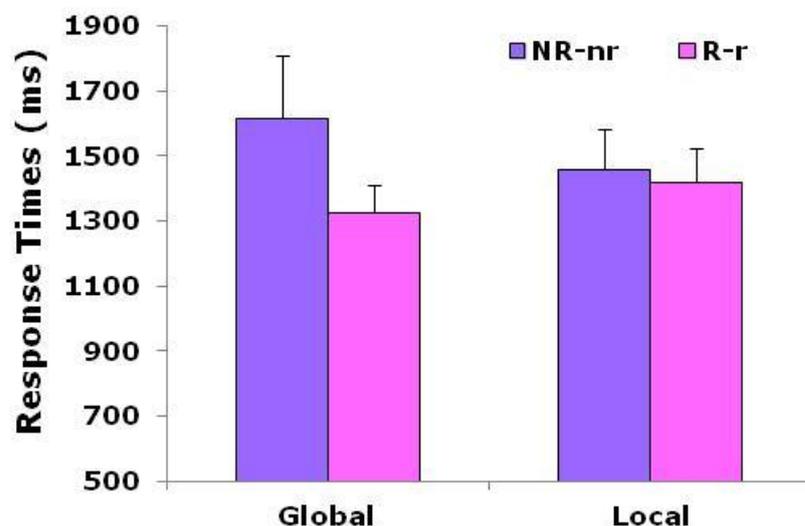


Figure 15. Mean RTs (ms) recorded for humans in the different trials of Experiment 1 with Consistent stimuli. Error bars represent one Standard Error.

### 3.2.2.2 Inconsistent Stimuli

#### 3.2.2.2.1 Accuracy

Figure 16 depicts the percentages of correct responses observed in the different trials for the two species. Moreover, individual percentages of correct responses recorded with each monkey are presented in Table 2.

Table 2. Mean individual percentages of correct responses recorded for each monkey with Inconsistent stimuli of Experiment 1

Subjects	Local		Global	
	NR-r	R-nr	NR-r	R-nr
<b>Gal</b>	79.2	87.5	79.2	83.3
<b>Patè</b>	79.2	95.8	75	66.7
<b>Pippi</b>	100	87.5	83.3	87.5
<b>Rubens</b>	83.3	70.8	70.8	83.3
<b>Vispo</b>	87.5	70.5	66.7	62.5

A 2 (Level of Processing) X 2 (Redundancy) X 2 (Species) mixed model ANOVA was carried out on the percentage of correct responses observed in trials featuring inconsistent stimuli with a high degree of redundancy at one level of processing only (i.e., R-nr and NR-r). The analysis revealed significant main effects for Species,  $F(1, 15) = 40.72, p < .001, \eta_p^2 = 0.731$ , and Level of Processing,  $F(1, 15) = 10.87, p < .01, \eta_p^2 = .420$ . Therefore it indicates that, overall, humans performed better ( $M = 95.4\%$ ) than monkeys ( $M = 80.0\%$ ) and that, in general, local trials were performed better ( $M = 90.0\%$ ) than global ones ( $M = 85.4\%$ ). The analysis revealed also the following interactions: Species by Level of Processing,  $F(1, 15) = 7.146, p < .05, \eta_p^2 = 0.323$ , and Species by Level of Processing by Redundancy,  $F(1, 15) = 4.649, p < .05, \eta_p^2 = .237$ .

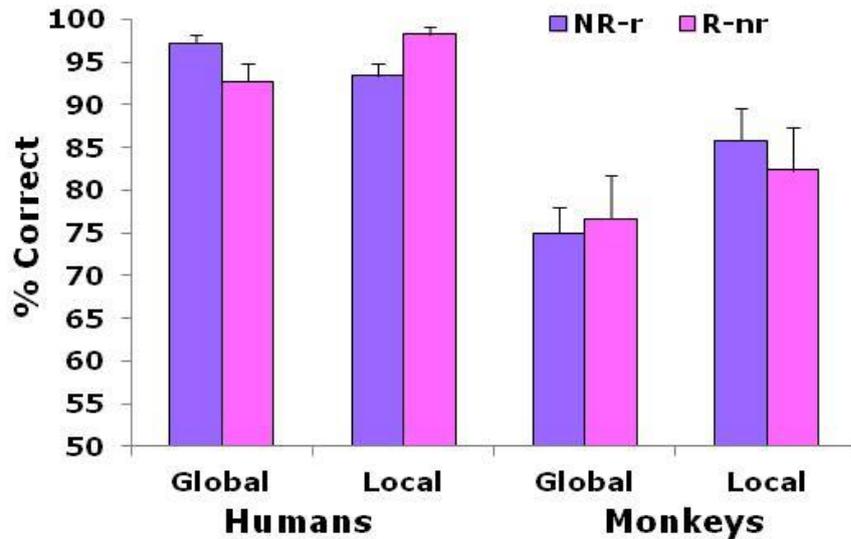


Figure 16. Mean percentages of correct responses recorded for both species in the different trials of Experiment 1 with Inconsistent stimuli. Error bars represent one Standard Error.

Pair-wise comparisons (*t*-tests with Bonferroni correction) revealed that, in the local trials, humans' performance was better when the stimuli featured local, non-redundant configurations (R-nr,  $M = 98.3\%$ ) than when they featured local, redundant configurations (NR-r,  $M = 93.4\%$ ),  $t(11) = 3.924$ ,  $p < .01$ . Moreover, humans showed a tendency towards a local advantage for stimuli redundant at global level and non-redundant at local level, R-nr: local trials,  $M = 98.3\%$ , global trials,  $M = 92.8\%$ ,  $t(11) = 2.68$ ,  $p < .05$ , ns with Bonferroni correction. Conversely, humans showed a tendency towards a global advantage for stimuli non-redundant at global level and redundant at local level, NR-r: local trials,  $M = 93.4\%$ , global trials,  $M = 97.5\%$ ,  $t(11) = 2.93$ ,  $p < .05$  ns with Bonferroni correction.

In monkeys, accuracy levels for R-nr and NR-r stimuli were similar in both local (R-nr,  $M = 82.4\%$ , NR-r,  $M = 85.8\%$ ) and global trials (R-nr,  $M = 76.7\%$ ; NR-r,  $M = 75.0\%$ ).

### 3.2.2.2.2 Response Times

Only latencies for correct responses were included in this analysis.

A 2 (Level of Processing) x 2 (Redundancy) repeated measures ANOVA was carried out on the latencies recorded with inconsistent stimuli and featuring a high level of redundancy at one level of processing only. The analysis did not reveal any significant main effect, but it revealed a significant interaction Level of Processing by Redundancy,  $F(1, 11) = 19.212$ ,  $p = .001$ ,  $\eta_p^2 = .636$ .

Post-hoc comparisons ( $t$ -test with Bonferroni correction) revealed that global trials ( $M = 1389.5$  ms) were processed faster than local ones ( $M = 1549.1$  ms) when stimuli were non-redundant at global level but redundant at local ones,  $t(11) = 5.573$ ,  $p < .001$ . However, global trials ( $M = 1638.9$  ms) tended to be processed slower when the local ones ( $M = 1383.3$  ms) when stimuli were redundant at global level but non-redundant at local level,  $t(11) = 2.759$ ,  $p < .05$ , ns with Bonferroni correction. Furthermore, when the task required global processing, trials featuring non-redundant shapes at the global level but redundant at local were processed faster than trials featuring redundant shapes at global level but non-redundant at local level, NR-r,  $M = 1389.5$  ms; R-nr,  $M = 1638.8$  ms;  $t(11) = 3.037$ ,  $p < .05$ . Conversely, when the task required local processing, trial featuring non-redundant shapes at the global level but redundant at local were processed slower than trials featuring redundant shapes at global but non-redundant at local, NR-r,  $M = 1549.1$ ; R-nr,  $M = 1383.3$ ;  $t(11) = 4.485$ ,  $p = .001$ .

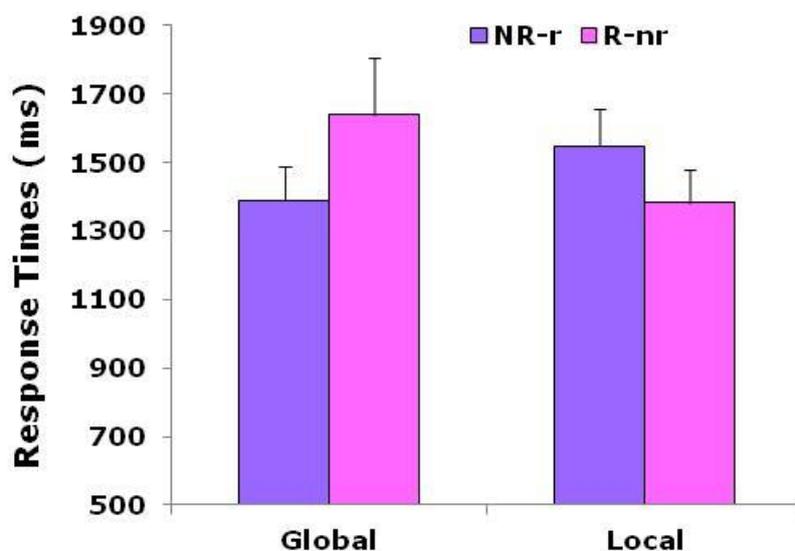


Figure 17. Mean of RTs recorded for humans in the different trials of Experiment 1 with Inconsistent stimuli. Error bars represent one Standard Error.

### 3.2.3 Discussion Experiment 1

The results of this first experiment indicate a general better performance in humans and a higher accuracy level for local processing in capuchins, which has been repeatedly observed in previous literature with this species (Spinozzi *et al.* 2003). The results of the analyses carried out to disentangle the complex pattern of interactions obtained for the two species under different conditions is more informative. As was done with the results, the two conditions will be discussed separately.

#### 3.2.3.1 Consistent Stimuli

The most interesting results emerged under this condition. In fact, in this condition, it is possible to unambiguously look at the role played by stimulus redundancy and how it interacts with the level of processing in the two species. The results obtained with capuchins revealed that monkeys tended to show a local advantage when

redundant stimuli had to be matched. Indeed, an inspection of Figure 14 indicates that monkeys' performance for redundant stimuli was higher in the local trials compared to the global trials. However, once applied the Bonferroni correction, this difference is not significant. This result, although not very strong, is still interesting, as it suggests that there could be a potential sensitivity to redundancy of shape in non-human primates.

However, this experiment highlighted that in humans redundancy plays a role in generating a higher and faster level of performance when two redundant stimuli have to be matched. However, this was true only for the global trials, suggesting that humans benefit from a high redundancy in the level of processing which is usually detected better by them. RT data confirmed this result revealing faster responses for redundant stimuli but only for global trials. On the other side, both accuracy and RT data on global-local trials did not reveal any significant advantage for either level of processing.

If possible, a similarity in the effect of redundancy in the two species can be found in the fact that both species proved sensitive to stimulus redundancy and this sensitivity was even more evident when the level that had to be processed was that one typically considered easier to attend to in that particular species. Therefore, the global level in humans and the local level in capuchin monkeys.

With regard to the level of processing, monkeys revealed a tendency in processing local trials better than global ones albeit this difference only approached the significance ( $p = .07$ ). However, humans did not display any advantage.

### ***3.2.3.2 Inconsistent stimuli set***

The analysis of results of trials featuring inconsistent stimuli produced a much more complex scenario. In fact, with inconsistent stimuli, which were characterised by the presence of redundancy only

at one level of stimulus structure, an overall difference in accuracy was observed once again between the two species. Humans performed better than monkeys in all conditions. However, with humans, a complex pattern of results was found. With regard to the factor redundancy, non-redundant local elements but redundant global shape (R-nr) enhanced humans' matching performance at local trials, whereas during global trials no difference was found between redundant and non-redundant stimuli. Furthermore, global trials were processed faster than local ones when stimuli were non-redundant at the global level but redundant at the local one (NR-r). Local trials were processed faster than global ones when stimuli were redundant at the global level but non-redundant at the local level (R-nr). This indicates a generally higher level of performance when non-redundant shapes had to be matched at each level of processing. Moreover, human participants showed a marginally significant global advantage when a high degree of redundancy featured the local shapes of the stimuli but not the global one (NR-r stimuli), but they tended to exhibit a local advantage when redundant shapes featured the global aspect of the patterns and so local elements where non-redundant (R-nr stimuli). Thus, with inconsistent stimuli, it seems like non-redundant stimuli were facilitating the global-local recognition at each level of processing. Although there is no literature specifically aimed at assessing the role played by stimulus redundancy in global-local processing, this result does not seem in agreement with the notion that redundant shape can ease the visual processing, notion well acknowledged in human literature (Garner, 1970; 1974).

Capuchins showed a different pattern of results. Coherently with previous literature, monkeys had a tendency to perform better in the local than in the global trials, but this tendency was independent of the different degree of redundancy featured by the global or the local aspects of the stimuli. Furthermore, no effect from stimulus redundancy was found.

However, it must be considered that in this experiment the inconsistency of the stimuli in terms of redundancy was confounded by the inconsistency of the stimuli in terms of the identity of the shapes presented as the two levels of the hierarchical stimulus. In other words, there were two different degrees of inconsistency that may have affected the general results. Therefore, it was considered important to carry out a second experiment specifically focused on the analysis of redundancy.

### **3.3 EXPERIMENT 2**

In Experiment 1, dot-patterns which could be either consistent for both levels of redundancy and shape or inconsistent for both levels of redundancy and shape were used. This means that the consistent set stimuli featured the same stimuli at both global and local level but they also featured the same level of redundancy at both levels of processing. Whereas the inconsistent stimuli featured always different stimuli at both global and local level and they also featured different level of redundancy (i.e., redundant or non-redundant shape) at both levels. Therefore, this kind of stimuli did not allow to disentangle the possible role played by the redundancy from the possible role played by the shape consistency as these two factors would necessary be (or not be) presented together. In addition, in the inconsistent set, the stimuli featured redundant and non-redundant shapes together, making more difficult to isolate the role played by redundancy itself.

In order to assess the role played by shape redundancy independently from the role played by shape consistency, a second experiment was carried out. Hence, in this experiment, one variable was kept constant by using only inconsistent stimuli. In this way, the role of stimulus redundancy could be assessed independently from

other stimulus characteristics. Moreover, each stimulus always featured the same level of redundancy at both levels of processing, making it easier to pinpoint the role this factor played in monkeys and humans pattern recognition.

### **3.3.1 Method**

#### ***3.3.1.1 Participants***

The monkey sample was the same as in experiment one.

In the present experiment, it was not possible to test the same human participants who took part in Experiment 1. Therefore, a new group of participants was recruited. It consisted of 12 volunteers, 6 males and 6 females. The requirements to take part in the experiment are described in Chapter II.

#### ***3.3.1.2 Stimuli and Procedure***

The set of hierarchical stimuli comprised 24 compound dot-patterns (Figure 18). They were similar to those adopted in Experiment 1. However, in this second experiment the stimuli were always inconsistent in shape but consistent in level of redundancy. This allowed us to produce stimuli featuring always a different shape at global and local level but featuring always the same degree of redundancy at both global and local level.

According to Garner, there are only two dot-patterns having the highest level of redundancy (rated = 1), these patterns are described in Figure 10 as pattern A (an X) and pattern B (a cross). However, with only two redundant patterns it was impossible to produce the right number of combinations necessary to present different global and local trials. Therefore, it was decided to adopt as redundant shapes, those patterns featuring a level of redundancy rated as 2.2. In this way, it was possible to use up to 4 redundant dot-patterns and

produce a sufficient number of global-local trials. Two subsets of hierarchical dot-stimuli were created:

a) The *redundant* subset, featuring 12 redundant stimuli at both global and local levels (i.e., the R-r subset), with a mean redundancy rating = 2.2.

b) The *non-redundant* subset, featuring 12 non-redundant stimuli at both global and local levels (i.e., the NR-nr subset) with a mean redundancy rating = 5.8.

### Garner's (1974) dot patterns

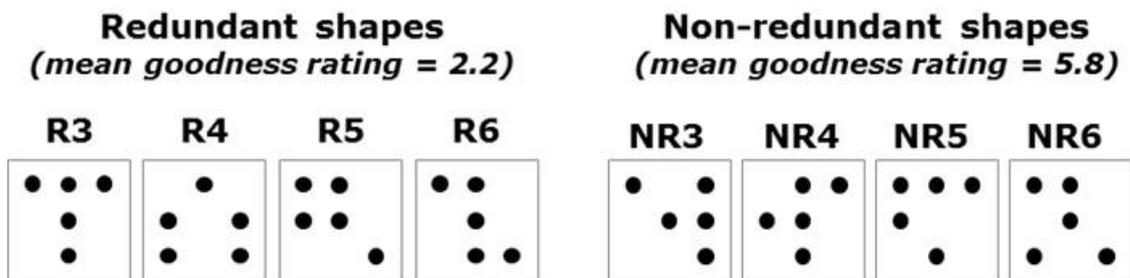


Figure 18. Medium-high redundant and non-redundant dot-patterns according to Garner (1974) used to produce the redundant and non-redundant dot stimuli in Experiment 2.

In both sets (R-r, NR-nr), stimuli featured always a different shape at global and local level (e.g., R5-r3 refers to a global redundant "R3" shape made up of five local redundant "r4" shapes).

## Hierarchical dot stimuli

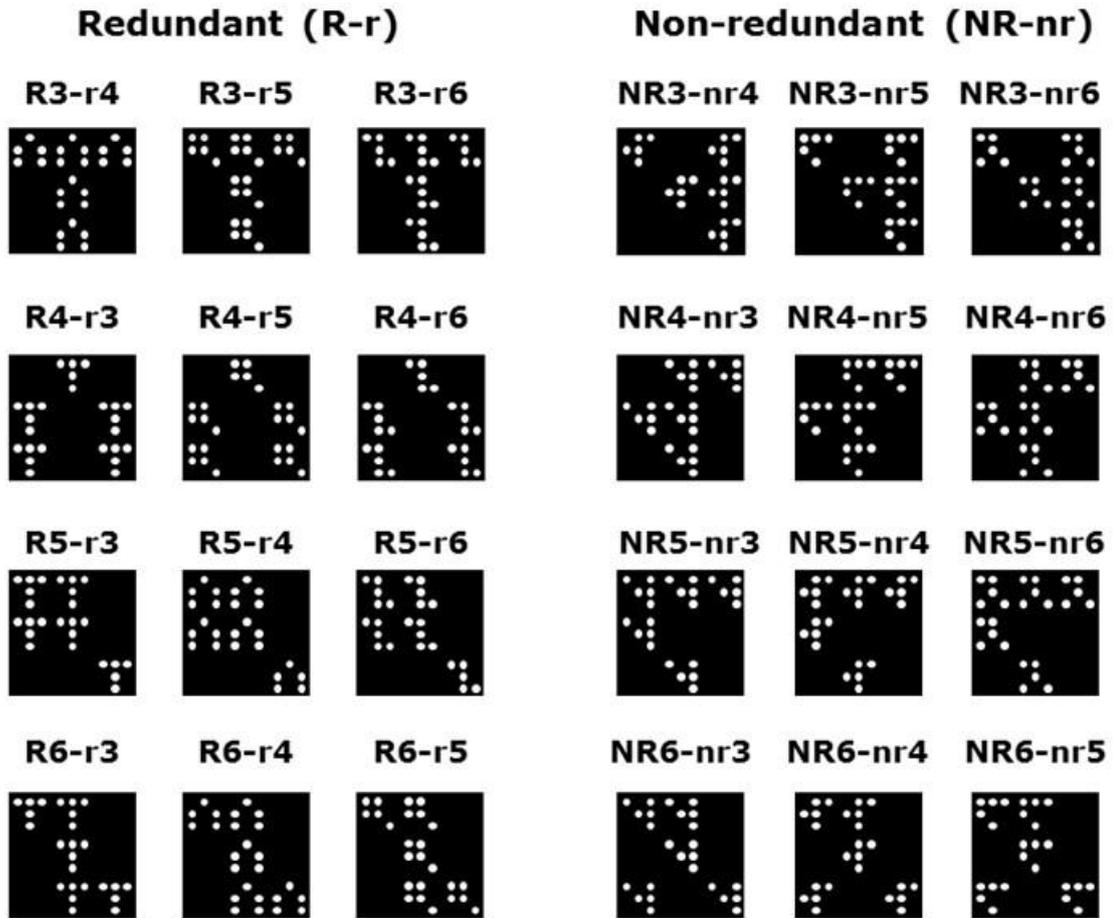


Figure 19. Stimulus set used in Experiment 2 (adapted from De Lillo, Palumbo, Spinozzi, Giustino, 2012).

Experimental design, task and procedure were all the same as described in Experiment 1.

Each monkey performed 1 daily session including all the 24 hierarchical stimuli shown in Figure 19, with each stimulus being presented once as sample. Every session featured 12 redundant (R-r) and 12 non-redundant (NR-nr) trials, in which the sample stimulus featured either non-redundant (e.g., NR6-nr5) or redundant (e.g., R6-r5) shapes at both levels of processing. Each session was blocked for either local or global trials and included redundant and non-redundant sample stimuli randomly intermixed.

Each human participant performed one session comprising 192 trials (96 global trials and 96 local trials). Within the global or local matching trials, 48 trials featured redundant shapes and 48 trials featured non-redundant shapes as sample stimuli, randomly intermixed.

### 3.3.2 Results Experiment 2

#### 3.3.2.1 Accuracy

Figure 20 depicts the percentages of correct responses recorded in Experiment 2. Moreover, individual percentages of correct responses recorded with each monkey in Experiment 2 are presented in Table 3.

*Table 3. Mean individual percentages of correct responses recorded for each monkey in Experiment 2*

<b>Subjects</b>	<b>Local trials</b>		<b>Global trials</b>	
	<b>NR-nr</b>	<b>R-r</b>	<b>NR-nr</b>	<b>R-r</b>
<b>Gal</b>	79.2	83.3	70.8	72.9
<b>Patè</b>	81.3	79.2	62.5	72.9
<b>Pippi</b>	72.9	87.5	79.2	70.8
<b>Rubens</b>	85.4	85.4	75.0	77.1
<b>Vispo</b>	81.3	81.3	64.6	81.3

A 2 (Level of Processing) × 2 (Redundancy) × 2 (Species) mixed model ANOVA was carried out on the mean percentage of correct responses recorded with the two species. The ANOVA revealed the following significant main effects: Species,  $F(1, 15) = 122.24, p < .001, \eta^2_p = .89$ , Level of Processing,  $F(1, 15) = 21.31, p < .001, \eta^2_p = .59$ , and Redundancy,  $F(1, 15) = 15.15, p < .01, \eta^2_p = .50$ ; *R-r*,  $M = 88.1\%$ ; *NR-nr*,  $M = 85.1\%$ . Therefore, the analysis of variance

proved that in addition to a general better performance displayed by humans ( $M = 96.0\%$ ) in comparison to *Monkeys* ( $M = 77.2\%$ ), overall local trials were processed better ( $M = 88.8\%$ ) than global one ( $M = 84.4\%$ ). Furthermore, redundant stimuli were processed better ( $M = 88.1\%$ ) than non-redundant ones ( $M = 85.1\%$ ). There were no significant interactions. The lack of interaction between redundancy and species suggests that both species were more accurate in processing redundant stimuli than non-redundant ones (*Monkeys*: R-r,  $M = 79.2\%$ ; NR-nr  $M = 75.2\%$ ; *Humans*: R-r,  $M = 97.0\%$ ; NR-nr,  $M = 95.0\%$ ). Analogously, the lack of interaction redundancy by level of processing suggests a lack of relationship between redundancy and the level of processing in this experiment. However, the interaction between Level of Processing and Species was significant,  $F(1, 15) = 23.03, p < .001, \eta^2_p = .61$ .

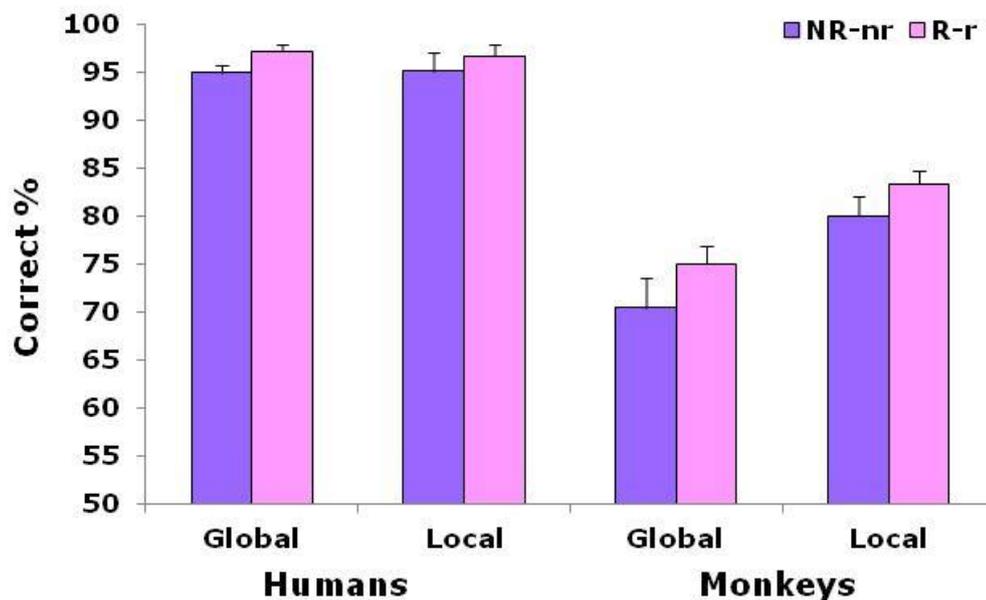


Figure 20. Mean percentages of correct responses recorded for both species in the different trials of Experiment 2. Error bars represent one Standard Error.

Planned comparisons (paired sample  $t$ -test) carried out to understand this last significant interaction showed that monkeys performed the local trials significantly better than the global ones, Local trials:  $M = 81.7\%$ ; Global trials:  $M = 72.7\%$ ,  $t(4) = 7.616$ ,  $p < .005$ . The same kind of effect was not observed with humans, Global trials,  $M = 96.1\%$ ; Local trials,  $M = 95.9\%$ , ns (adapted from De Lillo *et al.*, 2012).

### 3.3.2.2 Response Times

A 2 (Level of Processing)  $\times$  2 (Redundancy) ANOVA was performed on the mean of RTs, filtered per correct answer, recorded with humans. The ANOVA revealed a significant main effect for the factor Redundancy,  $F(1, 11) = 39.83$ ,  $p < .001$ ,  $\eta^2_p = .78$ , suggesting that redundant stimuli ( $M = 1586.7$  ms) were processed faster than non-redundant ones ( $M = 1874.8$  ms) overall. Conversely, as found with the accuracy results, the factor Level of Processing did not prove significant (Global trials,  $M = 1757.4$  ms; Local trials,  $M = 1703.7$  ms; ns). The ANOVA also revealed a significant interaction between the factors Level of Processing and Redundancy,  $F(1, 11) = 8.33$ ,  $p < .05$ ,  $\eta^2_p = .43$ .

Planned comparisons ( $t$ -test) revealed that redundant stimuli were processed faster than non-redundant in both global, R-r,  $M = 1656.2$  ms; NR-nr,  $M = 1858.6$  ms;  $t(11) = 3.651$ ,  $p < .01$ , and local trials, R-r,  $M = 1517.2$  ms; NR-nr,  $M = 1890.2$  ms,  $t(11) = 7.013$ ,  $p < .001$ . However, the difference was sharper with local trials and this may explain the significant interaction (adapted from De Lillo *et al.*, 2012).

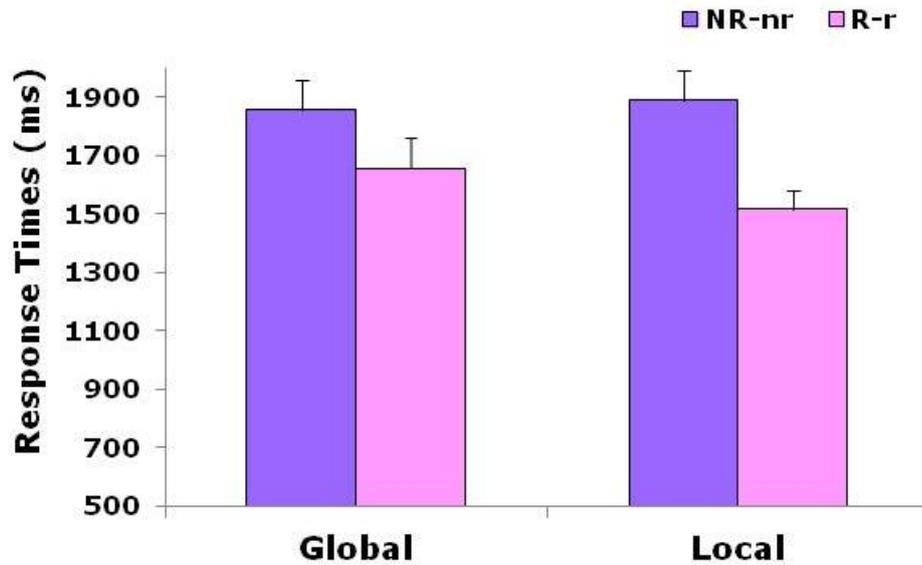


Figure 21. Mean RTs (ms) recorded for humans in the different trials of Experiment 2. Error bars represent one Standard Error.

### 3.3.3 Discussion Experiment 2

The results obtained with this experiment suggest that in both species the stimulus redundancy led to a significant benefit during the visual processing. No interaction species by redundancy was found suggesting that the beneficial effect elicited by the stimulus redundancy was equivalent in both species. Analogously, no interaction between redundancy and level of processing was found, suggesting that there was no relationship between these factors and therefore, that the effect of redundancy on the processing of hierarchical stimuli was not confined to a particular level of processing.

Previous findings proved that capuchins are sensitive to grouping cues like proximity, similarity of shape and orientation of local elements and to the internal spatial relationship between parts of the same stimulus (De Lillo *et al.*, 2007; Spinozzi *et al.*, 2009). All these properties contribute in the grouping abilities. However, the

possibility that monkeys' local advantage could persist even with stimuli requiring grouping at local level was never investigated before. This experiment, together with Experiment 1, demonstrated that capuchin monkeys' local advantage persists even when the monkeys have to process hierarchical stimuli that require grouping at the local level as well as the global one. These results indicate that monkeys' local advantage does not depend on a type of difficulty in grouping elements at the global level.

Experiments 1 and 2 were carried out with stimuli which required grouping at both levels of processing, they demonstrated that the local advantage typical of capuchin monkeys persists also in this condition. This finding suggests that monkeys do not have any particular difficulty in grouping elements into a whole and therefore, that this factor cannot be an explanation for their typical local advantage. However, since the hierarchical stimuli adopted in Experiment 1 and 2 had never been used before, it is important to verify whether or not the beneficial effects of redundancy could be present with stimuli more similar to those traditionally employed in studies of global-local processing, with local configurations featuring solid shapes (i.e., hierarchical pattern where grouping is required at global level only). For this reason, 2 further experiments were carried out. The aim of Experiment 3 and 4 was to assess the effect of stimulus redundancy on the global-local processing of humans and monkeys in conditions featuring the same shapes of Experiment 2 and 1 respectively. However, in Experiment 3 and 4 the local elements were depicted as solid lines rather than clusters of dots. This was done in order to produce stimuli analogous with the hierarchical stimuli typically used in previous studies on local-global processing.

### **3.4 EXPERIMENT 3**

In this experiment, the same patterns used in Experiment 2 were used, but the dots featuring each local element were connected in order to produce a local solid shape and therefore the requirement to group dots at the local level was removed. In this way, traditional hierarchical stimuli (like those adopted by Navon, 1977) were produced. However, stimulus shape was based on redundant and non-redundant patterns proposed by Garner (1974).

#### **3.4.1 Method**

##### ***3.4.1.1 Participants***

The monkey sample was the same as in previous experiments. The human sample was the same as in Experiment 2.

##### ***3.4.1.2 Stimuli and Procedure***

The stimuli were 24 hierarchical Navon-like patterns with five local elements. The shapes of the global and the local level of the hierarchical stimuli were the same as those used in Experiment 2 (see Figure 19), however, here the dots at the local level were connected by solid lines (see Figure 22). Experimental design, task and procedure were all the same as described in previous experiments.

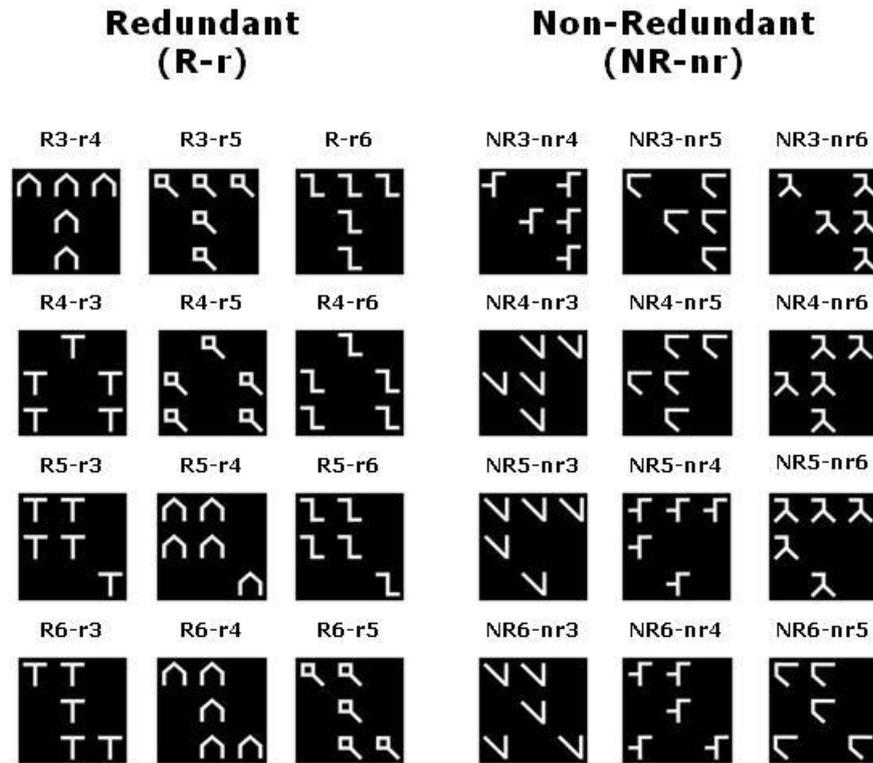


Figure 22. Stimulus set used in Experiment 3 (adapted from De Lillo et al., 2012).

### 3.4.2 Results Experiment 3

#### 3.4.2.1 Accuracy

Accuracy scores obtained by monkeys and humans for both redundant and non-redundant hierarchical stimuli, in the global and the local trials are presented in Figure 23. Moreover, individual percentages of correct responses recorded with each animal are presented in Table 4.

Table 4. Mean individual percentages of correct responses recorded for each monkey in Experiment 3

Subjects	Local		Global	
	NR-nr	R-r	NR-nr	R-r
<b>Gal</b>	79.2	95.8	77.1	75.0
<b>Patè</b>	81.3	83.3	70.8	72.9
<b>Pippi</b>	79.2	85.4	70.8	64.6
<b>Rubens</b>	85.4	91.7	72.9	79.2
<b>Vispo</b>	70.8	89.6	66.7	79.2

A 2 (Level of Processing)  $\times$  2 (Redundancy)  $\times$  2 (Species) mixed model Analysis of Variance was carried out. The ANOVA revealed significant main effects for all the three factors: Species,  $F(1, 15) = 151.82$ ,  $p < .001$ ,  $\eta^2_p = .91$ , Level of Processing,  $F(1, 15) = 34.86$ ,  $p < .001$ ,  $\eta^2_p = .70$ , and Redundancy,  $F(1, 15) = 16.59$ ,  $p = .001$ ,  $\eta^2_p = .53$ . Therefore, the ANOVA showed that, overall, humans ( $M = 96.9\%$ ) performed better than monkeys ( $M = 78.5\%$ ), that local trials ( $M = 91.5\%$ ) were processed better than global ones ( $M = 83.9\%$ ) and redundant stimuli ( $M = 89.7\%$ ) were processed better than non-redundant ( $M = 85.8\%$ ). Furthermore, all the two-way interactions were significant: Species by Level of Processing,  $F(1, 15) = 8.19$ ,  $p < .05$ ,  $\eta^2_p = .35$ , Species by Redundancy,  $F(1, 15) = 5.63$ ,  $p < .05$ ,  $\eta^2_p = .27$ , Level of Processing by Redundancy,  $F(1, 15) = 6.47$ ,  $p < .05$ ,  $\eta^2_p = .30$ . Finally, there was a significant three-way interaction Species by Level of Processing by Redundancy,  $F(1, 15) = 10.32$ ,  $p < .01$ ,  $\eta^2_p = .41$ .

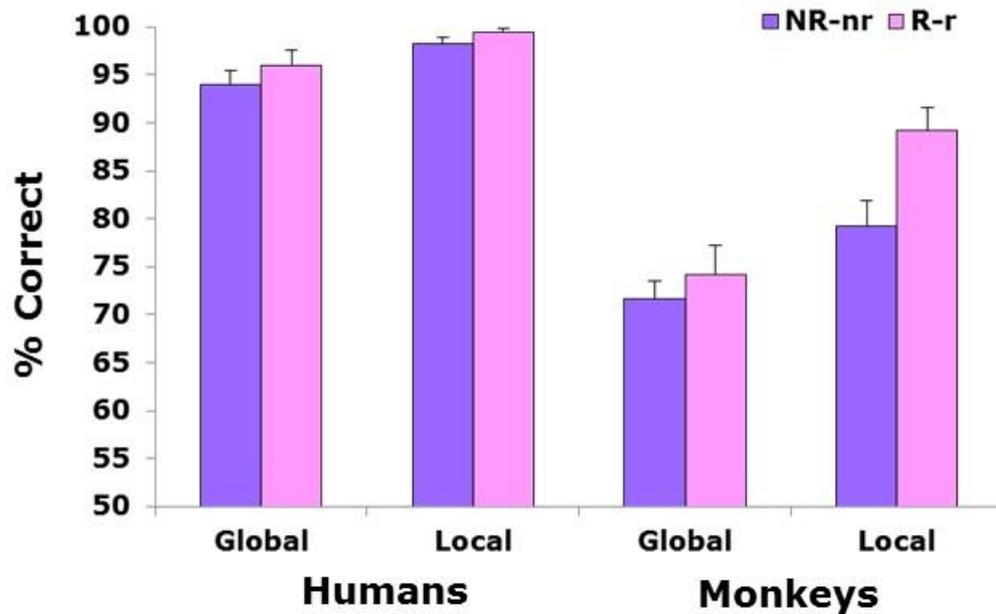


Figure 23. Mean percentages of correct responses recorded for both species in the different trials of Experiment 3. Error bars represent one Standard Error.

In order to explain this complex pattern of interactions, separate post hoc comparisons (paired sample *t*-tests) were performed on the data recorded with each species. Monkeys performed redundant stimuli better than non-redundant ones but only in the local trials, *Local trials*: R-r,  $M = 89.2\%$ ; NR-nr,  $M = 79.2\%$ ,  $t(4) = 3.057$ ,  $p < .05$ ; *Global trials*: R-r,  $M = 74.2\%$ ; NR-nr,  $M = 71.7\%$ , ns. These results suggest that in this experiment monkeys' local advantage emerged with both, redundant and non-redundant, stimuli.

In humans, in the global trials, the accuracy level observed with redundant stimuli was higher than that one observed with non-redundant ones, *Global trials*: R-r,  $M = 96.0\%$ ; NR-nr,  $M = 93.9\%$ ,  $t(11)=2.253$ ,  $p < 01$ . However, in the local trials, the performance difference between stimuli featuring a different degree of redundancy only approached the significance (*Local trials*: R-r,  $M = 99.5\%$ ; NR-nr,  $M = 98.3\%$ ,  $p = .06$ ; adapted from De Lillo *et al.*, 2012).

### 3.4.2.2 Response Times

A 2 (Level of Processing) x 2 (Redundancy) ANOVA was carried out on the response times, filtered per correct answer, recorded with humans. The ANOVA revealed a significant main effect for the factors Level of Processing,  $F(1, 11) = 47.12$ ,  $p < .001$ ,  $\eta^2_p = .811$ , and Redundancy,  $F(1, 11) = 54.83$ ,  $p < .001$ ,  $\eta^2_p = .833$ . Therefore it suggests that, overall, local trials ( $M = 1220.8$  ms) were processed faster than global ones ( $M = 1416.6$  ms) and that redundant stimuli ( $M = 1225.2$  ms) were processed faster than non-redundant one ( $M = 1412.2$  ms). The interaction between the two factors was not significant (adapted from De Lillo *et al.*, 2012).

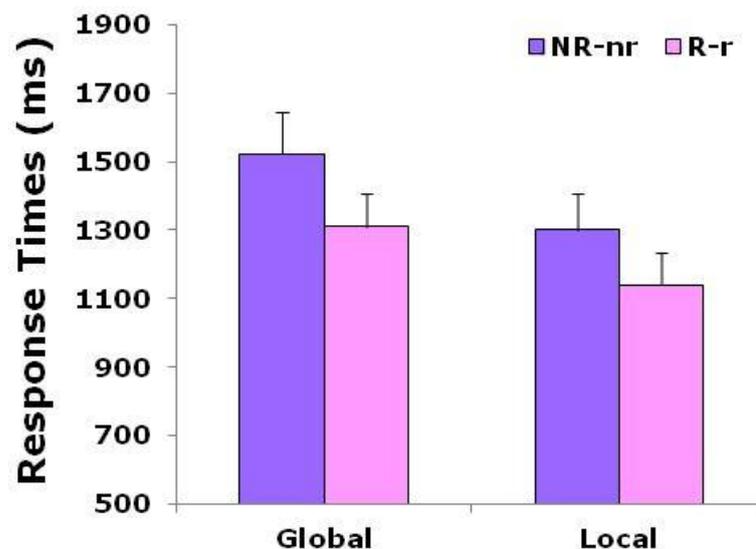


Figure 24. Means RTs (ms) recorded for humans in the different trials of Experiment 3. Error bars represent one Standard Error.

### 3.4.3 Discussion Experiment 3

In this experiment, in contrast with Experiment 1 and 2, stimuli which did not require grouping at local level were used. The results of this experiment confirmed the presence of an effect of redundancy in both species.

Monkeys displayed a positive effect coming from processing redundant stimuli in the local trials but not in the global trials, whereas with humans the same positive effect coming from stimulus redundancy was observed in the global but not in the local trials. However, the lack of interaction between the factors Redundancy and Level of Processing in the data relative to the response times shows an analogous increase in the speed of responding to redundant stimuli in both local and global trials. Therefore, it is possible to envisage that ceiling effect, due to the very high level of performance recorded from humans in this task, was masking the effect played by the redundancy in the accuracy scores for the local trials.

In addition to the effect discussed above, this experiment revealed a general better performance in humans along with higher levels of accuracy in the local trials in both species. This latter result contrasts with those emerged in Experiment 1 and 2, where no advantage was found. Furthermore, it does not seem to be in agreement with previous literature which reports that humans perform faster and better the global aspect of hierarchical stimuli unless specific factors are manipulated. However, it has to be considered that in the present and the following experiment, stimuli sustained a visual angle of  $11^\circ$  at the global level, a well wider visual angle compared to previous experiments on the same species (e.g., Spinozzi *et al.* 2003, global aspect of stimuli:  $7^\circ$  of va) and this can account for human local advantage (see also discussion to Experiment 4).

### **3.5 EXPERIMENT 4**

The aim of Experiment 4 was to evaluate whether the same pattern of results obtained in Experiment 1 would have been observed in a situation where the hierarchical Navon-like figures

featured consistent stimuli, in which identical redundant or non-redundant shapes were present at the global and the local level of the stimuli. For this purpose, the same shapes used in Experiment 1 (consistent set only) were used. However, as was done for Experiment 3 in this experiment the local elements consisted of solid shapes obtained from joining together the 5 dots featuring each local cluster (see Figure 22). Therefore, in this way, hierarchical Navon-like stimuli were produced but with stimuli based on redundant and non-redundant patterns proposed by Garner (1974).

### **3.5.1 Method**

#### ***3.5.1.1 Participants***

The group of monkeys was the same as in previous experiments.

The human sample comprised 12 participants (8 females, 4 males; mean age: 35) including 8 of the 12 individuals who had took part in Experiment 3 (6 females, 2 males) and a new group of 4 individuals (2 females, 2 males).

#### ***3.5.1.2 Stimuli and Procedure***

The stimuli were eight hierarchical Navon-like global/local figures. The shapes (redundant and non-redundant) of the global and the local level of the stimuli were identical to those used in Experiment 1 consistent condition (see Figure 12, consistent set). The stimulus set is depicted in Figure 25.

The procedures used with both humans and monkeys were identical to those used in the previous experiments.

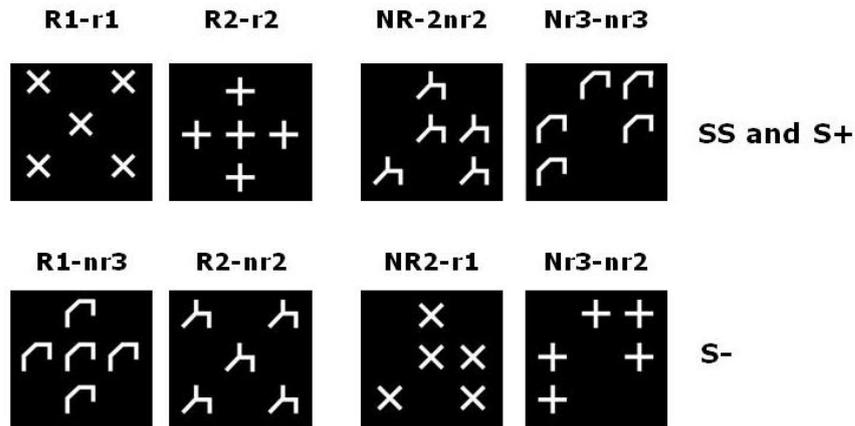


Figure 25. Stimuli adopted in Experiment 4. Stimuli were always consistent in shape and in redundancy at both levels of processing.

### 3.5.2 Results Experiment 4

#### 3.5.2.1 Accuracy

The mean percentage of correct answers recorded with the two species in the global and local trials is depicted in Figure 26. Moreover, individual percentages of correct responses recorded for each subject are presented in Table 5.

Table 5. Mean individual percentages of correct responses recorded for each monkey in Experiment 4

Subjects	Local		Global	
	NR-nr	R-r	NR-nr	R-r
<b>Gal</b>	89.6	87.5	79.2	89.6
<b>Patè</b>	72.9	87.5	72.9	79.2
<b>Pippi</b>	70.8	93.8	66.7	81.3
<b>Rubens</b>	87.5	83.3	77.1	79.2
<b>Vispo</b>	79.2	91.7	77.1	72.9

A 2 (Level of Processing) x 2 (Redundancy) x 2 (Species) mixed ANOVA was carried out on the accuracy data recorded for the two species. The analysis revealed significant main effects for Species,  $F(1, 15) = 96.112, p < .001, \eta_p^2 = .865$ , Level of Processing,  $F(1, 15) = 29.426, p < .001, \eta_p^2 = .662$ , and Redundancy,  $F(1,15) = 15.819, p < .01, \eta_p^2 = .513$ . Therefore, the presence of these main effects highlights that, overall, humans performed at a higher level of accuracy ( $M = 97.5\%$ ) than monkeys ( $M = 81.0\%$ ) and that local trials ( $M = 91.6\%$ ) were processed better than global ones ( $M = 86.9\%$ ). Likewise, in general, redundant shapes ( $M = 91.7\%$ ) were processed better than non-redundant ones ( $M = 86.7\%$ ). The ANOVA proved also a significant interaction Species by Level of Processing,  $F(1, 15) = 5.947, p < .05, \eta_p^2 = .284$ , whereas the interaction Species by Level of Processing by Redundancy only approached the significance,  $F(1, 15) = 4.347, p = .055, \eta_p^2 = .225$ .

Pair-wise comparisons carried out in order to explain the interaction Species by Level of Processing revealed that in both species, matching performance was higher in the local compared to the global trials, *monkeys*, local trials = 84.4%, global trials = 77.5%,  $t(4) = 5.582, p < .01$ ; *humans*, local trials = 98.8%, global trials = 96.2%,  $t(11) = 2.611, p < .05$ . As the interaction Species by Level of processing by Redundancy approached the significance ( $p=.055$ ), further pair-wise comparisons ( $t$ -test) on these factors considering the two species separately were carried out. In monkeys this analysis did not reveal any difference between Redundant and Non-redundant stimuli in both local and global trials. By contrast, in humans, redundant stimuli were processed better than non-redundant ones but only in the global trials, *Global trials*: R-r,  $M = 99.3\%$ , NR-nr,  $M = 93.1\%$ ;  $t(11) = 3.318, p < .01$ . Moreover, accuracy level for non-redundant stimuli was higher in the local trials compared to the global trials, *NR-nr*: Local trials,  $M = 99.3\%$ ; global trials,  $M = 93.1\%$ ;  $t(11) = 3.448, p < .01$ .

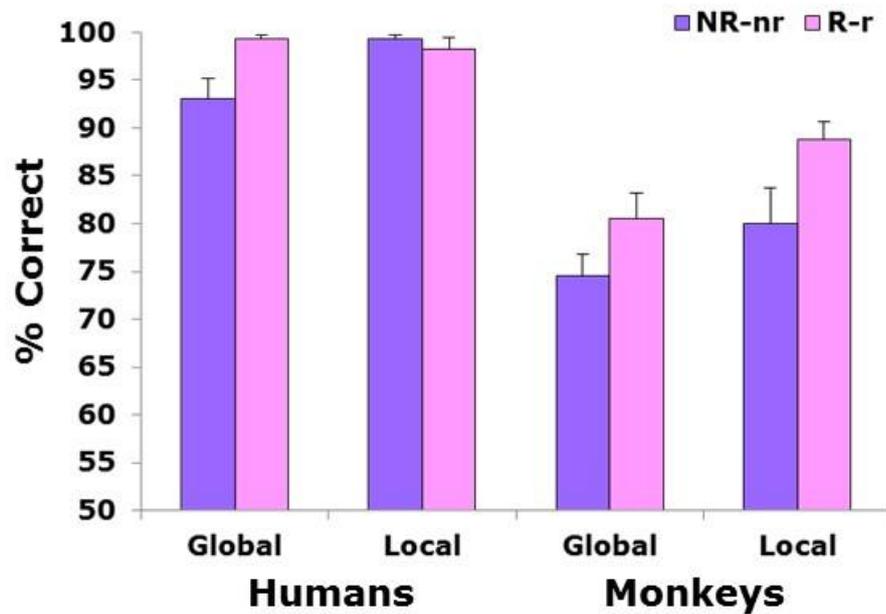


Figure 26. Mean percentages of correct responses recorded for both species in the different trials Experiment 4. Error bars represent one Standard Error.

### 3.5.2.2 Response Times

The 2 (Level of Processing) x 2 (Redundancy) ANOVA carried out on the latencies, filtered per correct answers, recorded for humans revealed a significant main effect for redundancy,  $F(1, 11) = 10.157$ ,  $p < .01$ ,  $MSE = 27189.8$ ,  $\eta_p^2 = .480$ , with redundant shapes ( $M = 1113.0$  ms) being processed faster than non-redundant shapes ( $M = 1264.7$  ms). The effect of level of processing only approached significance ( $p = .087$ ).

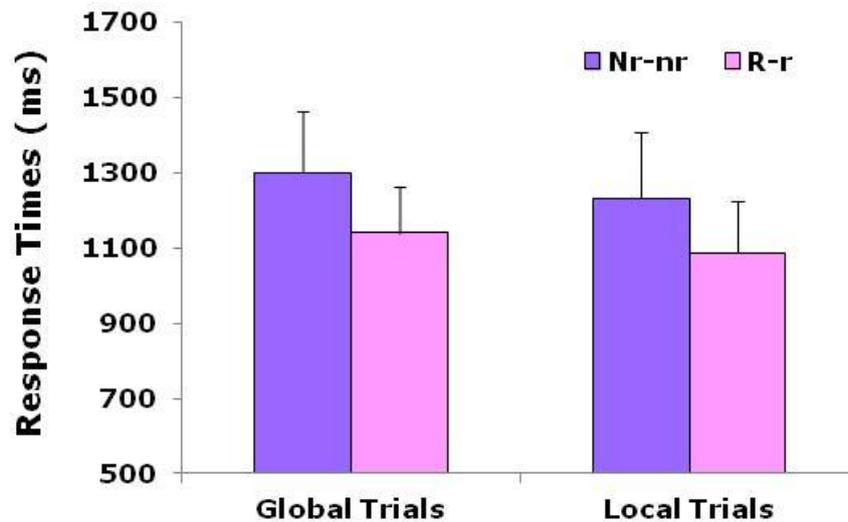


Figure 27. Means RTs (ms) recorded for humans in the different trials of Experiment 4. Error bars represent one Standard Error.

### 3.5.3 Discussion Experiment 4

In this experiment, a redundancy effect was observed in humans, but only when the participants had to focus on the global level of the stimulus, which is typically processed better and faster in this species. However, when RT data are taken into consideration, it emerged that human benefit from stimulus redundancy yielded to faster answers in both global and local trials. By contrast, no redundancy effect on the visual processing emerged in monkeys. This latter result will be discussed in the general discussion when a comparison between all the experiments will be possible. Moreover, Experiment 4 revealed an overall local processing advantage in both humans and monkeys. This finding is comparable to that observed in Experiment 3, where a local bias was found in the two species for inconsistent, hierarchical Navon-like figures. However, if response times are taken into consideration, humans did show only a tendency in processing faster local trials in comparison to global ones.

Overall, the results obtained for humans indicate that, when no grouping is required at the local level of the stimuli, this level of processing starts to develop an advantage also in this species with stimuli featuring such visual angle ( $11^\circ$  at global-level and  $2.6^\circ$  at local-level). Besides, in capuchin monkeys, a local bias emerged in conditions requiring local grouping as well as in conditions that did not require any grouping operation at the local level.

In Experiment 3 and 4, a general local advantage in both capuchins and humans was found. Human global advantage is a quite strong feature, however, it can be affected by the size of the stimuli (Kimchi, 1998; Kinchla, Wolfe, 1979) and also by the amount of local elements. As stimuli adopted in Experiment 3 and 4 sustained a visual angle much wider than those adopted in previous literature in humans (e.g., Spinozzi *et al.* 2003) to better understand the role played by the visual angle together with the numerosity of local elements a fifth experiment was carried out.

### **3.6 EXPERIMENT 5**

Previous literature in humans (Kimchi, 1998; Kinchla, Wolfe, 1979) suggests that the global–local processing of hierarchical patterns can be affected by some stimulus properties, such as the perceived visual angle and the number or relative size of the local elements. For example in humans, with stimuli subtending a large visual angle or featuring few and relatively large local elements, the global precedence tend to fade. In all previous experiments relatively large stimuli were used (sustaining a visual angle of  $11^\circ$  at global level and  $2.6^\circ$  at local level) compared to those often used in the literature on humans and monkeys (see Spinozzi *et al.*, 2003, which sustained a visual angle of  $7^\circ$  at global level and  $0.9^\circ$  at local level). Thus, the local advantage that was observed in humans in

Experiments 3 and 4 could be explained by the visual angle subtended by the stimuli. In fact, it is well-known that in humans the global advantage can be affected by stimulus size (see, for example, Kinchla & Wolfe, 1979) as well as local element numerosity (Kimchi, 1998). Therefore, the aim of this last experiment is to clarify whether this was the case. To do so, stimulus size at both levels of processing and the amount of local elements featuring the stimuli were manipulated. In this way, two sets of stimuli, one featuring few relatively large local elements and one featuring many small local elements were produced.

### **3.6.1 Method**

#### **3.6.1.1 Participants**

The monkey sample was the same as in previous experiments.

The human sample included 12 subjects, of which 8 had participated also in Experiment 2, 3 and 4, however it was not possible to recruit 4 subjects from the same sample and therefore 4 new subjects were enrolled.

#### **3.6.1.2 Stimuli and Procedure**

For this last experiment, the stimuli were created using 10 patterns from the 24 patterns used in Experiment 3 in addition to the 8 patterns used in Experiment 4. In both cases, the stimulus' size was reduced. In this way, all the stimuli created subtended a visual angle of about 7° at the global level. This visual angle was the same of the stimuli adopted in previous literature (Spinozzi *et al.*, 2003).

Figure 28 depicts the stimulus set used in this experiment. It included Consistent and Inconsistent stimuli. Both types of stimuli could be further divided into two subsets: one subset featured few and relatively large local elements (Few subset) whereas the other

subset featured many and relatively small local elements (Many subset).

Therefore, in total there were 36 stimuli divided as follows:

1) The *Consistent* stimuli featured 16 patterns obtained from those adopted in Experiment 4. The consistent set could be further divided in 2 sub-sets: the Consistent Few subset and the Consistent Many subset as described above. Both subsets featured 8 hierarchical patterns each, 4 redundant (R-r) and 4 non-redundant (NR-nr) (see Figure 28a).

2) The *Inconsistent* stimuli featured 20 stimuli obtained from those adopted in Experiment 3. The inconsistent set could be further divided into 2 sub-sets: the Inconsistent Few subset and the Inconsistent Many subset as described above. Both subsets featured 10 hierarchical patterns each, 5 redundant (R-r) and 5 non-redundant (NR-nr) (see Figure 28b).

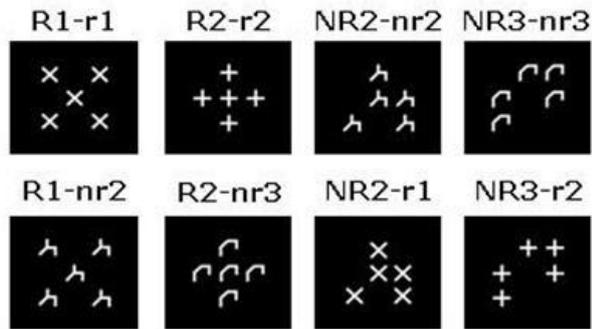
In both sub-sets, the global level of the stimuli featured always  $7^\circ$  of  $va$ , whereas the local elements measured about  $1.7^\circ$  in the few-elements subset and about  $0.7^\circ$  in the many-elements subset. Each subset featured five redundant (R-r) and five non-redundant (NR-nr) forms at both levels of processing.

Task and procedure were as in the previous experiments.

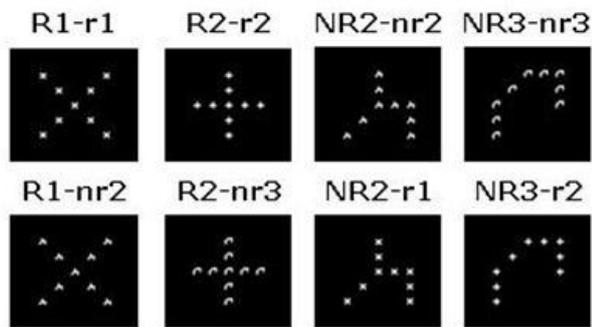
*Figure 28. (Next page) Set of Consistent (a) and Inconsistent (b) stimuli utilised in Experiment 5. Each set is further divided into two subsets featuring either few and large local elements or many and small local elements (adapted from De Lillo et al., 2012).*

a)

**Few Large Elements**

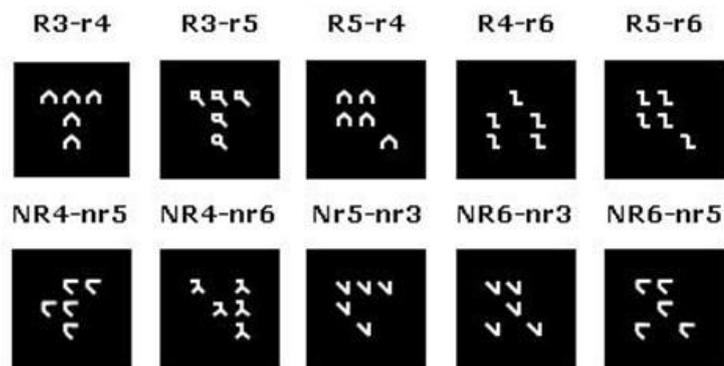


**Many Small Elements**

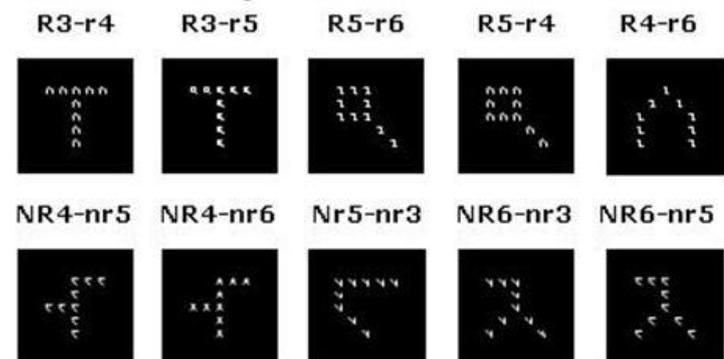


b)

**Few Large Elements**



**Many Small Elements**



### 3.6.2 Results Experiment 5

#### 3.6.2.1 Results Subset 1: Consistent stimuli

##### 3.6.2.1.1 Accuracy

Figure 29 illustrates the percentage of correct answers recorded with the two species in the two conditions: (a) few and large elements, (b) many and small elements. Moreover, individual percentages of correct responses recorded for each monkey with the different stimuli are presented in Table 6.

*Table 6. Mean individual percentages of correct responses recorded for each monkey with the different stimuli (few/many) of the Consistent stimuli subset.*

Subjects	Local				Global			
	Few		Many		Few		Many	
	NR-nr	R-r	NR-nr	R-r	NR-nr	R-r	NR-nr	R-r
<b>Gal</b>	93.8	93.8	100.0	93.8	62.5	93.8	81.3	75.0
<b>Patè</b>	81.3	93.8	81.3	81.3	56.3	100.0	68.8	87.5
<b>Pippi</b>	93.8	81.3	81.3	100.0	62.5	93.8	62.5	68.8
<b>Rubens</b>	93.8	93.8	87.5	87.5	75.0	75.0	75.0	75.0
<b>Vispo</b>	87.5	93.8	81.3	93.8	68.8	93.8	56.3	68.8

A 2 (Numerosity: Few, Many) × 2 (Level of Processing) × 2 (Redundancy) 2 (Species) mixed ANOVA was carried out. The ANOVA revealed that all the factors played a significant main effect: Species,  $F(1, 15) = 241.83, p < .001, \eta_p^2 = .942$ , Numerosity,  $F(1, 15) = 8.01, p < .05, \eta_p^2 = .348$ , Level of Processing,  $F(1, 15) = 62.876, p < .001, \eta_p^2 = .807$ , and Redundancy,  $F(1, 15) = 24.671, p < .001, \eta_p^2 = .622$ . Therefore, humans performed better ( $M = 97.8\%$ ) than monkeys ( $M = 82.4\%$ ), overall. Furthermore, in general, the few-elements subset was processed better ( $M = 94.1\%$ ) than many-elements subset ( $M =$

92.5%). Finally, in addition to a general better performance with redundant stimuli ( $M = 95.3\%$ ) compared to non-redundant one ( $M = 91.2\%$ ), overall, in this experiment local trials were processed better ( $M = 95.6\%$ ) than global ones ( $M = 91.0\%$ ). The ANOVA revealed also the following significant interactions: Level of Processing x Species,  $F(1, 15) = 58.578, p < .001, \eta_p^2 = .796$ , Redundancy x Species,  $F(1, 15) = 11.234, p < .005, \eta_p^2 = .434$ , Numerosity x Redundancy,  $F(1, 15) = 7.307, p < .05, \eta_p^2 = .328$ , Level of Processing x Redundancy,  $F(1, 15) = 22.704, p < .001, \eta_p^2 = .602$ , Numerosity x Level of Processing x Species,  $F(1, 15) = 4.375, p < .05, \eta_p^2 = .290$ , and, finally, Numerosity x Level of Processing x Redundancy x Species,  $F(1, 15) = 8.013, p < .05, \eta_p^2 = .351$ .

In order to explain this extremely complex pattern of significant interactions, planned comparisons were carried out considering the two species separately. Given the high number of comparisons (12), after applying the Bonferroni correction, only results with  $p < 0.0042$  were considered significant. Planned comparison carried out on data recorded for monkeys revealed that, in the 'few' condition, monkeys performed the non-redundant stimuli worse at global level than at local one, *NR-nr*: global trials,  $M = 64.1\%$ ; local trials  $M = 90.1\%$ ;  $t(4) = 8.884, p < .005$ . Also in the 'many' condition, they matched the non-redundant stimuli with a lower level of accuracy at the global level than at the local one, *NR-nr*: global trials,  $M = 71.9\%$ ; local trials,  $M = 87.5\%$ ;  $t(4) = 8.660, p < .005$ , ns with Bonferroni correction. Furthermore, in both conditions (few and many) they processed local trials better than global ones, *Few condition*: global trials,  $M = 77.4\%$ , local trials,  $M = 90.7\%$ ,  $t(4) = 5.668, p < .05$ ; *Many condition*: global trials,  $M = 74.2\%$ , local trials,  $M = 89.1\%$ ,  $t(4) = 3.186, p < .05$ , ns with Bonferroni correction.

In humans the planned comparisons revealed that, in the 'few' condition, the performance in global trials was better with redundant than with non-redundant stimuli, *Global trials*: R-r,  $M = 99.3\%$ , NR-

nr,  $M = 94.1\%$ ,  $t(11) = 2.917$ ,  $p < .05$ , ns with Bonferroni correction. However, they performed non-redundant stimuli better at the local level than at the global level, *NR-nr*: local trials,  $M = 99.3\%$ ; global trials,  $M = 94.1\%$ ,  $t(11) = 3.564$ ,  $p < .005$ . Furthermore, a significant difference was observed between global non-redundant stimuli featuring few and many-elements, *Global trials, NR-nr*: few-elements,  $M = 94.1\%$ , many-elements,  $M = 98.3\%$ ,  $t(11) = 2.346$   $p < .05$ , ns with Bonferroni correction. A similar pattern was recorded for local non-redundant stimuli, *Local trials, NR-nr*: few-elements,  $M = 99.3\%$ , many-elements,  $M = 95.8\%$ ,  $t(11) = 2.804$ ,  $p < .05$ , ns with Bonferroni correction. Finally there was a significant difference between local redundant stimuli featuring few and many-elements, *Local trials, R-r*: few-elements,  $M = 99.7\%$ ; many-elements,  $M = 96.9\%$ ,  $t(11) = 2.968$ ,  $p < .05$ , ns with Bonferroni correction.

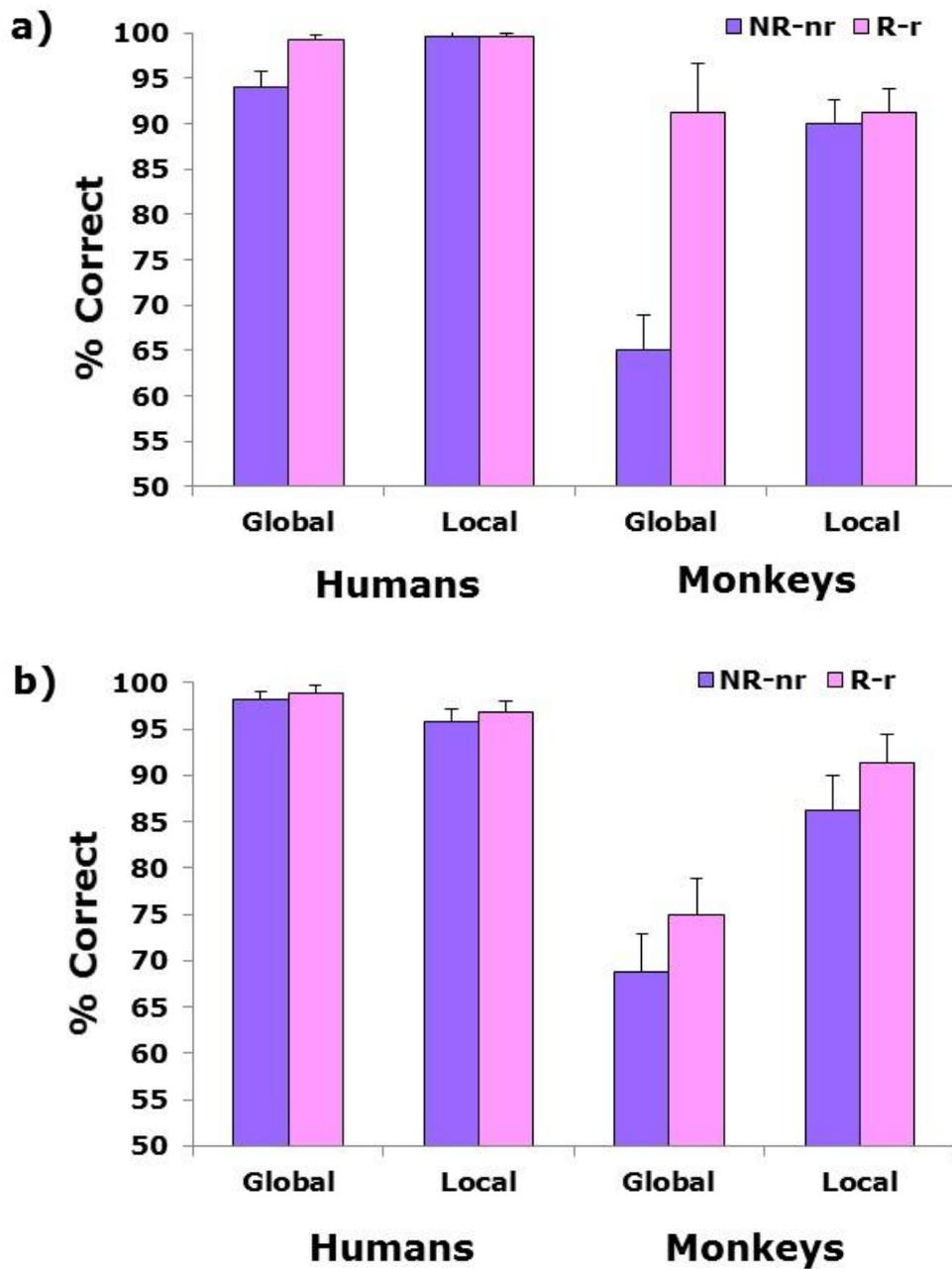


Figure 29. Mean percentages of correct responses recorded for both species in the different trials of Experiment 5 with Consistent stimuli. The two conditions are presented in separate graphs: a) Few-sparse elements b) Many-dense elements. Error bars represent one Standard Error.

### 3.6.2.1.2 Response Times

A 2 (Numerosity) × 2 (Level of Processing) × 2 (Redundancy) ANOVA was carried out on RTs, filtered by correct answers only, recorded for humans. The analysis revealed a significant main effect of Redundancy,  $F(1, 11) = 8.910$ ,  $p < .05$ ,  $\eta_p^2 = .448$ , indicating that, overall, redundant stimuli were processed faster ( $M = 977.1$  ms, ms) than non-redundant ones ( $M = 1105.7$  ms). It revealed also the following significant interactions: Numerosity by Level of Processing,  $F(1, 11) = 19.227$ ,  $p = .001$ ,  $\eta_p^2 = .636$ , and Redundancy by Level of Processing,  $F(1,11) = 5.014$ ,  $p < .05$ ,  $\eta_p^2 = .313$ .

Given the two-way interactions, post-hoc comparisons were carried out. They revealed that, regardless of the factor redundancy, in the 'few' condition, local trials were processed faster than global one, *Few-condition*: local trials,  $M = 976.7$  ms, global trials,  $M = 1062.2$  ms,  $t(11) = 3.618$ ,  $p < .005$ . However, in the 'many' condition the situation was reversed, with global trials processed faster than local ones, *Many-condition*: global trials,  $M = 987.8$  ms, local trials,  $M = 1061.3$  ms,  $t(11) = 5.086$ ,  $p < .001$ . Furthermore, regardless of the factor 'numerosity', global trials were processed faster when stimuli were redundant than non-redundant, R-r,  $M = 942.6$  ms, NR-nr,  $M = 1107.4$  ms,  $t(11) = 3.133$ ,  $p < .05$ . Also local trials were processed faster when the stimuli were redundant than when they were non-redundant, R-r,  $M = 963.1$  ms, NR-nr,  $M = 1074.9$  ms,  $t(11) = 2.631$ ,  $p < .05$ .

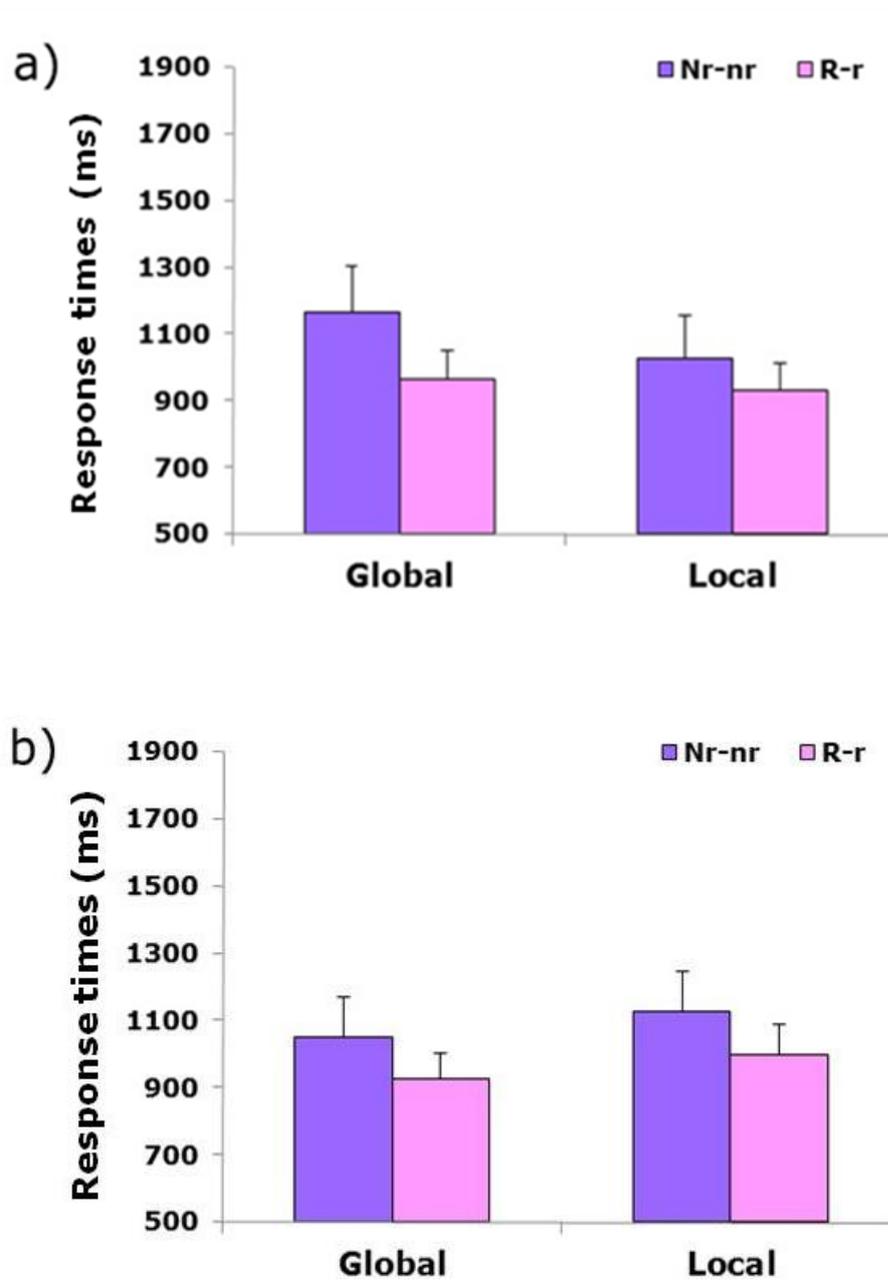


Figure 30. Means of Reaction Times (ms) registered for humans in the different trials of Experiment 5 with Consistent stimuli. The two conditions are presented in separate graphs: a) Few-sparse elements b) Many-dense elements. Error bars represent one Standard Error.

### 3.6.2.2 Results Subset 2: Inconsistent stimuli

#### 3.6.2.2.1 Accuracy

Figure 31 depicts the percentage of correct responses recorded in the few/large (a), and in the many/small (b) element conditions, considering the two species separately. Moreover, individual percentages of correct responses recorded with each monkey with the different stimuli are presented in Table 7.

*Table 7. Mean individual percentages of correct responses recorded for each monkey with the different stimuli (few/many) of the inconsistent stimuli subset*

Subjects	Global				Local			
	Few		Many		Few		Many	
	NR-r	R-nr	NR-r	R-nr	NR-r	R-nr	NR-r	R-nr
<b>Gal</b>	75.0	87.5	68.8	81.3	87.5	93.8	81.3	75.0
<b>Patè</b>	62.5	93.8	68.8	62.5	81.3	93.8	93.8	75.0
<b>Pippi</b>	50.0	81.3	75.0	75.0	50.0	81.3	87.5	93.8
<b>Rubens</b>	87.5	81.3	62.5	68.8	93.8	100	75.0	75.0
<b>Vispo</b>	68.8	87.5	81.3	50.0	75.0	93.8	81.3	75.0

A 2 (Numerosity) × 2 (Level of Processing) × 2 (Redundancy) × 2 (Species) mixed ANOVA was carried out. The analysis revealed significant main effects for the following factors: Species,  $F(1, 15) = 138.141$ ,  $p < .001$ ,  $\eta_p^2 = .882$ , Level of Processing,  $F(1, 15) = 44.668$ ,  $p < .001$ ,  $\eta_p^2 = .468$ , and Redundancy,  $F(1, 15) = 12.91$ ,  $p < .005$ ,  $\eta_p^2 = .463$ . Therefore, it suggests that, overall, humans performed at a higher level of accuracy ( $M = 96.7\%$ ) than monkeys ( $M = 78.9\%$ ) and that, in general, local trials ( $M = 92.9\%$ ) were processed better than global ones ( $M = 91.6\%$ ). Likewise, the general performance recorded with redundant stimuli was better (94.6%) than that recorded with non-redundant ones ( $M = 89.9\%$ ).

The ANOVA revealed also the following interactions: Species x Level of Processing,  $F(1, 15) = 63.975, p < .001, \eta_p^2 = .810$ , Numerosity x Redundancy,  $F(1, 15) = 12.838, p < .01, \eta_p^2 = .461$ , Species x Numerosity x Level of Processing,  $F(1, 15) = 6.868, p < .05, \eta_p^2 = .314$ , and Species x Numerosity x Redundancy,  $F(1, 15) = 15.714, p < .005, \eta_p^2 = .512$ .

Planned comparisons were carried out on the two species separately to explain the third order interactions and results were corrected (Bonferroni) considering 4 comparisons ( $p < .0125$ ). Planned comparisons revealed that monkeys had a local advantage with stimuli featuring both many-small elements, *Many condition*: local trials,  $M = 81.3\%$ ; global trials,  $M = 69.4\%$ ,  $t(4) = 4.404, p < .05$ , and few-large elements, *Few condition*: local trials,  $M = 85.0\%$ ; global trials,  $M = 77.5\%$ ,  $t(4) = 3.540, p < .05$ . Humans showed a different pattern of results since they displayed a global advantage when stimuli with many and small elements had to be processed, *Many condition*: local trials,  $M = 93.9\%$ ; global trials,  $M = 98.8\%$ ,  $t(11) = 3.023, p < .05$ , and a local advantage when subjects had to process stimuli featuring few and large local elements, *Few condition* = local trials,  $M = 98.6\%$ ; global trials,  $M = 95.5\%$ ,  $t(11) = 2.570, p < .05$ . These results can explain the emergence of a significant two-way interaction between the factor Numerosity and the factor Level of Processing.

Finally, in the 'few' condition, monkeys revealed better performance with redundant stimuli in comparison to non redundant ones, *Few-condition*: R-r,  $M = 89.4\%$ ; NR-nr,  $M = 73.1\%$ ,  $t(4) = 3.033, p < .05$ . On the other hand, humans performed better with redundant stimuli in comparison to non-redundant ones in both conditions, *Many-condition*: R-r,  $M = 98.6\%$ ; NR-nr,  $M = 94.1\%$ ,  $t(11) = 2.86, p < .05$ ; *Few-condition*: R-r,  $M = 98.8\%$ ; NR-nr,  $M = 95.3\%$ ,  $t(11) = 2.499, p < .05$  (adapted from De Lillo et al., 2012).

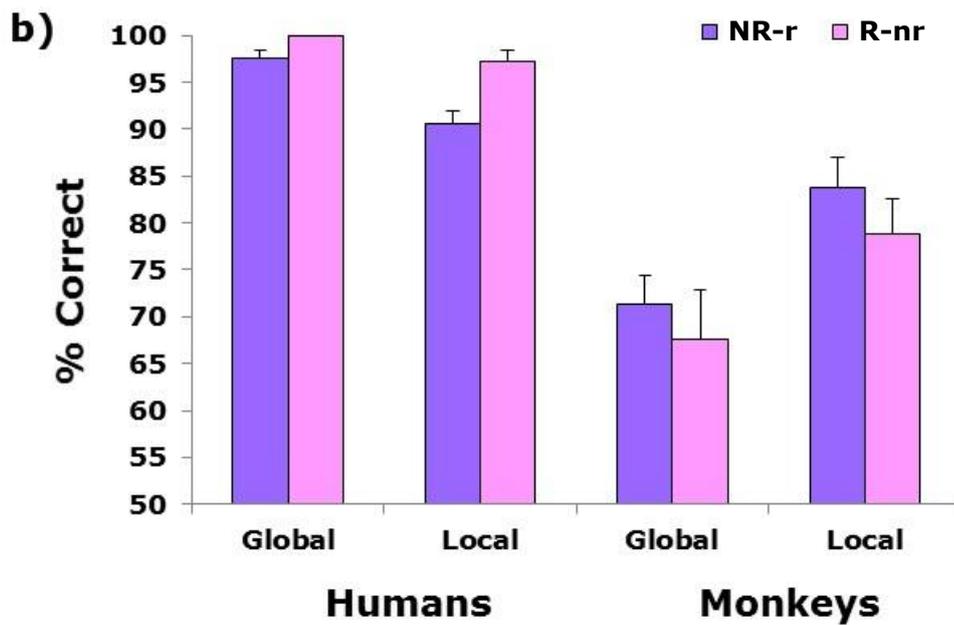
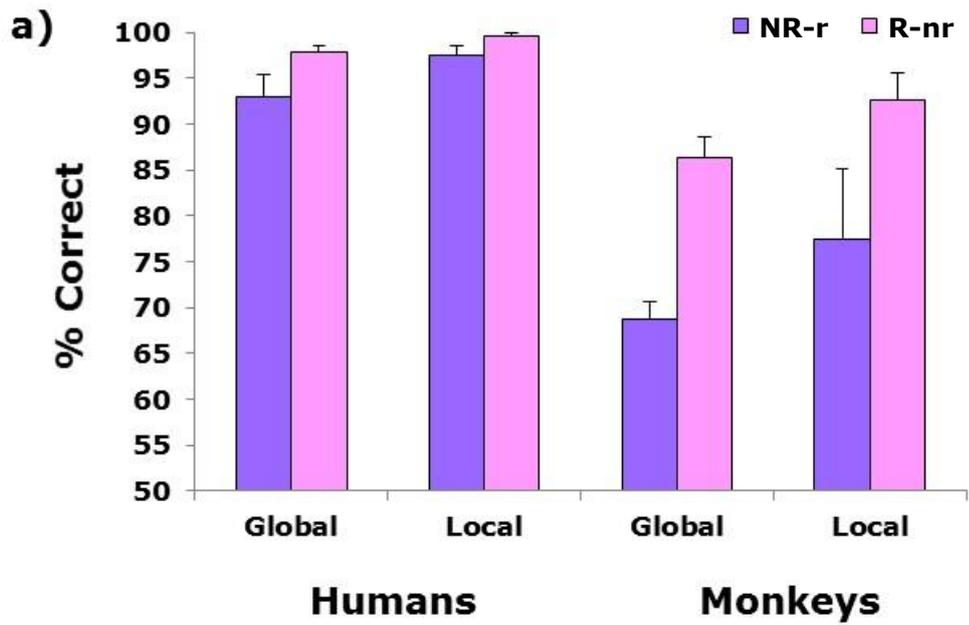


Figure 31. Mean percentages of correct responses recorded for both species in the different trials of Experiment 5 with inconsistent stimuli. The two conditions are presented in separate graphs: a) Few-sparse elements b) Many-dense elements. Error bars represent one Standard Error.

### 3.6.2.2.2 Response Times

A 2 (Numerosity)  $\times$  2 (Level of Processing)  $\times$  2 (Redundancy) ANOVA on RTs recorded with humans, filtered for correct answers only, was carried.

The analysis revealed a significant main effect of redundancy,  $F(1, 11) = 21.57, p = .001, \eta_p^2 = .662$ , with redundant stimuli ( $M = 1009.8$  ms) processed faster than non-redundant ones ( $M = 1230.7$  ms). It also showed the following significant interactions: Numerosity by Level of Processing,  $F(1, 11) = 25.76, p < .001, \eta_p^2 = .701$ , and Level of Processing by Redundancy,  $F(1, 11) = 5.75, p < .05, \eta_p^2 = .343$ .

Paired sample  $t$ -test were carried out in order to explain the two-way interactions. This last analysis showed that, overall, in the condition featuring few and large local elements, the local trials were processed significantly faster than the global ones, *Few condition*: local trials,  $M = 1051.2$  ms, global trials,  $M = 1158.1$  ms,  $t(11) = 4.49, p < .001$ . Conversely, in the condition featuring many and smaller elements, global trials were processed significantly faster than the local ones, *Many condition*: global trials,  $M = 1095.1$  ms, local trials,  $M = 1176.6$  ms;  $t(11) = 4.26, p < .001$ . This latter result is consistent with the accuracy results reported above. Finally, regardless of the numerosity of local elements, in both the global and the local trials, redundant stimuli were processed faster than non-redundant ones, *Global trials*: R-r,  $M = 1004.6$  ms; NR-nr,  $M = 1248.5$  ms;  $t(11) = 4.900, p < .001$ . *Local trials*: R-r,  $M = 1014.9$  ms, NR-nr,  $M = 1212.9$  ms;  $t(11) = 4.191, p < .01$  (adapted from De Lillo *et al.*, 2012).

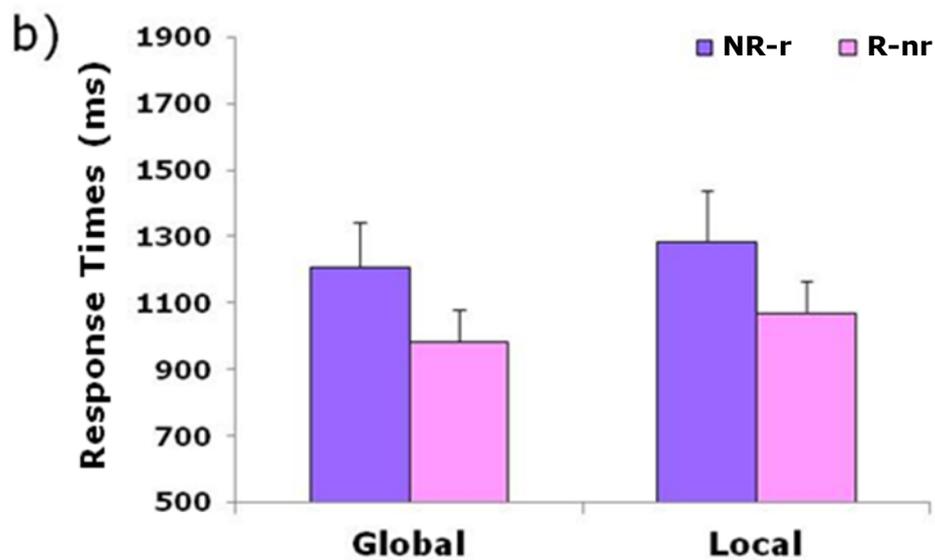
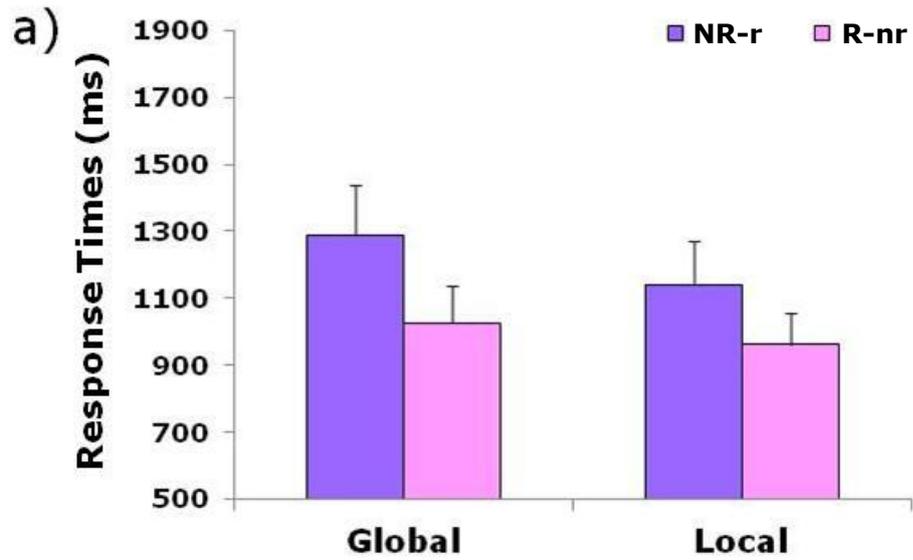


Figure 32. Means of Reaction Times (ms) registered for humans in the different trials of Experiment 5 with Inconsistent stimuli. The two conditions are presented in separate graphs: a) Few-sparse elements b) Many-dense elements. Error bars represent one Standard Error.

### **3.6.3 Discussion Experiment 5**

#### *3.6.3.1 Consistent stimuli*

The accuracy results obtained in Experiment 5 with consistent stimuli revealed significant main effects for Species, Numerosity, Level of Processing and Redundancy. They revealed also a complex network of interactions between these factors.

Planned comparisons revealed that monkeys processed global trials significantly worse than local ones in both 'few' and 'many' condition, but only with stimuli featuring non-redundant shapes. The poorer performance in global trials with non-redundant stimuli may indicate, once again, that the beneficial effect of stimulus redundancy may manifest itself in particular in the level of stimulus structure typically processed better by this species.

However, planned comparisons did not yield significant results when the Bonferroni correction was applied. A clearer pattern emerged from RT data. It showed that in the 'few' condition local trials were processed faster than global ones. Conversely, in the 'many' condition global trials were processed faster than local ones. Furthermore, in both conditions, redundant stimuli were processed faster than non-redundant ones.

#### *3.6.3.2 Inconsistent Stimuli*

The results of Experiment 5 with inconsistent stimuli demonstrated, once again, the strength of monkey local advantage which occurred also in this experiment with both, few-large and many-small, stimuli. In relation to the factor redundancy, the present experiment confirmed that monkeys can benefit from this stimulus property as the performance increased with redundant stimuli. This result matches the findings coming from Experiments 2 and 3 where analogous stimuli were adopted. However, this beneficial effect was present only in trials featuring stimuli with few-large local elements.

It is difficult to provide a good justification for this selective effect of redundancy in monkeys. However, it is worth to pinpoint that whereas larger overall, the stimuli in the few-large condition preserved the same proportions of stimuli used in Experiment 2 and 3. This means that the ratio between the local elements size and the distance between them was the same in the two experiments. Since a similar effect of redundancy was obtained in Experiment 3, it is possible to envisage that this proportion between size and relative distance could be critical for the emergence of the effect.

In the present experiment, the beneficial effect played by stimulus redundancy on monkey global-local processing emerged also in global trials. This contrasts with the results of Experiment 3 where there was a clear link between the level of processing and benefits of redundancy. The reason for this difference in the results of the two experiments is unclear.

However, results recorded with humans support the idea that the emergence of the human local advantage observed in Experiment 3 and 4 could be explained mainly by the use of hierarchical stimuli subtending a relatively higher visual angle. In fact, consistently with previous literature (Amirkhiabani & Lovegrove 1998; Kimchi, 1998; Kinchla & Wolfe, 1979; LaGasse, 1993; Lamb & Robertson, 1989) patterns composed of many-small elements lead to a global advantage to humans. Therefore, with inconsistent stimuli, it was found that stimulus size and local element numerosity influence the preferred level of processing in humans.

### **3.7 DISCUSSION**

With few exceptions, related to some possible confounds derived by some internal stimulus properties (see also below), overall, the results of this study indicate that capuchin monkeys can

take advantage of the redundancy of hierarchical stimuli in their visual processing. However, this benefit emerged under different conditions across the five experiments. Furthermore, the results from the first two experiments suggest that capuchin local bias persists even when local configurations require grouping.

Presumably, this is the first research which demonstrated that the stimulus redundancy can lead to better performances in the visual processing by a non-human primate species. In fact, the only previous research in this area, which was carried in stump-tailed monkeys (Shrier *et al.*, 1979, see also the general discussion), did not prove any beneficial effect of stimulus redundancy in this species. However, it should be pointed out that Shrier *et al.* (1979) used Garner's dot stimuli, but they were not hierarchical and the type of task was different from that one used in this study. Therefore, it cannot be ruled out that, with a similar procedure, also stump-tailed monkeys may show a certain degree of sensitivity to stimulus redundancy.

Garner's work (1970; 1974) proved that stimulus redundancy can ease the visual processing. The present results suggest that at least one non-human primate species might also perceive shape "redundancy" in an analogous way to humans, highlighting another similarity with the human cognitive system.

Taking into account the diverse pattern of results obtained across the five experiments, it is not clear if there is a relation between the stimulus redundancy and the level of processing. On one hand, some experiments indicate that the benefit from redundancy seems to occur mostly on the level of processing processed better by the two species, as it occurred in global trials with humans and local trials with monkeys (see Exp. 3 and 4 for humans). On the other hand, the results of both Exp. 2 and 5 (inconsistent condition) seem to indicate otherwise as they proved a beneficial effect of stimulus redundancy regardless of the level of

processing. In fact, in Experiment 5, humans processed redundant stimuli at a higher level of accuracy in every condition, while monkeys revealed a beneficial effect from stimulus redundancy in both levels of processing, but only with stimuli featuring stimuli few-large local elements. However, when RT data are taken into consideration, the results become more homogeneous. In fact, RT data in humans revealed faster answers for redundant stimuli in almost every experiment. Although not possible in the present study, the collection of response times also in monkeys would provide further information which may help to clarify whether or not there could be a relationship between stimulus redundancy and level of processing in capuchin monkeys.

Some experiments of the present study did not produce a clear pattern in particular with regard to the factor redundancy. In fact, in some experiments, no advantage in either level of processing was found (see for example humans in Exp. 1) nor a clear evidence of a beneficial effect from stimulus redundancy (see for example monkeys in Exp. 4). However, it is interesting to highlight the general consistency across experiments featuring similar stimuli. In fact, coherent results emerged from Experiment 2, 3 and 5 (this latter in the inconsistent condition), whereas unclear patterns emerged from experiment 1, 4 and 5 (consistent set). These latter experiments all featured the same shapes, manipulations occurred in the requirement to group local elements or in the stimuli size and local elements numerosity. Analogously, the same can be alleged for stimuli adopted in Experiment 2, 3 and 5 (inconsistent). It is not clear what caused these differences in the results, but this coherency across each group of experiments (where each group featured similar shapes) suggests that this fluctuation in the results of this study should not be considered by chance and may be due to some underlying factor intrinsic on each shape. A possible explanation might be that, as the shape in Exp. 1 (cons), 4 and 5

(cons) was always consistent in shape and in redundancy, perhaps the consistency in shape facilitated the task leading to better performance also with non-redundant stimuli. Another possible explanation can be found in the MTS procedure adopted with these stimuli. The MTS task featured as SS and S+ stimuli consistent in shape and redundancy at both levels of processing. Besides, the non-matching stimuli were shapes always redundant at one level and non-redundant at the other, with differences occurring at the level of processing that was processed at that moment. Perhaps, the presence of a degree of redundancy at either level of processing even with non-redundant trials, and vice versa (see Table 8 as example), affected the general performance.

*Table 8. Examples of MTS trials displaying the difference in the structure (in bold) of the non-matching stimuli between Experiment 1 and 2.*

		<b>S+</b>	<b>SS</b>	<b>S-</b>	<b>S+</b>	<b>SS</b>	<b>S-</b>
<b>Exp. 1</b>	<b>Global trial</b>	R <sub>1</sub> -r <sub>1</sub>	R <sub>1</sub> -r <sub>1</sub>	<b>NR<sub>1</sub>-r<sub>1</sub></b>	NR <sub>1</sub> -nr <sub>1</sub>	NR <sub>1</sub> -nr <sub>1</sub>	NR <sub>1</sub> - <b>r<sub>1</sub></b>
	<b>Local trial</b>	R <sub>1</sub> -r <sub>1</sub>	R <sub>1</sub> -r <sub>1</sub>	R <sub>1</sub> - <b>nr<sub>1</sub></b>	NR <sub>1</sub> -nr <sub>1</sub>	NR <sub>1</sub> -nr <sub>1</sub>	<b>R<sub>1</sub></b> -nr <sub>1</sub>
<b>Exp. 2</b>	<b>Global trial</b>	R <sub>3</sub> -r <sub>4</sub>	R <sub>3</sub> -r <sub>4</sub>	R <sub>5</sub> -r <sub>4</sub>	NR <sub>3</sub> -nr <sub>4</sub>	NR <sub>3</sub> -nr <sub>4</sub>	NR <sub>5</sub> -nr <sub>4</sub>
	<b>Local trial</b>	R <sub>3</sub> -r <sub>4</sub>	R <sub>3</sub> -r <sub>4</sub>	R <sub>3</sub> -r <sub>5</sub>	NR <sub>3</sub> -nr <sub>4</sub>	NR <sub>3</sub> -nr <sub>4</sub>	NR <sub>3</sub> -nr <sub>5</sub>

Furthermore, even if RT data on monkeys are not available, it is still worth to mention those recorded on human subjects. In fact, RT data revealed information hidden by the accuracy data demonstrating that in every experiment redundant stimuli were processed faster than non-redundant ones in both global and local trials. Perhaps, if RT data were recorded also on monkeys, a clearer pattern would have emerged. For this reason, further experiments which could record RT data also on monkeys may provide additional

information about the role played by redundancy on monkey visual cognition.

In Experiment 1 and 2 a local advantage in monkeys was found even with stimuli requiring grouping at local level. A possible interpretation of these results could be that the local advantage was determined merely by the need to use grouping resources twice and therefore, that a certain difficulty in grouping elements leads to their typical local bias. If this was the case, a difference in performance between experiments featuring the same shapes but a different requirement to group elements at the global level should emerge. In order to assess this possibility, a paired sample *t*-test was carried out comparing monkey performance in the global and local trials, considered separately, of experiments featuring the same shapes. Therefore, Experiment 1 vs. 4 and Experiment 2 vs. 3 respectively. The analysis carried out between global trials across Experiment 2 and 3 did not reveal a significant difference, *Global trials*: Exp. 2,  $M = 72.7\%$ ; Exp. 3,  $M = 72.9\%$ , ns. Similarly, a comparison of monkey performance in the local trials of Experiment 2 (where grouping was required at that level) and of Experiment 3 (where local grouping was not required), did not reveal a significant difference, *Local trials*: Exp. 2,  $M = 81.7\%$ ; Exp. 3,  $M = 84.2\%$ , ns. The same analysis was carried out between Experiment 1, consistent set, and Experiment 4, as they featured the same shapes whereas organised in a different way. Once again, paired sample *t*-test comparing monkey performance in the global trials of Experiments 1 and 4 did not reveal a significant difference, *Global trials*: Exp. 1 (cons. condition),  $M = 76.3\%$ ; Exp. 4,  $M = 79.6\%$ , ns. Similarly, a comparison of monkey performance in the local trials of Experiment 1 (where grouping was required at that level) and of Experiment 4 (where local grouping was not required), did not reveal any significant difference, *Local trials*: Exp. 1,  $M = 85.9\%$ ; Exp. 4,  $M = 84.2\%$ , ns.

These analyses indicate that the double grouping required to process the hierarchical stimuli used in Experiment 1 and 2 did not increase the difficulty in monkeys' visual processing and therefore, that grouping requirement cannot be considered as a satisfying explanation of their typical local advantage. Nevertheless, it should be pointed out that in Experiment 1 and 2 the visual angle was wider (global level: 11°; local level: 2.6°) in comparison to that adopted in previous literature (global level: 7°; local level: 0.7°-1.7°) on the same species and this may still account for the local advantage observed in monkeys. Although no longer possible in the present work because of procedural and technical reasons, perhaps further experiments adopting Garner's dot-patterns, specifically like those adopted in Experiment 2, but featuring the same visual angle of the stimuli adopted in Experiment 5 and in previous literature (Spinozzi *et al.* 2003) may help to better address this issue.

Another interesting result is the general no advantage or local advantage displayed by humans across Experiments 1-4. Humans did not show any advantage in Experiments 1 and 2, where there was a need to group elements at both the local and the global level. Conversely, in Experiments 3 and 4, humans revealed a local bias. First of all, it is interesting to pinpoint that, whereas no global-local bias was found in conditions featuring double grouping, a general local advantage emerged in both experiments featuring Navon-like stimuli which still maintained the proportion of the first two experiments. This pattern suggests that different factors may be involved in the processing of *Gestalt* clues, but also that the salience of the local elements increases with the size. Thus, a trade-off between these two factors may have caused the absence of an effect of level of processing in Experiment 1 and 2 and the emergence of a local-bias in Experiments 3 and 4.

In Experiments 3 and 4, there was no requirement to group local elements. Therefore, the need to use attentional resources

required to process that level were reduced. This factor, together with the fact that the stimuli used in the four experiments featured relatively few and large local elements, may have caused the emergence of the present local advantage, which is particularly unusual in humans. This hypothesis was tested in Experiment 5. Therefore, stimuli were manipulated in order to produce stimuli similar in size to those adopted in previous literature. In this experiment, humans displayed a global advantage but only in the many-small elements condition, in which the local elements appeared less salient than in the other condition. Conversely, monkeys displayed their typical local bias again. This latter result is consistent with previous studies in humans which demonstrated that the relative size of the local elements of hierarchical visual stimuli can have an effect on the way in which humans process each level of stimulus structure (Kimchi, 1992).

Finally, Experiment 5 proved again a local advantage in monkeys even when the stimulus size was reduced.

In conclusion, overall this study highlights an additional similarity between monkeys and humans in their visual processing as both species seem to benefit from stimulus redundancy in their visual processing. Furthermore, this study proved again that the capuchin monkey local bias is a very strong feature.

So far it has been proved that monkey are able to group elements into a whole and are sensitive to the relationship between the parts composing the stimulus and to some *Gestalt* grouping clues like the proximity, the similarity and the orientation of local elements (De Lillo *et al.*, 2007; Spinozzi *et al.*, 2009). Furthermore, capuchin monkeys seem to be sensitive to some visual illusions like the *Müller-Lyer* illusion (Sagunama *et al.*, 2007) and possibly the *Solitaire* illusion (Agrillo *et al.*, 2014b). Finally, the results of the current study support the idea that monkeys' local bias is very

strong but they also indicate that capuchins can benefit from the stimulus redundancy in their visual processing.

All these results, taken together, highlight several similarities between humans and capuchin monkeys in their visual cognition and suggest that the search for possible explanations of the observed differences in their global-local processing should point toward higher cognitive mechanisms like the attention set. For this reason, two additional studies, aimed at assessing the role played by the visual attention on global-local processing in tufted capuchin monkeys and humans were carried out.

## **CHAPTER IV**

### **STUDY ON ATTENTION**

#### **EFFECT OF ATTENTION ALLOCATION TOWARDS A PARTICULAR LEVEL OF HIERARCHICAL STIMULI ON GLOBAL-LOCAL PROCESSING**

##### **4.1 INTRODUCTION**

It is well-known that attentional biases are effective in modulating the speed of processing of a particular level of hierarchical stimuli in humans (Kinchla *et al.*, 1983; Lamb & Robertson, 1987, 1988; Miller, 1981; Robertson *et al.*, 1993; Ward, 1982). Some studies demonstrated that visual attention plays an important role also in other animals. For instance, pigeons can selectively shift their attention between different levels of hierarchical stimuli (Fremouw *et al.*, 1998; 2002). However, to my knowledge, there are no studies which have evaluated the role played by the attention allocation to global or local level of hierarchical visual patterns in tufted capuchin monkeys.

The aim of the present study is to evaluate whether or not capuchin monkeys, in comparison to humans, are able to switch their attention between the different levels of hierarchical stimuli, once again using an identity-MTS task.

Monkeys and humans were tested with the same set of hierarchical stimuli previously adopted in these kinds of studies (De Lillo *et al.*, 2005; Fagot & Deruelle, 1997; Spinozzi *et al.*, 2003). However, in previous studies sessions featuring either global or local trials were used. Pervious literature on humans proved that attentional shifts may be generated by changing the proportion of

trials requiring attending to a particular level of stimulus structure within trial sessions (Kinchla et al., 1983; Lamb & Robertson, 1987). Therefore, in this study, in order to evaluate the role of attention in the processing of hierarchical patterns, the proportion of trials featuring global or local processing was manipulated. Two conditions were produced: in the local-bias condition, trials requiring the local processing of the stimulus were more likely to occur than trials requiring the global processing, whereas in the global-bias condition, global processing was required more often than local processing. So in either condition each kind of trial, either global or local, would occur on roughly 86% of times, whereas the other only on roughly 14% of times and vice versa. Sessions featuring global and local trials in different proportions should be effective in producing an attentional bias toward each level of processing. Therefore, by comparing the performances on global and local trials under different bias conditions should be useful to highlight the relative ease, or the relative difficulty, in allocating attention to a particular level of the stimuli in the two species.

As opposed to the first study, where results were analysed using a mixed, between species ANOVA, in this study the experiments were analysed separately. Therefore, the same kind of task will be presented as two separate experiments run on two different species.

## **4.2 EXPERIMENT 1**

The first experiment was addressed to understand how attention allocation can affect monkey global-local processing.

## 4.2.1 Method

### 4.2.1.1 Participants

The same five subjects tested on the previous Study on Redundancy took part in this experiment. They were 1 female (Pippi) and 4 males (Gal, Patè, Rubens and Vispo) ranging in age from 7 to 28 years at the moment of the beginning of the test.

### 4.2.1.2 Stimuli and Procedure

The stimuli used in this experiment are presented in Figure 33. They were generated using *Microsoft PowerPoint* and featured white forms on a black background. The stimulus set comprised the eight compound forms used by Fagot & Deruelle (1997) with baboons and subsequently by Spinozzi *et al.* (2003) with capuchin monkeys.

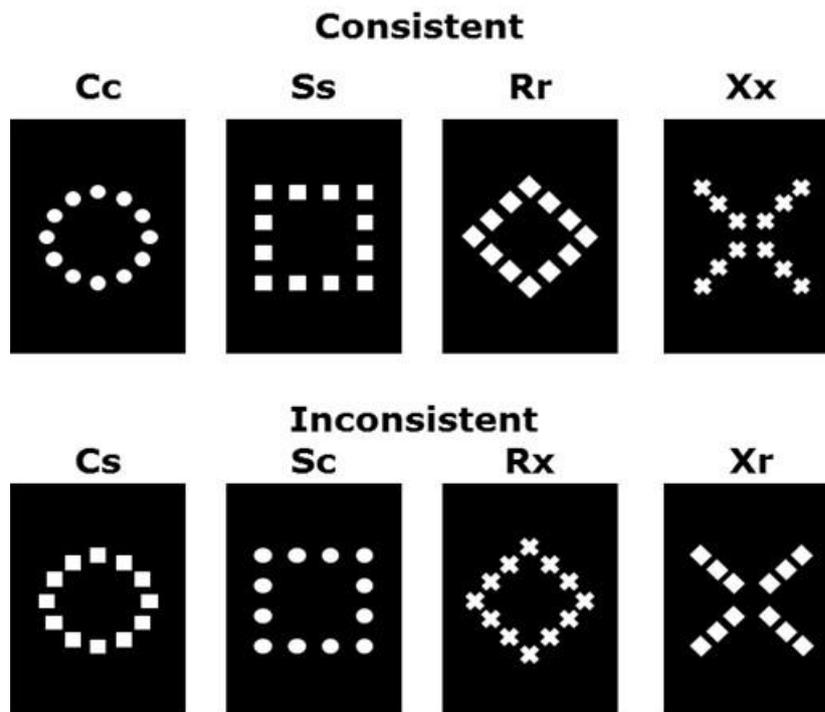


Figure 33. Set of stimuli adopted in the study on attention.

The stimulus set included large rhombi (R), squares (S), circles (C) and letter Xs (X) formed by smaller rhombi (r), squares (s), circles (c) and letters Xs (x). The shape of the global level could be identical (consistent stimuli) or dissimilar (inconsistent stimuli) from the shape of the local level. Stimuli measured about 4 x 4 cm at the global level and had 12 local elements measuring about 0.5 x 0.5 cm. Monkeys viewed the stimuli from about 30 cm distance. At this distance, the stimuli subtended about 7° of va at the global level and 0.9° of va at the local level.

An identity-MTS task was adopted as described in the dedicated session of Chapter II.

As was done in the Study on Redundancy, the sample stimulus was presented between the two comparison stimuli but above them (see Figure 7a, Chapter II).

The task involved two types of Identity-MTS trials. In both global and local trials S+ was always identical to the sample stimulus SS. By contrast, S- was different from SS only at the global level in the global trials and at the local level in the local trials. An example of a local and a global trial is presented in Figure 34.

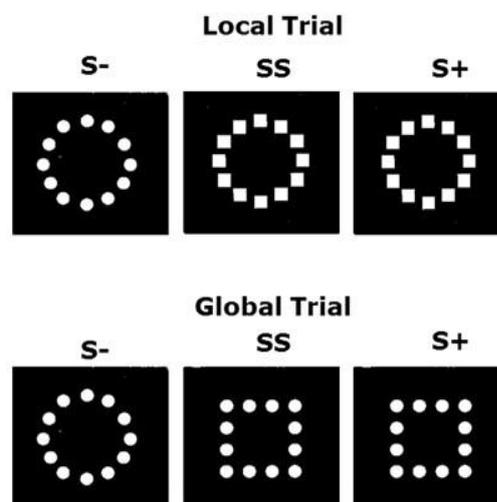


Figure 34. Example of local (above) and global (below) trials with hierarchical stimuli.

Two different bias conditions were produced in this experiment. In the global-bias condition, 85.7% of trials required the processing of the global level of the stimuli (i.e., global trials) and the remaining 14.3% of trials required the processing of the local elements of the stimuli (i.e., local trials). In the local-bias condition, these probabilities were reversed. Therefore, 85.7% of trials required the processing of the local elements whereas the remaining 14.3% global trials required the processing of the global level. In other words, each daily session consisted of 24 trials featuring either global or local trials plus 4 trials featuring either local or global trials. Each subject performed 16 sessions of 28 trials each, one session a day, for a total 448 trials. Either the global-bias or the local-bias condition was presented in each session, with the non-bias trials randomly intermixed. For each bias condition, stimuli could be consistent (Cc, Ss, Rr and Xx) and inconsistent (Cs, Sc, Rx and Xr) in equal number and pseudo-randomly intermixed. This was done to make sure that the same comparison would not appear more than twice consecutively and that S- and S+ appeared on both left and right sides with the same frequency. Each subject performed four consecutive sessions featuring the same bias condition. After completing a 4-session block the bias condition was reversed. Two subjects started with the local-bias condition whereas the remaining subjects started with the global-bias condition.

Before each experimental session, 9 practice identity-MTS trials were administered using non-hierarchical stimuli (e.g., simple white forms on a black background). The aim of these trials was to assess the MTS performance level of the subjects before each testing session. The criterion to be achieved in order to proceed to the test was to score at least eight correct responses out of nine. If subjects did not reach the criterion, the session was interrupted. This only happened on five occasions.

## 4.2.2 Results

### 4.2.2.1 Accuracy

Table 9 reports the percentage of correct responses recorded with each animal in the different conditions of Experiment 1.

*Table 9. Mean individual percentages of correct responses recorded for each monkey in the different conditions of Experiment 1*

Subjects	Local-bias		Global-bias		Combined	
	Local trials	Global trials	Local Trials	Global trials	Local trials	Global trials
<b>Gal</b>	85.4	75.0	59.4	82.3	72.4	78.7
<b>Patè</b>	81.8	71.9	62.5	75.5	72.2	73.7
<b>Pippi</b>	86.5	81.3	77.8	81.5	82.2	81.4
<b>Rubens</b>	72.9	59.4	65.6	76.0	69.3	67.7
<b>Vispo</b>	81.8	68.8	56.3	77.6	69.1	73.2

To assess whether monkeys' performance was above the chance level both, one-sample *t*-tests (for the whole group) and binomial tests (on each subject) were performed. The one sample *t*-test revealed that the percentage score obtained by the group for each type of trial in the different conditions was significantly above the 50% expected by chance, *Local-bias*: local trials,  $t(4) = 13.26$ ,  $p < .001$ ; global trials,  $t(4) = 5.88$ ,  $p < .01$ . *Global-bias*: local trials,  $t(4) = 3.86$ ,  $p = .05$ ; global trials,  $t(4) = 20.49$ ,  $p < .001$ . The binomial tests carried out on the frequencies of correct responses recorded for each subject in the global and the local trials, combining the two bias conditions, confirmed that all the subjects responded correctly above the 50% expected by chance in both types of trials (all  $ps < .01$ ).

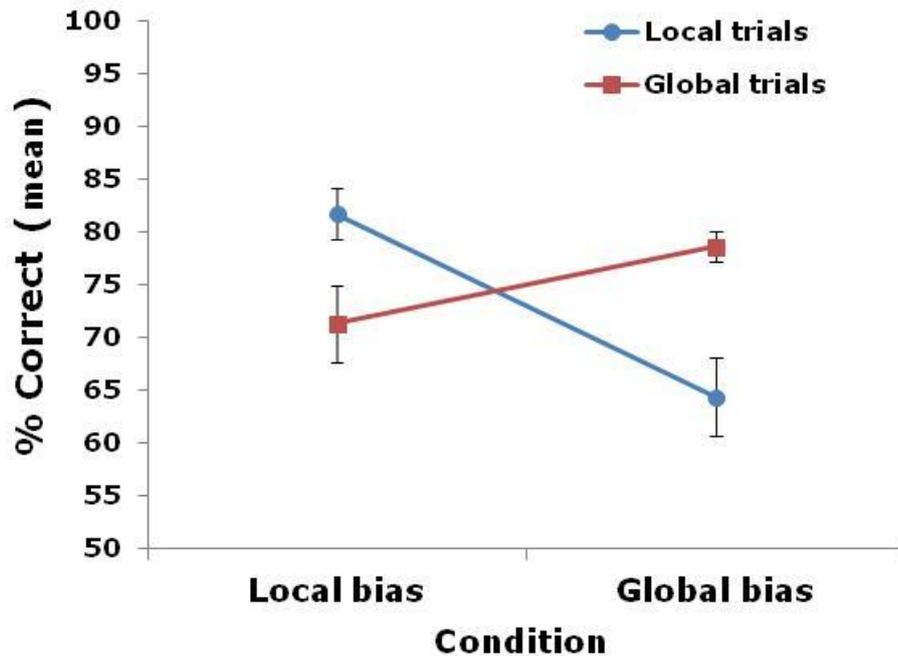


Figure 35. Percentages of correct responses recorded for monkeys in the local and global trials in the two bias conditions of Experiment 1. Error bars represent one Standard Error.

By inspecting Figure 35, it is visibly evident a cross-over of the two lines representing the overall percentage of correct responses recorded in the local and global trials, which suggest that the attention bias affected the global-local performance. A 2 (Bias Conditions) x 2 (Level of Processing) x 2 (Stimulus Consistency) repeated measures ANOVA confirmed this effect. In fact, the ANOVA did not show any significant main effect, however, it revealed a significant interaction between Bias condition and Level of Processing,  $F(1, 4) = 28.99, p < .01, \eta_p^2 = .879$ . None of the other interactions yielded significant results.

In order to explain in detail the significant interaction between bias condition and level of processing, post-hoc comparisons (Fisher's LSD test) were carried out. The post-hocs revealed that accuracy scores registered in the local-bias condition were higher for local trials than for global trials (*Local-bias*: local trials,  $M = 81.7%$ ; global trials,

$M = 71.3\%$ ;  $p < .05$ ). Conversely, in the global bias condition accuracy scores were higher for global trials than for local trials (*Global-bias*: local trials,  $M = 78.6\%$ ; global trials,  $M = 64.3\%$ ,  $p < .05$ ). Furthermore, accuracy scores for local trials were significantly higher in the local-bias condition than in the global-bias condition (*Local trials*: local-bias,  $M = 81.7\%$ ; global-bias,  $M = 64.3\%$ ,  $p < .01$ ). The same effect was not observed for global trials. In fact, although monkeys performance in global trials was higher in the global-bias condition compared to the local-bias condition (see Figure 35), this difference only approached significance (*Global trials*: local-bias,  $M = 71.3\%$ ; global-bias,  $M = 78.6\%$ ,  $p = .089$ ).

In order to assess if the amount of task exposure had an effect on the observed pattern of results, the results of the 8 sessions for each bias condition were divided into two blocks, each one featuring 4 sessions. Then, the same analyses were carried out for each of the two 4-session blocks (see Figures 36 and 37).

The ANOVA carried out on the first block did not reveal any significant main effects but it revealed a significant interaction Bias Condition by Level of Processing,  $F(1, 4) = 54.59$ ,  $p < .005$ ,  $\eta_p^2 = .932$ . Post-hoc comparisons (Fisher's LSD test) explained the nature of this interaction as revealed a significant difference between the level of accuracy shown by the monkeys in the local and global trials in the global-bias condition (*Global-bias*: global trials,  $M = 76.3\%$ ; local trials,  $M = 57.5\%$ ,  $p < .05$ ). However, in the local-bias condition this difference was not significant (*Local-bias*: local trials,  $M = 80.2\%$ ; global trials,  $M = 75.0\%$ , ns).

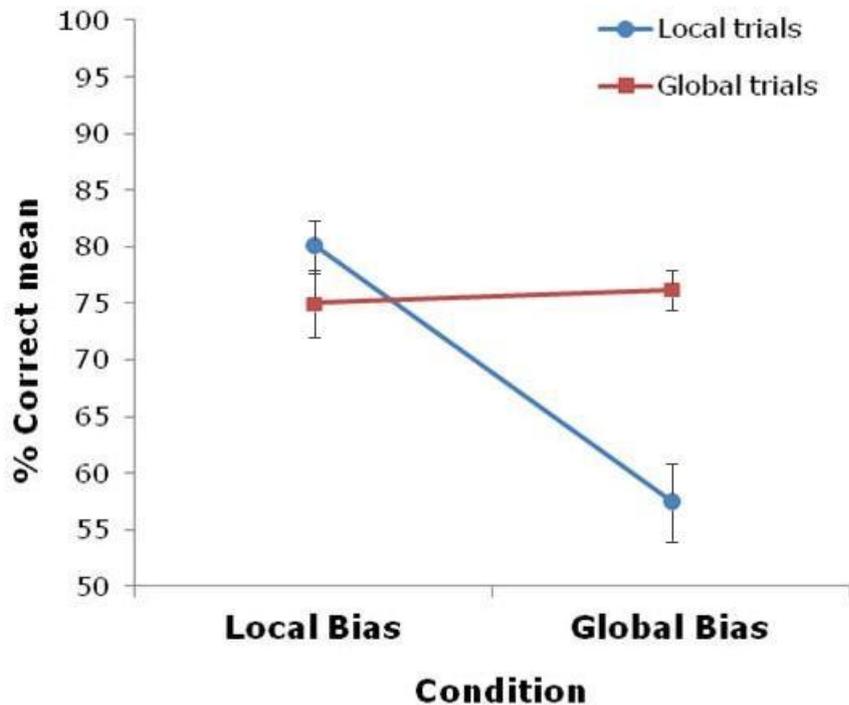


Figure 36. Percentages of correct responses recorded for monkeys in the local and global trials, in the two bias conditions, in the first 4-session block of Experiment 1. Error bars represent one Standard Error.

Furthermore, as was observed in the ANOVA for the two blocks combined, performance in the local trials was different in the two bias conditions (*Local trials*: global-bias,  $M = 57.5\%$ ; local-bias,  $M = 80.2\%$ ,  $p < .05$ ), whereas the global trials were not significantly affected by attention bias (*Global trials*: global-bias,  $M = 76.3\%$ ; local-bias,  $M = 75.0\%$ , ns).

The same analysis was carried out in the second block of trials not revealing any significant main effect but revealing a significant interaction between bias condition and level of processing,  $F(1,4) = 14.68$ ,  $p < .05$ ,  $\eta_p^2 = .786$ . In fact, post-hoc comparisons (Fisher's LSD test) revealed significant differences between the local and global trials in both bias conditions (*Global-bias*: global trials,  $M = 80.7\%$ ; local trials,  $M = 70.8\%$ ,  $p < .05$ ; *Local-bias*: local trials,  $M = 83.1\%$ ; global trials,  $M = 67.5\%$ ,  $p < .05$ ).

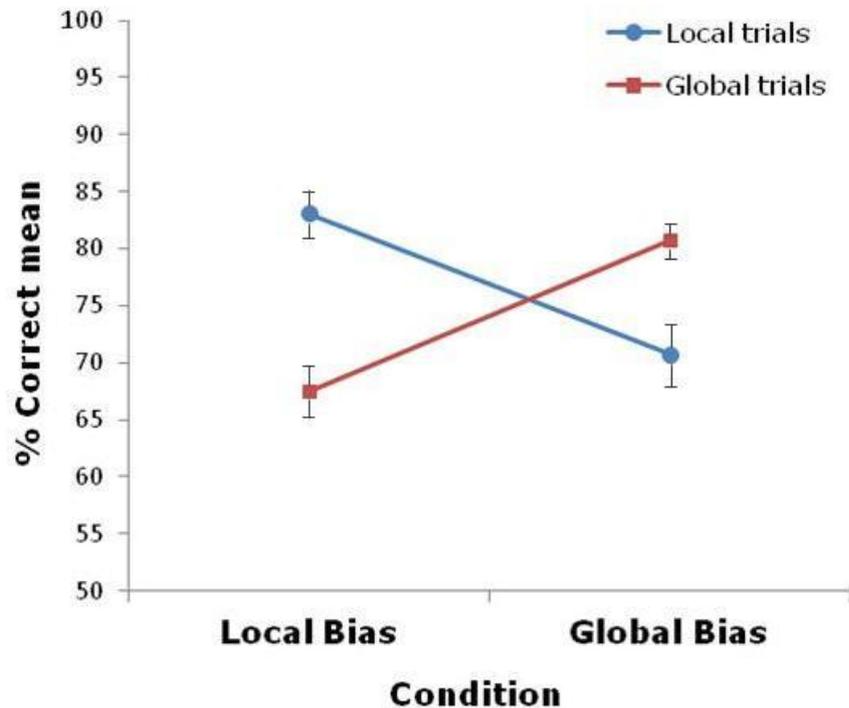


Figure 37. Percentages of correct responses recorded with monkeys in the local and global trials, in the two bias conditions, considering only the 4-session second block of Experiment 1. Error bars represent one Standard Error.

Moreover, in addition to a significant reduction in the performance in the local trials in the global-bias condition (*Local trials*: global-bias,  $M = 70.8\%$ ; local-bias,  $M = 83.1\%$ ,  $p < .05$ ), which was reported also in the first block, here the attention bias also affected the global trials, *Global trials*: global-bias,  $M = 80.7\%$ ; local-bias,  $M = 67.5\%$ ,  $p < .05$  (adapted from De Lillo, Spinozzi, Palumbo, Giustino, 2011).

#### 4.2.3 Discussion Experiment 1

The results of this experiment demonstrate that attentional bias produced by administrating session with a different amount of trials

across conditions was effective in reversing monkey typical local-bias. Monkeys displayed a local advantage in the local-bias condition and, for the first time, they displayed a global advantage in the global-bias condition. This is the first evidence that capuchin monkey local advantage can be reversed under appropriate attentional conditions. However, it has to be emphasised that the effect of the bias condition was predominantly evident in the local trials. The accuracy recorded on local trials was very high when subjects' attention was biased toward the local level of hierarchical stimuli. Conversely, it deteriorated dramatically when they were biased attending towards the global structure. On the other hand, whereas accuracy in processing local trials was reduced in the global-bias condition in comparison to the local-bias condition, performance on global trials across the two bias conditions failed to produce a significant difference. The analysis carried out on the two 4-session blocks revealed also that the effect of the bias condition emerged early in the first 4-session block for local trials, whereas for global trials the effect of the bias condition emerged only in the second 4-session block. In fact, percentage scores recorded for global trials in the first 4-session block according to the two bias conditions were very similar. However, the effect of the bias condition emerged clearly in the second 4-session block where a significant difference in accuracy was observed in the global trials according to the attention bias. In fact, the percentage of correct responses in the global trials was significantly higher when they were presented as part of the global-bias condition than when they were presented during the local-bias condition. Therefore, the changing in performance between the two bias conditions was complete only in the second 4-session block. These results indicate that, in capuchin monkeys, global processing requires more time to achieve the same results obtained with less time on local processing and therefore, that global processing is less sensitive to attentional bias conditions.

Taken together, these findings indicate that monkeys' global-local processing can be affected by attentional biases as matching performance changed across the two bias conditions. However, this pattern developed earlier and was particularly robust in local trials.

## **4.3 EXPERIMENT 2**

In order to allow interspecies comparisons, the same experiment carried out with monkeys was carried out with humans.

### **4.3.1 Method**

#### ***4.3.1.1 Participants***

The group of human participants comprised 12 (5 males and 7 females). The requirements to take part in the experiment are described in Chapter II.

#### ***4.3.1.1 Stimuli and Procedure***

The stimuli, converted in bitmaps, were presented using the experimental set-up described in Chapter II. The size of the stimuli on the screen and the distance between each subject and the screen were controlled so that all the stimuli always featured 7° of va at global level and 0.9° of va at local level. The Identity MTS trials were administrated as described in Chapter II.

### **4.3.2 Results**

#### ***4.3.2.1 Accuracy***

Figure 38 depicts the percentage of correct responses recorded with humans in the local and global trials across the two bias conditions (Local-bias condition and Global-bias condition). The

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

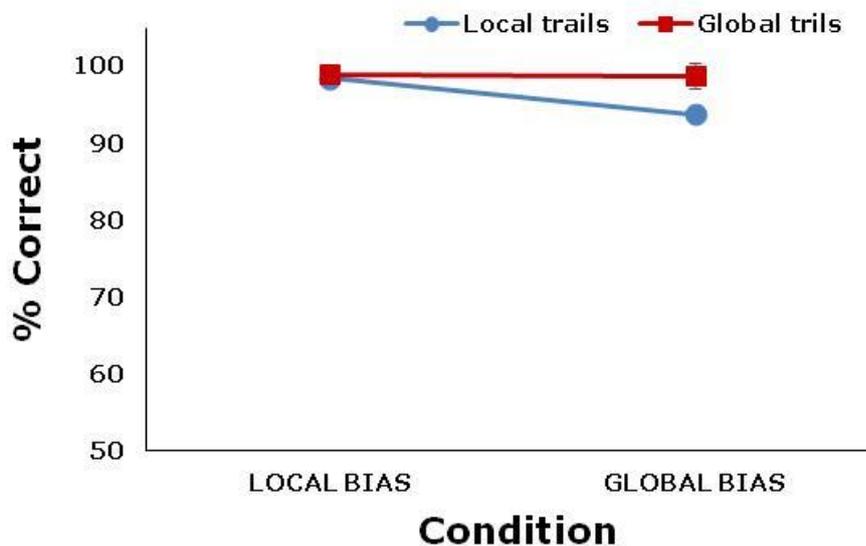


Figure 38. Percentages of correct responses recorded with humans in the local and global trials in the two bias conditions of Experiment 2. Error bars represent one Standard Error.

An inspection of Figure 38 suggests that in global trials, humans performed at a particularly high level of accuracy that was maintained regardless of the bias condition within which these trials were presented. A similar level of high performance can be observed in the local trials. However, performance in the local trials seems more vulnerable. In fact, the figure shows that the local trials seem to be deteriorating in the global-bias condition.

The above observations were confirmed by a 2 (Bias Condition) x 2 (Level of Processing) x 2 (Stimulus Consistency) repeated measures ANOVA carried out on the percentage of correct responses obtained in this experiment. The ANOVA revealed significant main effects for level of processing,  $F(1, 11) = 17.2, p < .01, \eta_p^2 = .610$ , and bias condition,  $F(1, 11) = 8.27, p < .05, \eta_p^2 = .429$ . Therefore, overall, global trials ( $M = 98.8\%$ ) were processed better than local

ones ( $M = 95.5\%$ ) and during the local-bias condition humans performed with higher level of accuracy ( $M = 98.7\%$ ) as opposed to the global-bias condition ( $M = 95.7\%$ ). Conversely, the factor consistency did not produce significant main effects. Importantly, the interaction Bias Condition by Level of Processing was significant,  $F(1,11) = 7.49, p < .05, \eta_p^2 = .405$ .

Post-hoc comparisons (Fisher's LSD test) carried out to better understand the two-way interaction showed that, in the global-bias condition, the performance level was significantly lower for local than for global trials (*Global-bias*: local trials,  $M = 92.7\%$ ; global trials,  $M = 98.7\%$ ,  $p < .01$ ). Conversely, in the local-bias condition, the percentages of correct choices were similar for both local ( $M = 98.4\%$ ) and global ( $M = 99.0\%$ ) trials. Moreover, performance level for local trials was significantly higher in the local-bias compared to the global-bias condition (*Local trials*: local-bias,  $M = 98.4\%$ ; global-bias,  $M = 92.7\%$ ,  $p < .01$ ). By contrast, the percentage of correct response for global trials was nearly identical in both conditions (*Global trials*: local-bias,  $M = 98.7\%$ ; global-bias,  $M = 99.0\%$ , ns).

Consistently with the analysis carried on monkeys, the total sessions were divided in 2 blocks of 4 sessions each and an analysis of variance was performed on each session block. The average percentage of correct responses was subjected to a 2 (Bias Condition) x 2 (Level of Processing) x 2 (Consistency) repeated measures ANOVA on the two blocks of trials featuring Experiment 2. However, as the pattern observed in each 4-session block is very similar to the overall pattern, and given the fact that this analysis has been reported for the more informative RT data (see below), for brevity it will not be reported here (adapted from De Lillo *et al.*, 2011).

#### 4.3.2.2 Response Times

The average RT observed in the local and global trials, filtered per correct answers only, in the two bias conditions is presented in Figure 39.

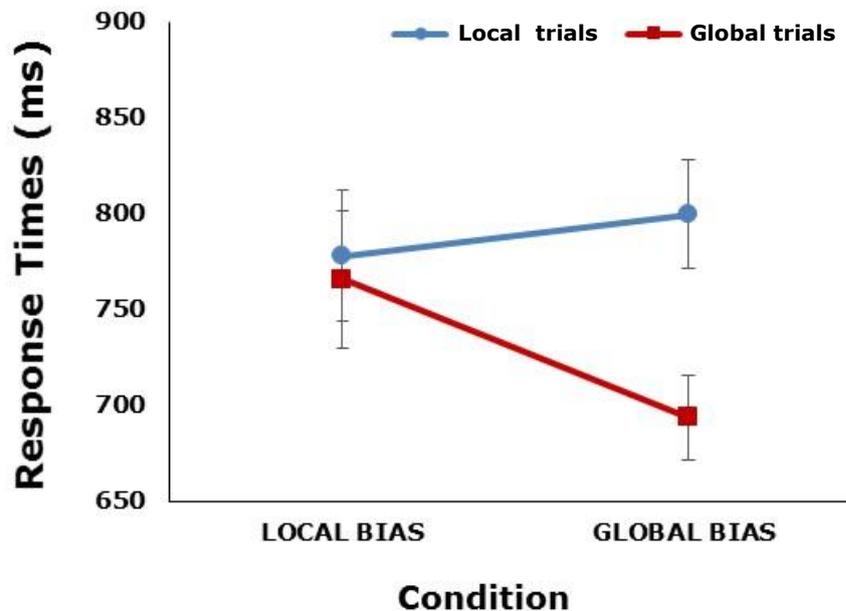


Figure 39. Mean of RTs (ms) recorded for correct responses performed by humans in the local and global trials across the two bias conditions of Experiment 2. Error bars represent one Standard Error.

Figure 39 displays that the participants were always faster in the global trials. RT appears to be dramatically reduced in the global trials in the global-bias condition indicating a benefit in performance from the bias condition. Moreover, there seems to be an indication that the local-bias reduced the time required to process the local trials whereas this effect of attention bias is not evident in the global trials.

Average RTs, filtered per correct answer, were subjected to a 2 (Bias Condition) x 2 (Level of Processing) x 2 (Consistency) repeated measures ANOVA. The analysis displayed significant main effects for

Level of Processing,  $F(1, 11) = 27.84, p < .001, \eta_p^2 = .717$ , and Consistency,  $F(1, 11) = 8.05, p < .05, \eta_p^2 = .423$ , whereas the factor Bias Condition was not significant. Therefore, humans proved faster when responding to global ( $M = 694.2$  ms) rather than to local trials ( $M = 748.8$  ms) and processed consistent stimuli faster ( $M = 706.3$  ms) than inconsistent ones ( $M = 736.7$  ms). Interestingly, the interaction Bias Condition by Level of Processing proved highly significant,  $F(1, 11) = 70.86, p < .001, \eta_p^2 = .866$ , indicating that bias condition played a role in the speed of processing of the stimuli. None of the other interactions was significant.

Post-hoc comparisons (Fischer's LSD test) revealed that responses to local trials were faster in the local-bias than in the global-bias condition (*Local trials*: local-bias,  $M = 734.8$  ms, global-bias,  $M = 762.9$  ms;  $p < .01$ ), whereas responses to global trials were faster in the global-bias than in the local-bias condition (*Global trials*: global-bias,  $M = 666.2$  ms, local-bias,  $M = 722.3$  ms,  $p < .001$ ). Thus, variation in the proportion of trials requiring the processing of a particular level (global or local) of the stimulus produced a change in the speed of responding at that level. Moreover, response times in the global and local trials were significantly different in the global-bias condition (*Global-bias*: global trials,  $M = 666.2$  ms; local trials,  $M = 762.9$  ms,  $p < .001$ ) but not in the local-bias condition (*Local-bias*: global trials,  $M = 722.3$  ms; local trials  $M = 734.8$  ms, ns).

Consistently with the analysis carried on monkeys, the total sessions were divided into 2 blocks of 4 sessions each and each 4-session block was subjected to the same analysis performed on the whole sample.

The ANOVA carried out on the first block revealed significant main effects for Level of Processing,  $F(1,11) = 29.866, p < .001, \eta_p^2 = .731$ , and stimulus Consistency,  $F(1,11) = 9.400, p < .05, \eta_p^2 = .461$ . Therefore, the ANOVA demonstrated that, as observed in the

overall analysis, humans were faster when had to respond to global trials ( $M = 755.4$  ms) than to local ones ( $M = 819.4$  ms) and they processed consistent stimuli ( $M = 765.9$  ms) faster than inconsistent ones ( $M = 808.8$  ms). Interestingly, the interaction Bias Condition by Level of Processing proved highly significant,  $F(1,11) = 32.305$ ,  $p < .001$ ,  $\eta_p^2 = .746$ , indicating that bias played a role in the speed of processing of the stimuli. Post-hoc comparisons (Fischer's LSD test) carried out to clarify the latter interaction, revealed that responses times to global trials were faster in the global-bias in comparison to the local-bias condition (*Global trials*: global-bias,  $M = 716.3$  ms; local-bias,  $M = 794.4$  ms;  $p < .05$ ). Moreover, there was a highly significant difference between the speed of responding to the global and local trials in the global-bias condition (*Global-bias*: global trials,  $M = 716.3$ ; local trials,  $M = 830.0$  ms;  $p < .001$ ) but not in the local-bias condition.

The same analysis was performed on the second 4-session block revealing a very similar pattern of results as depicted in Figure 40. The ANOVA revealed a significant main effect for level of processing,  $F(1, 11) = 1.064$ ,  $p < .01$ ,  $\eta_p^2 = .088$ , and a significant interaction Bias Condition by Level of Processing,  $F(1, 11) = 19.278$ ,  $p = .001$ ,  $\eta_p^2 = .637$ . Post-hoc comparisons (Fischer's LSD test) carried out to clarify the 2-way interaction revealed that in the global-bias condition global trials were processed faster than local ones (*Global-bias*: global trials,  $M = 670.8$  ms; Local trials,  $M = 737.9$  ms,  $p = .001$ ). Furthermore, global trials were processed faster in the global-bias condition rather than in the local one (*Global trials*: global-bias,  $M = 670.8$  ms; local-bias,  $M = 737.9$  ms,  $p < .05$ ), also local trials were processed faster in the local bias condition than in the global ones, *Local trials*: local-bias,  $M = 715.8$  ms; global-bias,  $M = 767.9$  ms,  $t(11) = 2.409$ ,  $p = .05$ . However, if the Bonferroni correction is applied, this last value does not remain significant (adapted from De Lillo *et al.*, 2011).

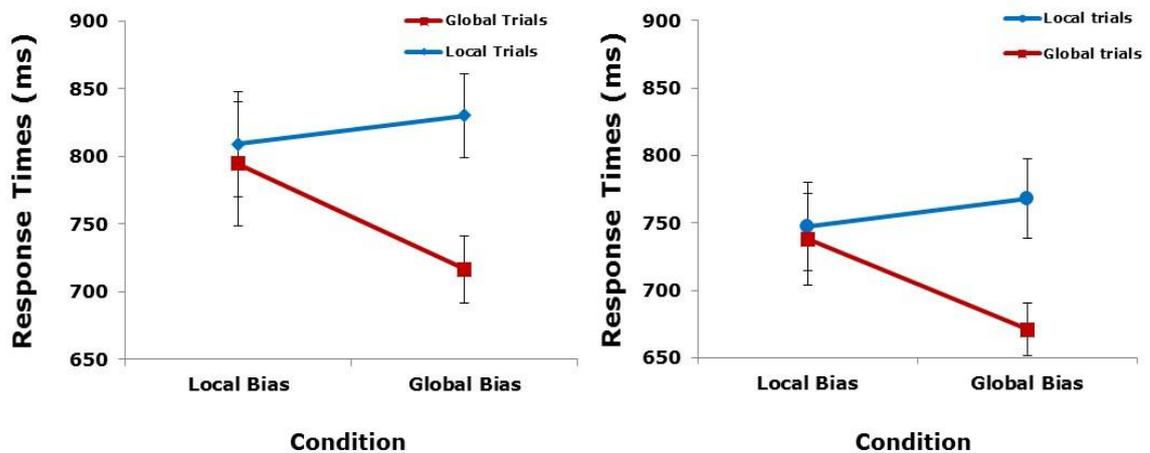


Figure 40. Mean RTs (ms) recorded for humans depicted as separate graphs for the first 4-session block (on the left) and second 4-session block (on the right). Error bars represent one Standard Error.

### 4.3.3 Discussion Experiment 2

Results on humans are quite informative in both accuracy and response times. Overall, in terms of accuracy, a general better performance was recorded when subjects were processing the global trials than the local ones. In particular, a clear global advantage emerged in the global-bias condition, whereas in the local-bias condition did not emerge any advantage. In fact, global processing was not significantly affected by the bias condition as performance for global trials was almost the same across conditions (local-bias,  $M = 99.0\%$ ; global-bias,  $M = 98.7\%$ ).

The results of the analysis performed on the RTs partly resemble that one of accuracy as they revealed an overall global advantage. Furthermore, during the global-bias condition, global trials yielded faster RTs in comparison to local ones. As was observed for accuracy data, no advantage emerged in the local-bias condition. In fact, in the

local-bias condition, the RT recorded for global and local trials was extremely similar. These results indicate that the attentional bias was not able to slow down the response times in the global trials in comparison to local trials. However, post-hoc comparisons between trials across conditions revealed that responses to local trials were faster in the local-bias than in the global-bias condition, whereas responses to global trials were faster in the global-bias than in the local-bias condition. This latter result is different to that found in the accuracy data where no difference was found in the global trials across conditions. Therefore, the attentional bias produced was effective even though it was not possible to produce a complete trade-off in performance across conditions. In fact, either level of processing was processed faster in the bias condition featuring it the most, rather than in the bias condition featuring it the least. Furthermore, a comparison between accuracy and RT data reveals that, whereas in the accuracy global trials were not affected by the bias conditions, this was not true for what concerns the RT data where responses to global trials were faster in the global-bias than in the local-bias condition when considered overall. However, in the local-bias RT values recorded for global and local trials were extremely similar. These data suggest that attentional allocation to the local level was not adequate to slow down global processing in humans and support the idea that global processing is a very robust feature of human visual cognition. Furthermore, both accuracy and RT data, although in a different way, indicate that global processing is less sensitive to attentional biases. This interesting result will be further discussed in the general discussion to the entire research work (see Chapter VI).

Finally, in contrast with monkeys, whose performance changed with practice, human performance was very similar across the two 4-session blocks revealing that the attentional bias started to be effective at an early stage of the experiment.

#### 4.4 DISCUSSION

In the previous study on redundancy, another similarity between humans and capuchin monkeys in their visual cognition was found, as results indicated that both species are sensitive to stimulus redundancy when processing hierarchical stimuli. Nevertheless, monkey typical local bias persisted in every experiment, proving to be a very strong feature as opposed to human typical global advantage. Therefore, the present study was another attempt to search for conditions under which monkey local advantage persists and, by doing so, suggest possible mechanisms responsible for this difference between monkey and human visual cognition.

The aim of this study was to assess the role played by visual attention in the global-local processing in monkeys in comparison with humans. In order to modulate attention allocation to different levels of hierarchical stimuli, the same procedure previously used in the literature in similar studies in human visual cognition (Kinchla *et al.*, 1983) was adopted in this study.

The results obtained here provide, for the first time, clear evidence that capuchins' typical local advantage can be reversed under appropriate conditions. In fact, monkeys showed an advantage in processing local trials in comparison to global trials in the local-bias condition and an advantage in processing global trials in comparison to local trials in the global-bias condition.

In the present study, there was no control condition which could be useful to compare the level of performance in absence of a requirement to shift attention from each level of processing across trials. However, some information can be obtained from previous studies carried out on capuchin monkeys using blocked sessions featuring entirely global or local trials (e.g., Spinozzi *et al.*, 2003; Spinozzi *et al.*, 2006). These experiments were carried out on the

same colony of monkeys and using the same stimuli and procedure, however, only two out of five subjects were the same. The overall performance recorded for monkeys on global trials in the present study combined for the two bias-conditions ( $M = 74.9\%$ ), was very similar to that observed in the global trials of those previous studies (74.1% average of values observed in Spinozzi *et al.*, 2003, Exp. 1, and Spinozzi *et al.*, 2006, Exp. 1). However, the observed level of performance in the local trials, combined for the two bias-conditions, was lower in the present study (73.0%), compared to that of the previous studies (89.1% average of values observed in Spinozzi *et al.*, 2003, Exp. 1, and Spinozzi *et al.*, 2006, Exp. 1). This is possibly due to the requirement to switch between different levels of processing. This difference is particularly sharp when considering local trials recorded during the global-bias condition ( $M = 64.3\%$ ). This tendency persists even when considering only the two subjects (Pippi and Gal) who took part in all studies (percentage of correct responses observed in the local trials for Spinozzi *et al.*, 2003 and Spinozzi *et al.*, 2006 combined, Pippi: 85.6%, Gal: 91.0%). The performance of local trials combined for the two bias-conditions Pippi: 82.2%, Gal: 72.4%). Again, also considering Pippi and Gal only, the differences become even sharper when considering the local trials presented as part of the local-bias condition only (see Table 9 for the values). These observations confirm the idea that, in monkeys, attention allocation using an MTS task affected principally local processing.

In the present study, humans showed a global advantage in their accuracy in the global-bias condition but not in the local-bias condition. In fact, whereas in the global-bias condition accuracy was higher in global trials than in local ones, in the local-bias condition performance recorded on each level of processing was very similar. Moreover, while accuracy for local processing was better in the local-bias condition compared to the global-bias condition, the same effect

was not observed for global processing across the two bias conditions. Accuracy for global trials appeared nearly identical during the two bias conditions. Furthermore, even reaction times recorded in global and local trials in the local-bias condition were extremely similar indicating that attentional bias was not able to slow down global trials in comparison to local trials.

Comparing the two experiments it is possible to see some similarities in the way in which visual attention acts on global-local processing in the two species. In fact, even if in a different way, in both species attentional biases seems to be less effective in global trials. This effect in humans is particularly evident in accuracy data but it also emerged in the reaction times when latencies between trials are compared in the local-bias condition.

In conclusion, in this study, attentional biases produced administering sessions with different proportions of trials using a matching-to-sample procedure were effective in determining a trade off in global-local performance in both species. However, results recorded for both species revealed that global trials were less sensitive to attentional biases. This interesting result will be further discussed in the general discussion.

## **CHAPTER V**

### **STUDY ON SPATIAL FREQUENCIES**

#### **EFFECT OF ATTENTION TOWARDS DIFFERENT SPATIAL FREQUENCIES ON GLOBAL-LOCAL PROCESSING**

##### **5.1 INTRODUCTION**

As mentioned in the introduction, global-local processing seems to be related to spatial frequency (SF) processing. Many factors have been considered in order to explain this relationship. Some investigators described it in terms of hemispheric specialization (see for example Boeschoten *et al.*, 2005; Evans *et al.*, 2000; Fink *et al.*, 1996; Heinze *et al.*, 1998) whereas others stressed more on the spatial frequency content of the stimulus (Shulman *et al.*, 1986; Shulman & Wilson 1987; Robertson, 1996) and its role in the global-local processing. The interaction between global-local processing and SFs processing can also be seen in relation to the distribution of attention. As suggested by Shulman and Wilson (1987), in humans sensitivity to particular spatial frequencies might be controlled by the areal spread of attention to local or global information. This hypothesis was supported also by a following study (e.g., Flevaris *et al.*, 2011) which replicated the same experiment but using compound grating patterns rather than simple grating patterns (see Chapter I). Flevaris's work demonstrated that an important factor in determining attentional bias was not the absolute value in cpd of each grating composing the pattern, but its relative role, either high or low, in the compound grating. In fact, the same frequency could elicit different

responses depending on its relative role, either high or low, in the compound stimulus. These findings support the idea that global-local processing and SF processing can be modulated by a flexible top-down mechanism.

Since the previous study proved that visual attention plays a very important role in capuchin and human global-local processing, the aim of this last study is to assess whether the distribution of the attention to high or low spatial frequencies can affect the ability to detect the local or global structure of the stimulus.

As it was not known how capuchins process different SFs, a first experiment was carried out in order to clarify which one, among six different spatial frequency patterns, was processed better by the two species. The patterns ranged from 0.25 to 8.0 cpd of visual angle, SFs within this range of cpd can be well discriminated by humans (De Valois & De Valois, 1988) but very little research has been carried out to highlight potential differences between human and non-human primates on their ability to detect some particular spatial frequencies. Furthermore, to my knowledge, the studies carried out in this direction involved mostly Old World primate species such as macaques and chimpanzees (see for example De Valois *et al.*, 1974 for macaques and Matsuno & Tomonaga, 2006 for chimpanzees) but never involved neo-tropical primate species such as tufted capuchin monkeys. Therefore, the main purpose of Experiment 1 was to identify the SFs which can be well detected by capuchin monkeys and humans and so be used in the second experiment.

In the previous study on attention (see Chapter IV) it was demonstrated that biasing attention allocation to one level of hierarchical visual stimuli significantly affects the detection to the other level in both species (see Chapter IV). The aim of the second experiment is to clarify whether or not biasing attention allocation towards either HSFs or LSFs can affect global and local visual processing in capuchin monkeys and humans. The rationale is that if

the preferential level of processing of hierarchical structure of visual stimuli is mediated by a preferential processing of particular bands of spatial frequency, then it should be affected by manipulations of the number of trials within a session which require focusing on particular spatial frequencies. Therefore, in the second experiment, tasks featuring SF trials intermixed with few tasks featuring global-local trials were administered. In fact, as it was demonstrated by the study on attention, administering a different proportion of trials within each session has been proved effective in manipulating attentional biases (see also Fremouw *et al.*, 1998; Kinchla *et al.*, 1983; Lamb & Robertson, 1987).

## **5.2 EXPERIMENT 1**

This experiment evaluated the ability of monkeys in comparison to humans to process low, medium or high spatial frequencies by presenting a sequence of trials requiring matching spatial frequency gratings of given frequencies. Therefore, the aim of this experiment was to identify the SFs which can be well detected by monkeys and humans in order to select the appropriate LSF and HSF patterns to be used in the second experiment to produce an attention bias towards them. To do so, an identity MTS task was administered in which subjects had to identify trials featuring six different sine-wave grating patterns ranging from 0.25 cpd of  $v_a$  and 8.0 cpd of  $v_a$ . SFs within this range of cpd have been previously demonstrated to be well discriminated by humans (De Valois & De Valois, 1988).

## 5.2.1 Experiment 1a: Monkeys

### 5.2.1.1 Method

#### 5.2.1.1.1 Participants

The monkey sample included three out of five monkeys which took part in the previous studies: 1 female (Pippi) and 2 males (Gal and Rubens) aged from 8 to 29 years. The subjects were already familiar with the MTS procedure as they had been previously tested using hierarchical patterns (see previous studies and De Lillo *et al.*, 2005; Spinozzi *et al.*, 2006). However, none of them had ever been tested with grating patterns before.

#### 5.2.1.1.2 Stimuli and Procedure

In this experiment, spatial frequency grating patterns were adopted as visual stimuli. Each stimulus consisted of a grating plus a Gabor-Mask. The stimuli were obtained by converting a sinusoidal function into an image using the software *Mat-lab.r2010a*. The Gabor-mask allowed a higher level of contrast in the centre of the grating that dropped down toward the edge of the pattern.

The stimulus set included 18 SF gratings. Among these patterns, those used as sample and correct comparison stimuli featured the following cpd values: 0.25, 0.5, 1.0, 2.0, 4.0 and 8.0 cpd. Conversely, the 12 stimuli used as negative comparison stimuli featured cpd values half of which were 30% above and the other half 30% below the value featured by each corresponding sample stimulus (e.g., SS/S+: 0.5 cpd; S- could be 30% above, namely, 0.65 cpd or 30% below, namely, 0.35 cpd).

The whole spectrum of cpd patterns has been proved to be detectable by humans (De Valois & De Valois, 1988) and it falls within the range of SF patterns previously used in similar studies (Dale & Arnell, 2014; Flevaris 2011; Shulman *et al.* 1986; Shulman & Wilson 1987). The stimuli were grouped in low (LSF), medium (MSF) and

high (HSF) spatial frequencies categories for the purpose of experimental manipulation, as described in Table 10.

Each grating pattern measured roughly 4 cm x 4 cm and was surrounded by a grey background. The whole stimulus measured 11 cm x 7 cm. Stimuli were positioned at 30 cm distance from the monkey and therefore, they subtended about 7° of visual angle.

*Table 10. Spatial frequency values (cpd) used in Experiment 1a and 1b.*

	<b>Sample (SS) and matching (S+) stimuli</b>	<b>Non-matching stimuli (S-)</b>	
	<b>Cpd</b>	<b>-30% cpd</b>	<b>+30% cpd</b>
<b>Low</b>	0.25	0.175	0.325
	0.5	0.35	0.65
<b>Medium</b>	1.0	0.7	1.3
	2.0	1.4	2.6
<b>High</b>	4.0	2.8	5.2
	8.0	5.6	10.4

Figure 41 reports the stimulus set adopted in this experiment.

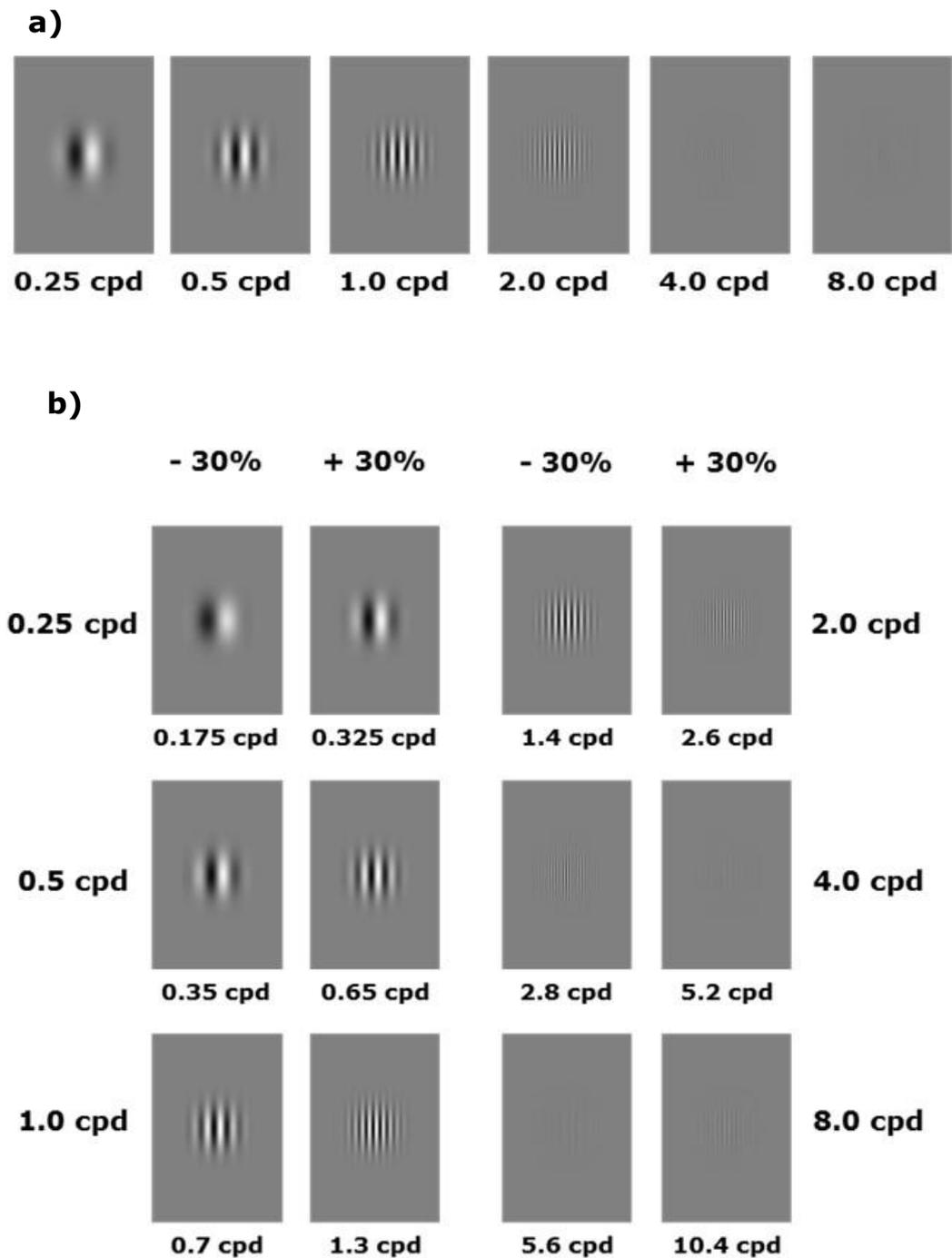
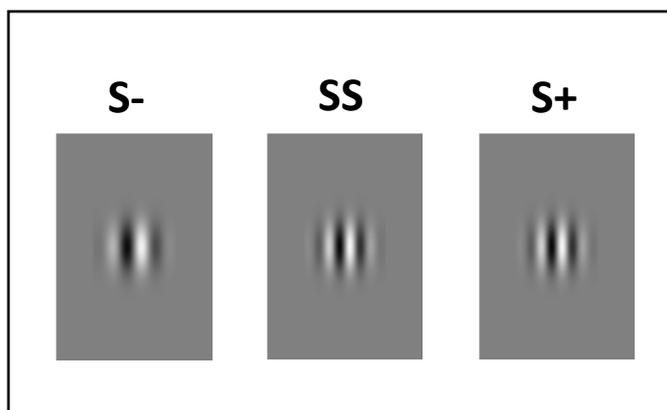


Figure 41. Stimulus set adopted in Experiment 1. The set comprised 6 main SF gratings used as sample and correct comparison stimuli (a) and 12 gratings used as non-matching stimuli (b). Half of the non-matching stimuli featured cpd values which were 30% above the corresponding sample stimulus. Conversely, the other half of the non-matching stimuli featured cpd values which 30% below the corresponding sample stimulus.

An Identity-MTS task was adopted. Each matching condition involved one sample stimulus (SS), one matching stimulus (S+) exactly alike SS, and one non-matching stimulus (S-) different from SS as described above. An example of a MTS trial with SF patterns is reported in Figure 42.



*Figure 42. Example of Identity-MTS trial between SF patterns. In this example, SS and S+ feature 0.5 cpd grating patterns. Conversely, S- features a 0.35 cpd grating, namely, a value 30% below 0.5 cpd.*

More details about the MTS procedure are reported in Chapter II.

Each monkey performed 8 sessions of 36 trials each. Each daily session included as sample stimulus all the 6 main gratings shown in Figure 41a and the 12 non-matching stimuli shown in Figure 41b (each featuring values either 30% above or 30% below the corresponding sample stimulus). The non-matching stimuli appeared in the same proportion in each session. Each monkey performed one session a day, for a total of 288 trials. The order of presentation of each SF main grating was randomized; however, they would appear in equal number within each session.

### 5.2.1.2 Results Experiment 1a: Monkeys

#### 5.2.1.2.1 Accuracy

Figure 43 reports the percentages of correct responses obtained with monkeys in each SF condition, namely, 0.25 cpd, 0.5 cpd, 1.0 cpd, 2.0 cpd, 4.0 cpd, 8.0 cpd. Furthermore, percentages of correct responses recorded for each monkey are presented in Table 11.

*Table 11. Mean individual percentage of correct answers recorded for each monkey in the different SF conditions of Experiment 1a*

<b>Subject</b>	<b>0.25 cpd</b>	<b>0.5 cpd</b>	<b>1.0 cpd</b>	<b>2.0 cpd</b>	<b>4.0 cpd</b>	<b>8.0 cpd</b>
<b>Gal</b>	60.4	68.8	51.0	66.7	58.3	72.9
<b>Pippi</b>	52.1	81.3	68.8	79.2	72.9	77.1
<b>Rubens</b>	53.8	62.7	76.9	58.0	86.3	72.0

The overall mean percentage of correct responses was 67.8%. The one-way ANOVA carried out comparing the accuracy scores obtained on each SF condition did not reveal significant differences among the six cpd conditions,  $F(5, 10) = 1.423$ , ns.

In order to evaluate whether or not monkeys' percentage of correct responses observed for each condition was significantly above the chance level of 50% correct responses, one-sample  $t$ -tests were carried out. The one sample  $t$ -test proved that monkeys performed at a level of accuracy significantly above the chance only for the 8 cpd condition,  $M = 74.0\%$ ,  $t(2) = 15.34$ ,  $p < .005$ , and approached significance for the 0.5 cpd condition,  $M = 70.9\%$ ,  $t(2) = 3.837$ ,  $p = .062$ . As the one sample  $t$ -tests revealed an unclear pattern on the majority of the cpd conditions, with the only exception of the 8.0 cpd condition, binomial tests were performed on accuracy scores recorded for each subject in each condition. This last analysis demonstrated

that discrimination performances for all three subjects were above level expected by chance for the 8.0 cpd condition (Pippi,  $z = 3.61$ ,  $p < .001$ ; Rubens,  $z = 2.97$ ,  $p < .01$ ; Gal,  $z = 3.03$ ,  $p < .005$ ) but they were at chance level for all the three subjects for the 0.25 cpd condition. Furthermore, the number of correct responses was above the chance level for two out of three subjects in the other conditions (0.5 cpd: Pippi,  $z = 4.19$ ,  $p < .001$ ; Gal,  $z = 2.45$ ,  $p < .05$ ; 1.0 cpd: Pippi,  $z = 2.45$ ,  $p < .05$ ; Rubens,  $z = 4.02$ ,  $p < .001$ ; 2.0 cpd: Pippi,  $z = 3.9$ ,  $p < .001$ ; Gal,  $z = 2.17$ ,  $p < .05$ ; 4.0 cpd: Pippi,  $z = 3.03$ ,  $p < .01$ ; Rubens,  $z = 5.04$ ,  $p < .001$ ).

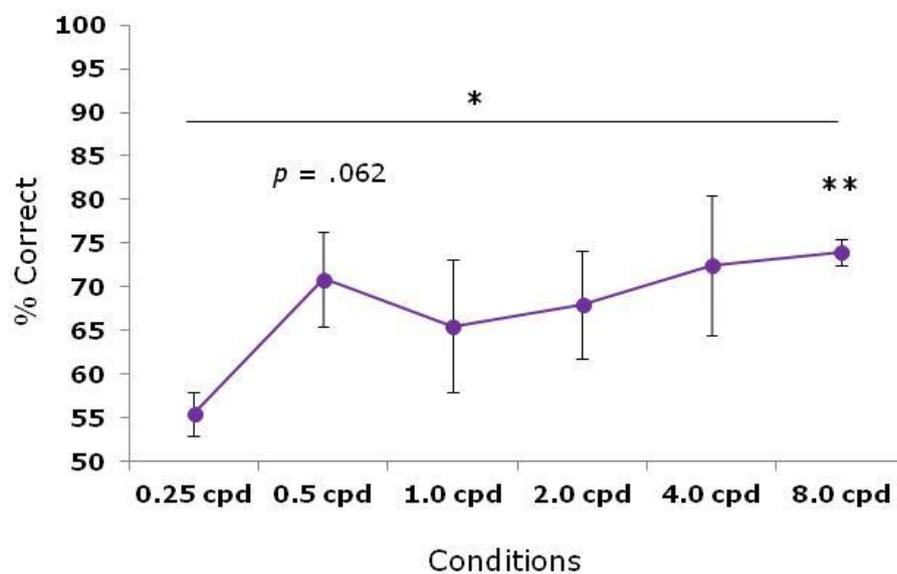


Figure 43. Percentages of correct responses recorded for monkeys in the different cpd conditions of Experiment 1a. (\*\*:  $p < .01$  one sample  $t$ -test). Error bars represent one Standard Error.

The finding that no monkey performed above the chance level in the 0.25 cpd condition, which entirely contrasts with the results obtained in the 8.0 cpd condition, suggests a difference between these two conditions that remained hidden in the one-way ANOVA. In order to assess this possibility, a paired samples  $t$ -test was carried out between these two conditions revealing an accuracy score

significantly higher recorded in the 8.0 cpd condition than in the 0.25 cpd condition,  $t(2) = 5.133, p < .05$ .

#### *5.2.1.2.1.1 Further analysis*

The relatively high level of accuracy recorded in the 8.0 cpd condition raised the doubt that monkeys may have used some alternative clues to solve the task. Given that the 10.4 cpd patterns consisted of extremely thin bars, it is possible to envisage that these bars might have been perceived by monkeys as grey patterns. Should this have been the case, trials featuring 10.4 cpd patterns could have resulted in matching tasks between proper gratings (as S+ and S+) versus uniform patterns. Therefore, discrimination tasks featuring 10.4 cpd gratings as non-matching stimuli would have been easier to solve than discrimination tasks featuring 5.6 cpd patterns as non-matching stimuli. If this was the case, performance in trials featuring 10.4 cpd gratings as S- should be significantly higher than performance of trials featuring 5.6 cpd gratings as S-. In order to rule out this possibility, a paired sample *t*-test was carried out to compare accuracy in trials featuring these two different non-matching stimuli. This analysis did not reveal any significant difference between the two non-matching trials for what it concerns the group of monkeys. In fact, as reported also in Table 12, trials involving 10.4 cpd patterns as S- were not processed any better than those involving 5.6 cpd patterns as S-, 10.4 cpd,  $M = 71.7\%$ , 5.6 cpd,  $M = 76.4\%$ ;  $t(2) = 1.158, ns$ . Instead, if any difference was observed, this was in the opposite direction, despite not significant.

*Table 12. Mean percentages of correct responses recorded for each monkey and for the group of animals in the 8.0 cpd condition with the two different types of non-matching stimuli of Experiment 1a.*

<b>Subjects</b>	<b>10.4 cpd (8.0 cpd +30%)</b>	<b>5.6 cpd (8.0 cpd -30%)</b>
<b>Gal</b>	75.0	70.8
<b>Pippi</b>	70.8	83.3
<b>Rubens</b>	69.2	75.0
<b>Means</b>	<b>71.7</b>	<b>76.4</b>

These results highlight that capuchin proficiency in discriminating 8.0 cpd gratings is a genuine result and suggest that they can process properly these SF patterns and match them accurately when a MTS paradigm is used.

### **5.2.2 Experiment 1b: Humans**

In order to enable an interspecies comparison, in this experiment the same stimuli and procedure used in Experiment 1 with monkeys were adopted with humans whereas a different apparatus was used as described in Chapter II.

#### **5.2.2.1 Method**

##### *5.2.2.1.1 Participants*

16 volunteers (8 males and 8 females) were enrolled in this experiments, ranging in age between 18 and 35. The general requirements to take part in the experiment are further described in Chapter II.

### *5.2.2.1.2 Stimuli and Procedure*

The stimuli were the same as those of Experiment 1a (see Figure 41). As for the monkeys, the stimuli-eye distance and the stimulus size were arranged in order to subtend a visual angle of approximately 7°. The distance between the computer screen and the participant's eyes was kept constant by using a chin rest.

The same identity MTS procedure used for Experiment 1a was adopted for Experiment 1b.

Each participant performed 48 trials featuring each main SF pattern for a total of 288 SF trials in one session. As for Experiment 1a, the non-matching stimuli were in equal number and appeared randomly. Each trial started with the three stimuli appearing aligned on the screen, the sample stimulus was always in the centre between the two comparison stimuli. Subjects had to answer using a response box as described in Chapter II.

## **5.2.2.2 Results Experiment 1b: Humans**

### *5.2.2.2.1 Accuracy*

The overall percentage of correct responses recorded with humans across the six SF conditions was 88.7% (see Figure 44).

One-sample *t*-tests revealed that the accuracy level of humans was significantly above the chance level of 50% for all the SF conditions, 0.25 cpd:  $t(15) = 26.081$ ,  $p < .005$ ; 0.5 cpd:  $t(15) = 44.393$ ,  $p < .005$ ; 1.0 cpd:  $t(15) = 30.028$ ,  $p < .005$ ; 2.0 cpd:  $t(15) = 30.064$ ;  $p < .005$ ; 4.0 cpd:  $t(15) = 25.689$ ,  $p < .005$ ; 8.0 cpd:  $t(15) = 20.858$ ,  $p < .005$ .

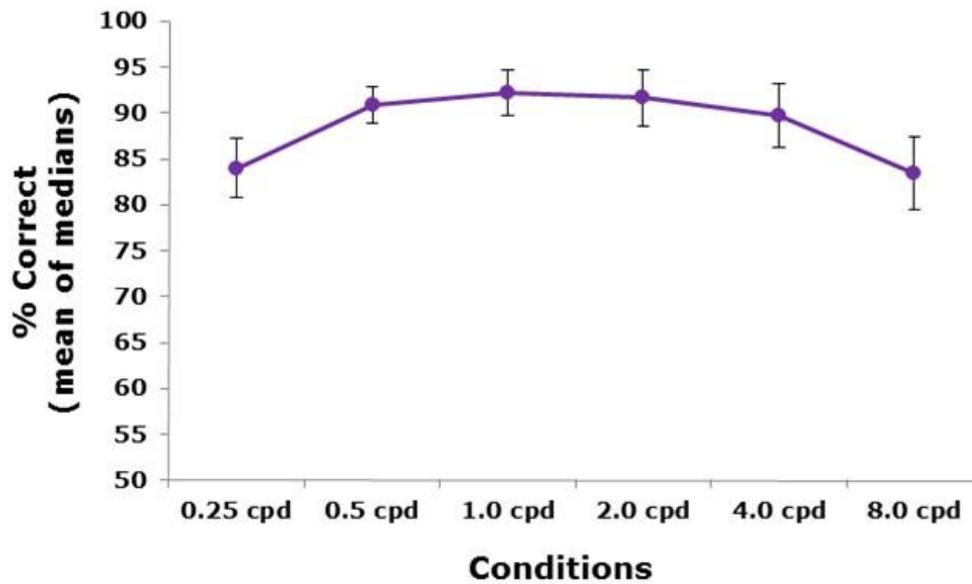


Figure 44. Accuracy observed with humans in the different cpd conditions of Experiment 1. Error bars indicate one Standard Error.

The one-way ANOVA carried out to compare the mean percentages of correct responses obtained for each SF condition proved significant,  $F(2.985, 44.782) = 6.886, p < .005, \eta_p^2 = .315$ .

Paired sample *t*-test were performed revealing a significant difference between the following conditions: 0.25 cpd vs. 0.5 cpd ( $p < .005$ ); 0.25 cpd vs. 1.0 cpd ( $p < .001$ ); 0.25 cpd vs. 2.0 cpd ( $p < .005$ ); 0.25 cpd vs. 4.0 cpd ( $p < .05$ ); 0.5 cpd vs. 8 cpd ( $p < .01$ ); 1.0 cpd vs. 8.0 cpd ( $p < .005$ ); 2.0 cpd vs. 8.0 cpd ( $p < .01$ ); 4.0 cpd vs. 8.0 cpd ( $p < .05$ ); while 0.25 cpd vs. 8.0 cpd was not significant. However, after applying the Bonferroni correction for 15 comparisons ( $\alpha = 0.0033$ ) only some of these differences remain significant (i.e., 0.25 cpd vs. 0.5 cpd; 0.25 cpd vs. 1.0 cpd; 0.25 cpd vs. 2.0 cpd; 1.0 cpd vs. 8.0 cpd).

In Experiment 1a, monkeys proved to process the 8.0 cpd patterns significantly better than the 0.25 cpd. In order to assess the presence of interspecies differences in the processing of these two

SFs, independent sample *t*-tests were performed on accuracy score recorded with monkeys and humans for the 0.25 cpd condition and the 8.0 cpd condition. This last analysis revealed that the accuracy score recorded for the monkeys in the 0.25 cpd condition was lower than that recorded for humans,  $t(17) = 3.720, p < .005$ . However, no significant interspecies difference emerged for 8.0 cpd condition.

#### *5.2.2.2.2 Response Times*

As with previous studies, the apparatus adopted with humans allowed the recording RT. The median RT for each condition, filtered for correct answers only, was computed for each subject to compensate potential effects of extreme values. Figure 45 reports means of medians and SE of the RTs recorded for each SF condition. The one-way ANOVA, carried out on these values revealed a significant difference between conditions,  $F(2.377, 35.653) = 5.063, p < .01, \eta_p^2 = .252$ .

Paired sample *t*-test proved significant the differences among the following conditions 0.25 cpd vs. 0.5 cpd ( $p < .05$ ); 0.25 cpd vs. 1.0 cpd ( $p < .05$ ); 0.25 cpd vs. 2.0 cpd ( $p < .05$ ); 1.0 cpd vs. 8.0 cpd ( $p < .01$ ); 2.0 cpd vs. 8.0 cpd ( $p < .05$ ); 4.0 cpd vs. 8.0 cpd ( $p < .05$ ); while 0.25 cpd vs. 8.0 cpd was not significant. However, none of these differences remains significant after applying the Bonferroni correction for 15 comparisons ( $\alpha = 0.0033$ ).

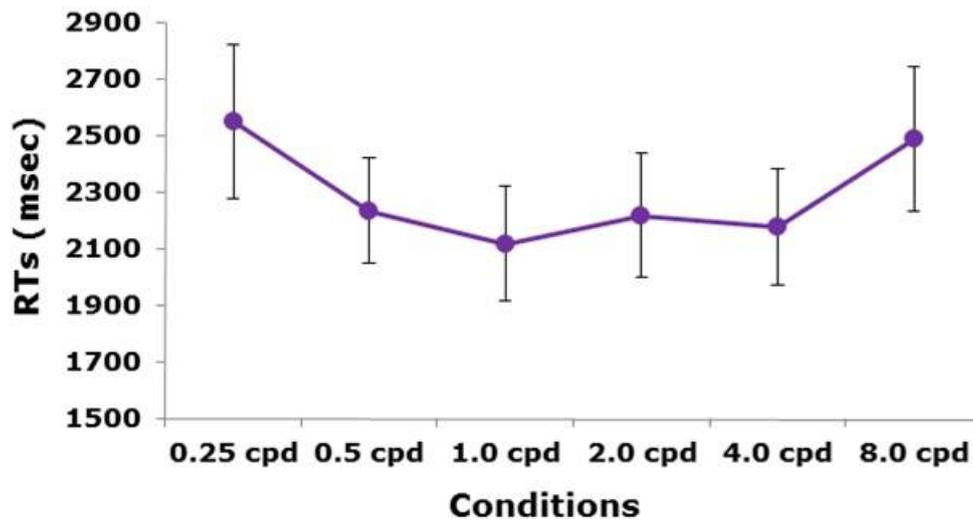


Figure 45. Medians of RTs observed in the different cpd conditions of Experiment 1 with humans. Error bars indicate standard errors.

### 5.2.3 Discussion Experiment 1

The results of this experiment show interspecies differences between the processing of Low, Medium and High Spatial Frequencies by humans and capuchin monkeys.

Humans' performance across the six SF conditions was above the level expected by chance, demonstrating that humans can detect the range of frequencies featured in this study and they can use them effectively in a Matching-to-Sample task. However, humans proved more accurate in trials featuring SFs ranging between 0.5 cpd and 4.0 cpd than with gratings featuring 0.25 cpd and 8.0 cpd as shown in Figure 44 and 45.

Capuchins showed a different pattern. In fact, their accuracy was above the chance level only in the 8.0 cpd condition. In addition, paired sample *t*-test demonstrated that their accuracy was significantly higher in trials featuring sample stimuli with 8.0 cpd gratings than in trials featuring sample stimuli with 0.25 cpd gratings.

Further analyses confirmed that this difference seems to be genuinely due to their ability to discriminate HSF patterns particularly accurately.

The results of the interspecies analysis performed on the accuracy recorded on the 8.0 cpd and 0.25 cpd condition indicate that monkeys process these last frequencies significantly worse than humans, whereas the two species do not differ in their processing of 8.0 cpd supporting the evidence, provided also by the binomial test and the one sample *t*-test, that monkeys process the 8.0 cpd condition significantly better than the 0.25 cpd condition even though the ANOVA did not show any significant difference across conditions.

Thus, from the first experiment it emerges that the peak of SF sensitivity is located around medium SFs in humans and around higher SFs in monkeys. In addition, both species found it more difficult to process the 0.25 cpd condition.

The main purpose of Experiment 1 was to identify the values of SF which could be discriminated at a reasonable level of accuracy by both monkeys and humans in order to use them in the second experiment to produce an attention bias towards HSF or LSF. The 8.0 cpd value was selected as HSF stimulus because it was processed above chance by monkeys. The 0.5 cpd value was selected as LSF stimulus as monkeys' performance approached significance there. The same stimuli were suitable for use with humans as they matched both above chance level (as they did with all other spatial frequencies used in Experiment 1).

### 5.3 EXPERIMENT 2

The previous study on attention (see Chapter IV), demonstrated that it is possible to induce in both, monkeys and humans, an attention set towards the global or the local level of structure of hierarchical visual patterns by manipulating the proportion of trial requiring the processing of one or the other level within a testing session. Such attention bias affects the quality of processing of the levels of structure of the stimuli and can produce an inversion of the global/local dominance shown by a given species (De Lillo *et al.*, 2011; Fremouw *et al.*, 1998). The aim of Experiment 2 is to evaluate whether or not the allocation of attention to high or low spatial frequencies can affect local and global processing in monkeys and humans in a similar way. It was, therefore important to identify with the previous experiment appropriate values of spatial frequency to be used to in Experiment 2. In the first experiment, humans showed better performances with SFs ranging from 0.5 and 4.0 cpd but their performance was above the chance level in every condition. By contrast, the group of monkeys performed above chance level only in the 8.0 cpd condition. Nevertheless, among the conditions where the group of monkeys did not perform above chance level, the 0.5 cpd condition closely approached significance ( $p = .062$ ). Moreover, binomial tests carried out on individual monkeys revealed that matching performances of two out of three subjects were above chance level in the 0.5 cpd condition. Therefore, in this second experiment it was decided to use the 8.0 cpd and the 0.5 cpd patterns as the HSFs and LSFs respectively.

The aim of this experiment is therefore to induce an attention bias towards either HSF or LSF, by administering 85.7% of trials requiring matching either HSFs or LSFs, randomly intermixed with a 14.3% of trials requiring, either global or local. These particular percentages were used following the procedure previously adopted in

the study on attention (see also Chapter IV) with monkeys and by Kinchla *et al.* (1983) with humans and Fremouw *et al.* (1998) with pigeons. In these previous studies, the use of these percentages of trials proved to be effective to bias their attention towards global or local levels of stimulus structure in hierarchical stimuli. Therefore, the same percentage was adopted in the current experiment. The use of trials featuring discrimination of SFs in order to bias attention towards global or local processing has not been attempted before with capuchin monkeys or, to my knowledge, with any other animal species. This rested in the rationale that if the preferential processing of one or the other level of the hierarchical structure of visual stimuli is mediated by a preferential processing of particular bands of spatial frequency, then it should be affected by manipulations of the number of trials within a session which require focusing on particular spatial frequencies.

### **5.3.1 Experiment 2a: Monkeys**

#### **5.3.1.1 Method**

##### *5.3.1.1.1 Participants*

The monkey sample consisted of the same participants who were tested in Experiment 1a.

##### *5.3.1.1.2 Stimuli and Procedure*

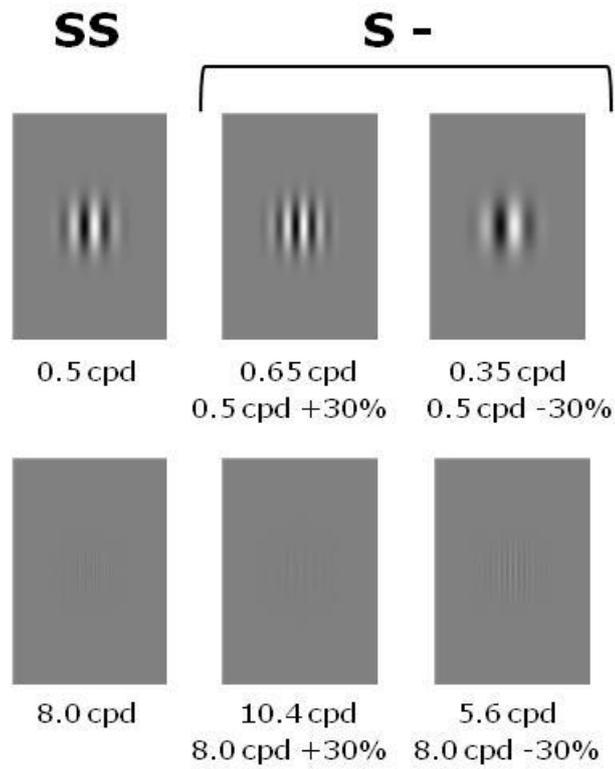
Figure 46a and 46b depicts the stimuli adopted in this second experiment. The stimulus set comprised a sub-set of SF patterns and a sub-set of hierarchical stimuli patterns.

Figure 46a depicts the first sub-set of SF stimuli which included the gratings with LSF and HSF identified as the most appropriate on the basis of the results of Experiment 1, therefore, the 0.5 cpd grating and the 8.0 cpd grating respectively. The figure reports also the non-matching stimuli. These were gratings whose value could be

30% above or 30% below the sample stimulus as was done in the first experiment. Hence, in the LSF condition the 0.5 cpd patterns were adopted as SS and S+, while as S- 0.65 cpd (+30%) and 0.35 cpd (-30%) were adopted. Analogously, in the HSF condition the 8.0 cpd patterns were adopted as SS and S+, while as S- 10.4 cpd (+30%) and 5.6 cpd (-30%) were adopted. The matching between the SF stimuli was the same reported in the first experiment (see Figure 42 as example).

Figure 46b depicts the second sub-set of hierarchical stimuli which comprised the same eight hierarchical patterns used in the previous study (see Chapter IV) and in previous literature (e.g., Spinozzi *et al.*, 2003; 2005) arranged along with the line described by Navon (1977). Since a detailed description of these stimuli has been already provided in Par. 4.2.1.2. (Chapter IV), for brevity it will be omitted here. As with the previous study, size and stimulus-eye distance were measured to obtain a visual angle of about 7° of at global level and 0.9° at local level.

a) Spatial frequencies patterns



b) Hierarchical patterns

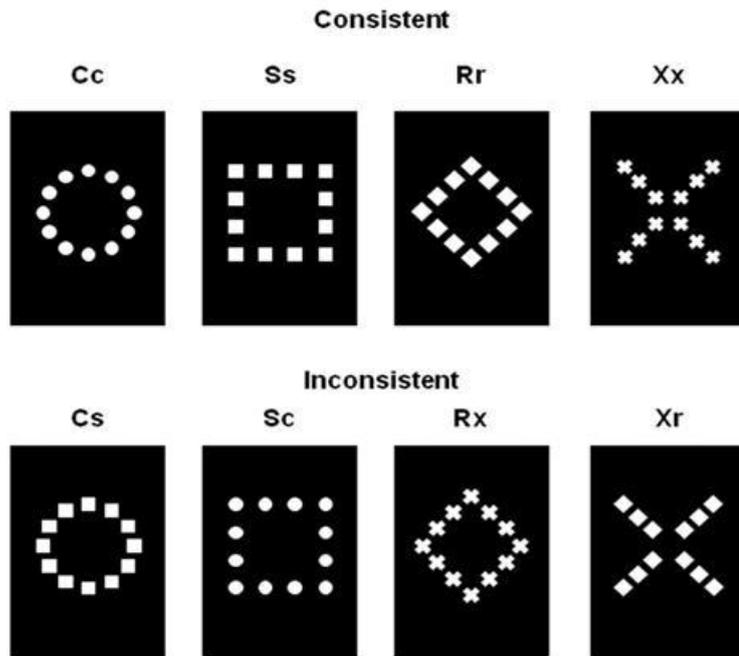


Figure 46. Stimulus set adopted in Experiment 2.

An identity matching-to-sample task was adopted using both SF stimuli and hierarchical patterns.

The matching between the SF stimuli was the same reported in the first experiment, with the only difference that the SF patterns adopted here were only the 8.0 cpd as HSF pattern and 0.5 cpd as LSF pattern. Thus, as was done in the first experiment, the non-matching stimuli (S-) were grating patterns obtained by adding or removing 30% of cpd from SS.

The MTS with hierarchical stimuli involved two matching conditions: in the global trials, S+ was identical to the sample and S- was differed from the sample only at the global level. In the local trials, S+ was identical to the sample and S- was differed from the sample only for local elements. An example of global and of a local trial is presented in Figure 34 (Chapter IV).

The procedure adopted resembled closely that adopted in the previous study on attention. Each daily session consisted of a sequence of 4 control trials (either global or local), followed by 24 SFs trials pseudo-random intermixed with 4 either global or local trials. The randomisation had the only constraint that the global/local trials should not appear in the first 7 trials. This was done to avoid that global/local trials appeared in the first positions and thus before an attention bias could be developed on the basis of the SF discriminations. Each daily session was preceded by a control session of 4 trials comprising either global or local trials. Each monkey performed a total of 16 sessions, one session per day, for a total of 512 trials, comprising 64 control trials (32 global, 32 local), 384 spatial frequency trials (192 HSF, 192 LSF) and 64 global or local trials (32 global, 32 local).

There were three conditions:

<b>HSF bias:</b>	<i>Global trials</i>	85.7% HSFs trials and 14.3% global trials
	<i>Local trials</i>	85.7% HSFs trials and 14.3% local trials
<b>LSF bias:</b>	<i>Global trials</i>	85.7% LSFs trials and 14.3% global trials
	<i>Local trials</i>	85.7% LSFs trials and 14.3% local trials
<b>Control:</b>	<i>Global trials</i>	Global trials only
	<i>Local trials</i>	Local trials only

As only three subjects were tested, it was not possible to fully counter balance the order of which monkeys started the experiment and it was considered more appropriate to follow the same order with all subjects (i.e., HSFs-Local followed by HSFs-Global then LSFs-Local followed by LSFs-Global). The whole sequence of conditions was repeated 4 times in total.

### **5.3.1.2 Results Experiment 2a: Monkeys**

#### *5.3.1.2.1 Accuracy for Spatial Frequency Matching Trials*

The overall mean percentage of correct responses for the group of monkeys for high and low SF trials combined was 71.4%. Table 13 shows the individual percentages of correct responses for trials involving HSFs and LSFs pattern discrimination registered during the local and global tasks. The average percentage of the group obtained combining the performance recorded on SF trials during the global and local condition was 68.1% for the LSF trials and 74.7% for the HSF trials. The one-sample *t*-test performed on the percentage of correct answers obtained combining the performance recorded on the SF trials, during the global and local tasks, revealed that the accuracy level shown by the monkeys was above the 50% level expected by chance in both HSF trials,  $t(2) = 6.64, p < .05$ , and LSF trials,  $t(2) = 5.77, p < .05$ . In addition, paired sample *t*-test performed on the

accuracy scores recorded between these 2 conditions, always combined for local and global tasks, did not reveal any significant difference demonstrating again that monkey performance in the LSF trials was as good as the one in the HSF trials.

*Table 13. Individual percentages of correct responses recorded for monkeys with HSF and LSF grating patterns during the local and the global tasks of Experiment 2.*

<b>Subjects</b>	<b>HSF</b>		<b>LSF</b>	
	<b>Local</b>	<b>Global</b>	<b>Local</b>	<b>Global</b>
<b>Gal</b>	78.1	85.4	65.6	58.3
<b>Pippi</b>	72.9	72.9	69.8	75.0
<b>Rubens</b>	67.7	70.8	75.0	64.6

#### 5.3.1.2.2 Accuracy for Compound Stimuli Matching Trials

The overall mean percentage of correct responses for global and local trials was 70.7%. Table 14 reports the individual percentages of correct responses shown by each monkey in the local and global trials of the Control, HSF-bias (8.0 cpd), and LSF-bias (0.5 cpd) conditions.

*Table 14. Individual percentages of correct responses recorded for monkeys with local and global trials across the different conditions of Experiment 2*

<b>Subjects</b>	<b>Local Trials</b>			<b>Global Trials</b>		
	<b>Control</b>	<b>HSF</b>	<b>LSF</b>	<b>Control</b>	<b>HSF</b>	<b>LSF</b>
<b>Gal</b>	75.0	56.3	87.5	59.4	50.0	68.8
<b>Pippi</b>	81.3	62.5	62.3	84.4	87.5	62.5
<b>Rubens</b>	71.8	68.8	75.0	68.8	75.0	75.0

A bar graph displaying the percentage of correct responses for the group of monkeys across the different conditions is presented Figure 47.

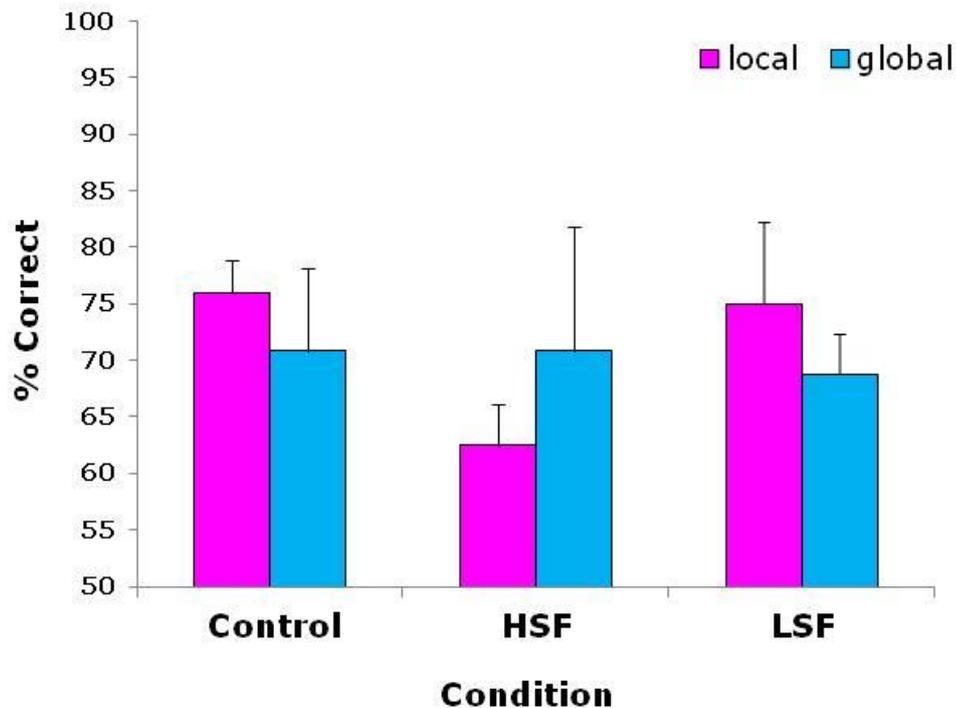


Figure 47. Percentages of correct responses observed with monkeys for local and global trials in the different conditions of Experiment 2. Error bars represent one Standard Error.

A 2 (Level of Processing) x 3 (Condition) repeated measures ANOVA was performed on the percentage of correct responses. The analysis did not display any significant main effect for either Level of Processing (*Local*,  $M = 71.2\%$ ; *Global*,  $M = 70.2\%$ ), or Condition (*Control*,  $M = 73.4\%$ ; *HSF*,  $M = 66.7\%$ ; *LSF*,  $M = 71.9\%$ ). Importantly, however, it proved that the interaction Level of Processing by Condition was significant,  $F(1,2) = 7.611$ ,  $p < .05$ ,  $\eta_p^2 = .792$ . None of the post-hocs (paired sample *t*-tests) carried out to interpret the interaction further yielded significant results. Nevertheless, an inspection of Figure 47 suggests that the interaction

can be explained by the reversal of the relative accuracy observed in local and global trials in the control and LSF bias condition (with higher values for the Local trials, compared to the Global trials), on the one hand, and the HSF bias condition (with higher values for the Global trials compared to the Local trials), on the other.

### **5.3.2 Experiment 2b: Humans**

In order to allow interspecies comparisons, in this experiment, the same stimuli and design of experiment 2a were used to test humans with a procedure as similar as possible to that used with monkeys.

#### **5.3.2.1 Method**

##### *5.3.2.1.1 Participants*

This experiment was carried out on the same subjects tested in Experiment 1b but two subjects (who did not perform above the chance level in at least one SF condition) were replaced with new subjects. However, in order to replicate as much as possible the procedure adopted with monkeys, in the analysis, only the 4 subjects who performed the sessions in exactly the same order as monkeys did (see next paragraph for a description) are taken into consideration.

##### *5.3.2.1.2 Stimuli and Procedure*

In this experiment, the same stimuli used with monkeys in Experiment 1a were adopted (see Figure 46a and 46b).

As was done with monkey, a MTS procedure was adopted.

Each subject performed 4 alternated sessions per day, instead of one session per day, and the whole sequence was repeated for 4 days.

Possible adaptation effects were minimised by administering only 4 sessions per day, each one reporting different condition (i.e., HSF-bias Local trials, HSF-bias global trials, LSF-bias local trials and LSF-bias global trials). The same sequence was repeated for 4 consecutive days. Furthermore, each session was separated by a time of approximately one minute and every trial was followed by a blank screen so that participants had to press a button to move to the next trial.

The whole sample was split into 4 groups each one receiving the sessions in a different order. However, in order to replicate as much as possible the procedure adopted with monkeys in Experiment 2a, only the subjects who performed in the same order as monkeys, (i.e., HSFs-Local followed by HSFs-Global then LSFs-Local followed by LSFs-Global) have been taken into account within data.

### **5.3.2.2 Results Experiment 2b: Humans**

#### *5.3.2.2.1 Accuracy for Spatial Frequency Trials*

The overall mean percentage of correct responses on SFs trials (high and low) recorded with the whole group of humans was high (96.4%). The average percentage of the group obtained combining the performance recorded on the SF trials during the global and local condition was 98.6% for the LSF trials and 94.3% for the HSF trials. A one sample *t*-test performed on the percentage of correct answers obtained combining the performance recorded on the SF trials during the global and local condition, revealed that the accuracy level shown by the group of humans was above the 50% level expected by chance in both LSF,  $t(7) = 69.913$ ,  $p < .001$ , and HSF,  $t(7) = 14.627$ ,  $p < .001$ . Finally, paired sample *t*-test performed on the percentage of correct answers recorded in the two conditions did not reveal any difference between the two SF trials.

#### *5.3.2.2.2 Reaction Times for Spatial Frequency Trials*

The median RT for each condition, filtered for correct answer, was computed for each subject to attenuate potential effects of extreme values. The average of the group obtained combining the performance recorded on the SF trials during the global and local condition was 1497.9 ms for the HSF trials and 1315.8 ms for the LSF trials. As observed with accuracy data, paired sample *t*-test performed on the medians of RTs recorded in the two conditions did not reveal a difference between the speeds of processing of the two SF trials.

#### *5.3.2.2.3 Accuracy for Compound Stimuli Matching Trials*

The level of accuracy of human subjects in the global/local trials was extremely high (Global trials:  $M = 100\%$ ; Local trials:  $M = 100\%$ ) in all conditions making their comparison meaningless. Hence, the analysis was confined to RTs, as described below.

#### *5.3.2.2.4 Response Times for Compound Stimuli Matching Trials*

Only RTs for correct responses were analysed. A 2 (Level of Processing) x 3 (Condition) ANOVA was performed on the medians of the RTs data recorded on 8 human subjects.

The ANOVA did not reveal any significant effect for Level of Processing and Condition but it showed that interaction between these two factors was significant,  $F(1,3) = 5.292$ ,  $p < .05$ ,  $\eta_p^2 = .638$ . Paired sample *t*-test revealed a significant difference between the local trials processed as part of the HSF conditions and those processed during the LSF condition, with the latter processed significantly faster,  $t(3) = 4.963$ ,  $p < .05$ . However, if Bonferroni correction is applied this difference does not remain significant.

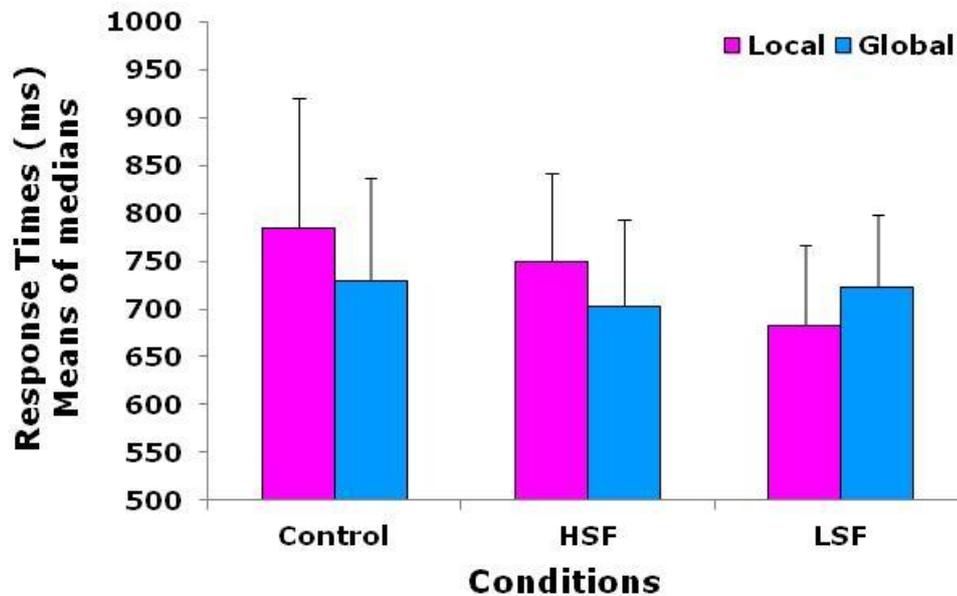


Figure 48. Means of the RT medians data recorded with humans for local and global trials according to the different conditions of Experiment 2. Error bars represent one Standard Error.

### 5.3.3 Discussion Experiment 2

First of all, it is important to discuss monkey performance in the SF trials. In the first experiment, the performance shown by monkeys in the majority of conditions was quite poor with the only exception of the 8.0 cpd condition. Even in the 0.5 cpd condition, one sample *t*-test showed that monkey performance only approached the significant difference from the chance level. However, the experimental design required to compare the effect due to the HSFs with the effect due to the LSFs. Therefore, it was important to ensure that in the second experiment the monkey accuracy in the LSFs condition was above the chance level. Importantly, both binomial test and one-sample *t*-test confirmed that accuracy scores recorded in the LSFs condition were significantly above the chance level in this second experiment with *p* values ranging from  $<.05$  and  $< 0.001$  in

the three subjects. These results suggest that the three subjects were performing the 0.5 cpd discrimination very well.

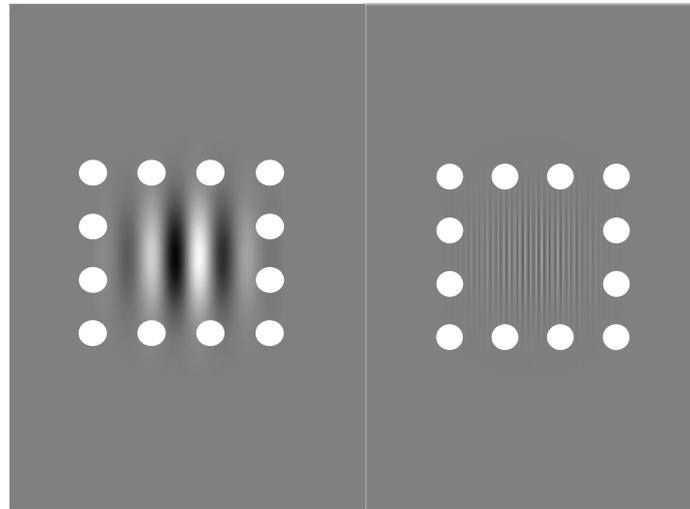
Overall, interesting results emerged from this second experiment. The ANOVA revealed a significant interaction between the SF processes and the global-local processing in both species. However, in monkeys, the paired sample *t*-test did not reveal any significant difference. It is possible to envisage that the small sample adopted in this experiment (only three subjects) can be a good explanation for this lack of significant difference in the post-hoc even after a significant interaction in the ANOVA. In fact, the huge variability associated with small samples is likely to affect the significance. Nevertheless, as the ANOVA revealed a significant interaction between the two factors, it is still possible to draw some interesting observations even only by inspecting the graphs. Figures 48 and 47 show the direction of such interaction: in both species, the effect seems to emerge mostly in the local trials, although with some important differences. In monkeys, this effect emerges as a reduction in performance of the local trials in the HSFs condition, since the local trials in this latter condition were processed worse than these performed in the other two conditions. Conversely, with humans, the effect on local trials emerges in the LSFs condition as a reduction in RTs.

A vast amount of literature on humans documented that global trials are mediated by LSF processing and local trials are mediated by HSF processing (Badcock *et al.*, 1990; Hughes *et al.*, 1990; Lamb & Yound, 1993; Robertson, 1996; Shulman *et al.*, 1986; Shulman & Wilson 1987). Instead, the present findings indicate otherwise, suggesting that higher cognitive mechanisms may be involved in these results. This experiment was addressed to better understand how attention allocation to either HSFs or LSFs can affect global-local processing and the present pattern of results is compatible with attentional interpretations. It is possible to envisage that the

attention allocation to a particular area of the visual scene can explain our results. It is a well documented phenomenon that attention can be allocated selectively to a particular area and so to a particular level of a hierarchical structure, in this way enhancing processing at that level or hindering processing at the other level. This phenomenon is considered related to a mechanism based on a spatial allocation of attention. Using the 'spotlight' metaphor of attention, some researchers suggested that the efficiency of responding to either level of a compound pattern can be affected by variations in the diameter of the 'spotlight' (Lamb & Robertson, 1988; Robertson, Egly, Lamb, Kerth 1993; Ward, 1982). According to this hypothesis, the processing of local trials is facilitated when attended area is small like the size of local elements, whereas the processing of global trials is facilitated when attended area is large like the size of a global structure. Other authors proposed the 'zoom lens' as metaphor (Eriksen & St. James, 1986; Stoffer, 1993, 1994). This last model suggests an inverse relation between the resolving power for detail and the size of the field of view, as the visual field increases the magnification decreases and so the processing of details. As the power of magnification increase the field of view constricts but with a compensating increase in the amount of information that is discernible about the remaining objects in the field. Besides, both models claim that stimulus level within the focus of attention benefits from more attentional resources than the stimulus level outside it.

In order to apply the spotlight model to this experiment it is necessary to compare, for each condition, the size of attentional window of both hierarchical and SF patterns. Thus, the actual size of either global level or local elements with the actual size of the single strips composing the whole SF patterns must be compared. To address this point, two sample patterns were realised by overlapping the HSF pattern and the LSF pattern with one hierarchical stimulus (see Figure 49). The two stimuli overlapped are scaled to the same

extent. Particularly interesting is the comparison between the width of each bar composing both HSF and LSF gratings with the size of both global and local level of hierarchical stimuli.



*Figure 49. Images obtained overlapping a hierarchical pattern with LSF (left) and HSF (right) patterns.*

By inspecting Figure 49, it is possible to draw a few important observations: 1) The real size of each bar in the HSFs pattern is much smaller than the local elements of hierarchical stimuli. 2) The size of each bar in the LSFs pattern is roughly of the same size of the local elements of hierarchical stimuli. 3) Coherently with the experimental design, the size of the entire SFs pattern is equivalent to the global level of hierarchical stimuli in every condition. Hence, using the attentional 'spotlight' paradigm, it is possible to envisage that the attentional window required to discriminate the SF patterns was essentially different in size from the attentional window required to process the hierarchical stimuli at both global and local levels. Therefore, an attentional bias toward either bigger or smaller area, depending on the different condition, was produced. Consequently, some possible expected scenarios can now be drawn:

As the attentional spotlight required to process the HSF patterns was narrower than that required for processing the local and global levels, subjects were biased toward a smaller attended visual area. Therefore, in the HSFs condition possible decrease in performance in both local trials and global trials may be expected.

As the attentional spotlight required to process the LSF patterns was of the same size of that required to process the local elements, it is like an attentional bias toward the local level was produced. Therefore, in LSFs condition, no effect or even a possible increased performance in local trials could be expected. Analogously, also a possible decreased performance in the global trials could be expected

The suggestion that allocating visual attention towards a smaller visual area can affect both global and local trials seems to be confirmed by the present results especially in monkeys. In fact, by inspecting Figure 47, it is evident that monkey performance in local trials decreased during exposition to HSFs. This result is confirmed by the observed significant interaction found between SF processing and global-local processing in the ANOVA. By contrast, in humans no difference in global-local processing in the HSF condition emerged. However, it should be highlighted that in the first experiment, HSFs grating were processed better by monkeys, while humans' performance in the same condition was relatively poor when compared to the other SF conditions. This poor performance may imply more dispersed attentional resources during the HSFs task, circumstance which may be interpreted as a less powerful attentional bias, resulting in no effect on global-local tasks. However, by inspecting the graph it emerges that both species did not show any difference on global trials. Further, possible interpretations of the observed general lack of any effect on global trials in both species are explored later on in the discussion.

The suggestion that allocating visual attention towards a visual area of the same size of the local elements of hierarchical stimuli

(e.g., LSF vs. Local elements, see also Figure 49 left) can induce no effect or even a possible increase in performance of local trials seems to be quite satisfied particularly in humans. In fact, as the LSF bars were substantially of the same size of the local elements of hierarchical stimuli, no effect or even an increase in performance in the local trials could be expected. By inspecting the graph, it is possible to envisage that these previsions are satisfied on both capuchins and humans. For capuchins the graph does not show any important changing in performance on local trials in the LSFs condition, when compared to the control condition. However, for humans, under the same condition, a better performance was found, showed by shorter RTs on local trials.

Given these results, it is worth analysing the chance that subjects were experiencing some kind of fatigue or adaptation due to repetitive exposure to the same SF task. In fact, it is a well-known phenomenon that neuron responses to grating patterns drops down with the time of exposure to the same grating (see also Blakemore & Campbell, 1969). In the present study each session was short and was presented only once per day on monkeys and four per day on humans, always alternated HSFs and LSFs. Furthermore, in humans each trial was separated by consecutive trials using a blank screen, with a time of exposure decided by the participant. On the other hand, in monkeys' experiment, between each trial, a few seconds were required by the experimenter to insert the stimuli in the apparatus. Thus, there was no intention to adapt the subjects to the same spatial frequencies, as was done in previous literature (e.g., Shulman *et al.* 1986). By contrast, the study was addressed in biasing the attention toward either HSFs (global/local) or LSFs (global/local). Using the present procedure, it is extremely unlikely that a phenomenon of fatigue to the same spatial frequencies occurred. Yet, a way to asses if subjects were adapting to either HSFs or LSFs consists in analysing the trend of performance across each

session. The rationale is that, if any fatigue occurred during the experiment, the performance in the SF trials should be affected, possibly showing a significant decrease in performance. In order to rule out this possibility, each session was divided into six blocks (four trials each). Then, monkeys' percentage of correct answers was calculated for each block of all the sessions reporting the same SF task (e.g., HSF-local or HSF-global). Similarly, humans' medians of RTs, filtered for correct answers, were calculated for each block. Then, a statistical analysis was performed.

In monkeys, the one-way ANOVA carried out on SF trials organised according to each condition (HSF-global, HSF-local, LSF-global and LSF-local) did not reveal any significant results in any condition, ruling out the possibility that the fatigue was occurring.

In humans, the one-way ANOVA carried out on the HSF-global, HSF-local and LSF-global conditions did not reveal any significant results. Only the HSF-local condition revealed a significant trend across the six blocks,  $F(5,35) = 2.942$ ,  $p < .05$ . However, the trend featured a significant quadratic component,  $F(1,7) = 9.365$ ,  $p < .05$ , indicating that RTs decreased and then increased again across the six sessions. Such quadratic pattern is unlikely consistent with the hypothesis that human subjects were experiencing some fatigue during the experiment.

Therefore, considering the procedure adopted together with the results of this last analysis, it is extremely unlikely the two species exhibited some kind of fatigue during the experiment.

## 5.4 EXPERIMENT 3

A third experiment was carried out on humans only to understand whether or not the interaction between the SF processing and the global-local processing could operate in the opposite way to what reported in earlier experiments. In fact, it has been demonstrated that administrating hierarchical patterns can affect subsequent SF recognition (Flevaris *et al.*, 2011; Shullman & Wilson, 1987; see also Chapter I, Par. 1.5.3).

Therefore, another experiment was carried out in which the proportion of SF stimuli and hierarchical stimuli was reversed (e.g., 85.7% hierarchical stimuli vs. 14.3% of SF stimuli).

As this experiment was designed after every study was performed, it was not possible to replicate it on monkeys. In fact, on one hand, unfortunately, few months after the ending of the second experiment two of the three subjects tested before (Rubens and Pippi) died of natural causes. On the other hand, given the amount of training required and the relative difficulty that monkeys experienced with SF tasks, it was not possible to train new subjects just for the purpose of this experiment.

### 5.4.1 Method

#### 5.4.1.1 Participants

As this experiment involved just humans and it was an additional experiment not planned in the original project, it was decided to test only 8 participants. Subjects were randomly chosen from the participants enrolled in the previous experiments.

#### 5.4.1.2 Stimuli and Procedure

In this experiment, the same stimulus set used in the previous experiments were adopted.

The identity MTS procedure was adopted using both SF stimuli and hierarchical patterns.

The matching between the SF stimuli is the same reported in Experiment 2. Also the procedure adopted is similar to that adopted in Experiment 2, but with an inversion of the causalities reporting SF trials vs. global-local trials. Each session consisted of a sequence of 4 control trials (either HSF or LSF), followed by 24 global-local trials pseudo-randomly intermixed with 4 SF trials, either high or low. The randomisation had the only constraint that the global/local trials should not appear in the first 7 trials. This was done to avoid that SF trials appeared in the first positions and before an attention bias could be developed on the basis of the global-local discriminations. Each subject performed 16 sessions, 4 sessions per day, for a total of 512 trials, which comprised 64 control trials (32 HSF, 32 LSF), 384 global-local trials (192 global, 192 local) and 64 SF trials (32 HSF, 32 LSF).

There were three conditions:

<b>GLOBAL bias:</b>	HSF trials	85.7% global trials and 14.3% HSF trials
	LSF trials	85.7% global trials and 14.3% LSF trials
<b>LOCAL bias:</b>	HSF trials	85.7% local trials and 14.3% HSF trials
	LSF trials	85.7% local trials and 14.3% LSF trials
<b>CONTROL:</b>	HSF trials	HSF trials only
	LSF trials	LSF trials only

## 5.4.2 Results Experiment 3

### 5.4.2.1 Response Times

A 2 (Spatial Frequency: HSF, LSF) x 3 (Condition: Control, Global-bias, Local-bias) analysis of variance (ANOVA) was performed on the medians of the RT data revealing a significant main effect for conditions,  $F(1,7) = 15.553$ ,  $p < .005$ ,  $\eta_p^2 = .690$ , with LSFs,  $M =$

1035.7 ms, processed faster than HSFs ( $M = 1438.0$  ms) overall. The interaction between SF processing and condition only approached significance ( $p = 0.06$ ).

An inspection of the graph reveals that performance in HSF slowed down during the global-bias condition ( $M = 1515.2$  ms) as opposed to the control condition ( $M = 1366.5$  ms). However, this difference only approached significance,  $t(11) = 2.221$ ,  $p = .062$ .

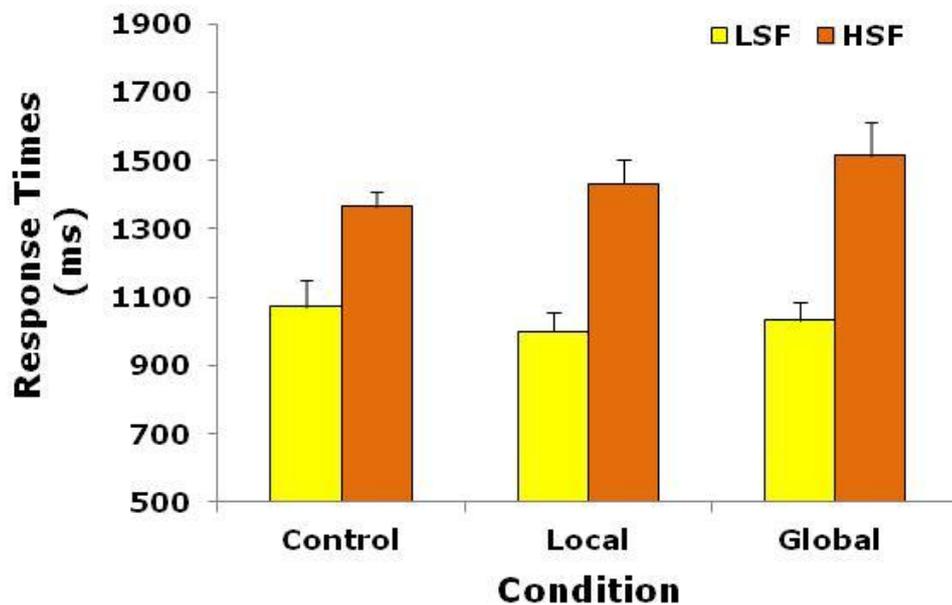


Figure 50. Mean of Response Times (ms) recorded for humans in the different conditions of Experiment 3. Error bars represent one Standard Error.

### 5.4.3 Discussion Experiment 3

In this last experiment, humans revealed faster latencies when processing the LSFs (0.5 cpd) in comparison to the HSFs (8.cpd) but the interaction SF by level of processing only approached significance ( $p = .06$ ). However, an inspection of the graph suggests that HSF tasks required more time to be processed in the global-bias condition

than in the control condition. Even if it represents just a tendency, this result provides us with some interesting information which deserves further discussion and may be used for further investigations.

As mentioned above, the 'zoom lens' metaphor proposed to describe visual attention (Eriksen & St. James, 1986; Stoffer, 1993, 1994) suggests that there is an inverse relation between the resolving power for detail and the size of the field of view. In other words, as the visual field increases the magnification decreases and so the processing of details. By contrast, as the power of magnification increases, the field of view shrinks but with a compensating increase in the amount of information that is discernible about the remaining objects in the field. According to the areal spread of attention proposed above (based on the images obtained by overlapping SF stimuli with hierarchical stimuli, discussion to Experiment 2, Par. 5.3.3) the attentional spread required to process both global and local level of hierarchical stimuli, was wider than that one required to process HSF patterns. Conversely, the attentional spread required to process the local level of hierarchical stimuli, was wider than that one required to process HSF patterns, but very similar to that one required to process LSF patterns. Therefore, in the present experiment, global trials should affect both HSF and LSF processing. However, local trials should still have an effect, although less pronounced, on the HSF processing, but it should have no effect or positive effect on LSF processing. By inspecting Figure 50, it is possible to see that RT data recorded on HSF trials during both global and local conditions, are higher when compared to the control condition. However, this effect was more pronounced in the global-bias condition, in which it approached the significance. Even though these results represent just a tendency, they are compatible with the notion that inverse relation between the resolving power for detail and the size of the field of view (Eriksen &

St. James, 1986; Stoffer, 1993, 1994). In other words, it is possible to envisage that during the global-bias condition, the areal spread of attention was wide and therefore, the processing of local details was affected. This can explain the increment, although not significant, in the speed of processing recorded on HSF trials which required a smaller attentional area. Perhaps, with a higher sample number, these results would become significant.

On the other hand, performance on LSF trials remained unvaried across conditions. Experiment 2 proved that LSFs were processed significantly better and faster than HSFs. Therefore, it is possible to envisage that, since matching LSF patterns was an easier task in comparison to HSF patterns, this may have led to more stable results across conditions. This result resembles that one on global trials of Experiment 2, where no significant effect on global trials was recorded across the different SF conditions. Further studies aimed at evaluating whether there is a difference in the speed of processing of a broader range of SF patterns may be of interest.

## **5.5 DISCUSSION**

The studies discussed before (Chapter III and IV) showed some important results. On one hand, the study on redundancy revealed another similarity between monkeys and humans in their visual cognition, and therefore that both species seem sensitive to stimulus redundancy. On the other hand, both studies proved that capuchin monkeys' local bias is a very strong feature that persists under several conditions. Notwithstanding this, it can be easily reversed following attentional manipulations.

The aim of the present study was to assess whether or not selective attention towards either HSFs or LSFs can affect global-local processing in capuchin monkeys and humans. Therefore, the present

study searched for a possible explanation of monkeys' typical local bias and the fact that it can be reversed with manipulations affecting selective attention (see previous study on attention).

In the first experiment, the ability of capuchin monkeys and humans to process different SFs was analysed. The results of the first experiment were particularly interesting in relation to capuchins' accuracy. They revealed that monkeys process higher spatial frequencies better than the lower ones. Conversely, humans detected slightly better and faster grating patterns featuring SFs ranging from 0.5 and 4.0 cpd of  $v_a$  than gratings featuring 8.0 and 0.25 cpd. Nevertheless, the performance of the group was above the chance level in every condition.

Overall, from the first experiment it emerges that the peak of spatial frequency sensitivity is shifted toward medium SFs in humans and toward higher SFs in monkeys. In addition, both species found it more difficult to process the 0.25 cpd condition. These results highlight some similarities but also some discrepancies in visual processes of capuchins and humans which can be relevant for the interpretation of some interspecies difference in the global-local visual processing of these species.

The aim of the second experiment was to determine whether or not global-local processing in monkeys and humans can be affected by having to process particular spatial frequencies within a testing session. The experiment rested on the rationale that a large proportion of trials requiring the processing of particular spatial frequencies would form an attention set towards those particular frequencies. The formation of such attention set would in turn affect global and local processing, if the latter it is mediated by attention towards particular spatial frequencies in monkeys and humans. Since in the previous study on attention it was found that biasing attention allocation toward either level of hierarchical stimuli can affect the local advantage, a similar procedure was used here. Therefore, the

aim of Experiment 2 was to evaluate whether or not selective attention toward either LSFs or HSFs can affect global-local processing in capuchin monkeys and humans. In fact, there is evidence that in humans some cognitive process such the attention allocation can play a prominent role in global-local processing and can be mediated by SF processing in humans (Flevaris *et al.*, 2011; Schulman & Wilson, 1987). As discussed in the introduction (par. 5.1) a large body of literature on level of processing in humans suggests that global detection can be mediated by LSF processing and local detection by HSF processing (see for example Shulman *et al.*, 1986; Shulman & Wilson, 1987; Robertson, 1996). Nevertheless, it is well-known that the global structure is still visible when LSFs are removed or attenuated and this effect has been confirmed by a good number of studies which adopted different stimuli such as natural images, including the face recognition (Fiorentini, Maffei, Sandini, 1983; Norman & Ehrlich, 1987; Parker, Lishman, Hughes, 1996; Peli, 1992; Schyns & Oliva, 1994) and synthetic images (Badcock *et al.*, 1990; Carlson, Moeller, Anderson, 1984; Hughes *et al.*, 1990). Moreover, Lamb and Yund (1993) showed that the removal of LSFs can slow global processing but does not eliminate the global bias, also it does not affect the capacity to move attention from global to local forms. In other words, the finding that low and high frequencies channels can play a different role in defining global and local structure of hierarchical stimuli does not require that each channel provides images information that can be separately accessed. Consequently, SFs are not necessary global or local in themselves (see also Sierra-Vázquez, Serrano-Pedraza, Luna, 2006). Another study which does not support the idea of a strict relationship between LSFs and global processing or HSFs and local processing respectively has been recently carried out by Dale and Arnell (2014). The main purpose of their study was to evaluate if dispositional global-local biases can be altered by various manipulations of high/low spatial frequencies on

humans. Subjects were asked to discriminate 0.76 cpd patterns as LSF trials and 7.2 cpd patterns as HSF trials. Before and after the discrimination tasks, subjects were asked to perform some global-local trials and scores were compared. Interestingly, they adopted LSFs and HSFs grating patterns with cpd values very similar to those adopted in the current study. Overall, they did not find substantial differences following SF manipulations with the only exception of an affected global performance after exposure to HSFs. However, since it was the only significant result out of five different experiments, authors argued that this effect could possibly have been found by chance and that it was not necessarily meaningful, thus they concluded that exposing to HSFs or LSFs do not affect global-local processing.

In contrast with Dale and Arnell (2014), a significant interaction between SF processing and global-local processing was found in both humans and capuchins when the majority of trials featured SF trials vs. a minority of global-local trials (Experiment 2a and 2b). This interaction was in both cases in an unexpected direction, drawing a complex final picture. Figure 47 and 48 suggest that monkeys performed worse in the local trials under HSFs conditions, while humans performed faster in the local trials under LSFs conditions. Moreover, in both species, the global trials were not affected by any SF condition.

As discussed above, the attentional spotlight can provide a useful explanation of the results of the present study (see discussion to Experiment 2). In a previous study (see Chapter IV), biasing attention to different level of hierarchical stimuli was effective in producing a shift in global-local performance in capuchin monkeys. This resulted in a global advantage when a global attention bias was induced, whereas the global bias was accounted mostly to a reduced performance in local trials during the global-bias condition (see also below). Similarly, in the present study, biasing areal spread of

attention resulted in a change in global-local performance. Nevertheless, by inspecting the graphs it emerges that the attentional bias was evident in particular on the local trials. In fact, with humans, an effect on local trials during exposition to LSFs was observed, whereas no effect was observed in the global trials. However, the global trials are typically processed faster and better by humans. Therefore, it is possible that, because of the robustness of the global advantage in human visual cognition, in humans these trials are less susceptible to attentional bias toward both HSFs and LSFs. Moreover, there was no effect on global trials across conditions also on monkey visual processing. Interestingly, this pattern of results resembles that one reported in the previous study on attention (see Chapter IV). In that study, the attentional bias toward one or the other level of hierarchical stimuli, obtained by varying the percentage of global-local trials in each condition, was effective in producing a switch in performance in the global-local processing. The final result was the emergence of global advantage in the global bias condition and a local advantage in the local bias condition in monkey visual processing. However, the data analysis revealed that whereas the local trials were significantly affected by the bias conditions, the attentional bias failed to have significant effect on global trials. Therefore, the global trials did not significantly change across the two bias conditions and the global advantage was accounted mostly to a detriment in performance of the local trials in the global-bias condition (see Chapter IV). In the present study, a procedure highly similar that one adopted in the previous study on attention was used. Both studies revealed that in monkey visual cognition the global trials are less susceptible to attentional bias and the explanation of this finding deserves further investigations.

The result that monkey local performance was not affected by the LSF condition also deserves further consideration. In fact, due to the size of local elements in comparison to LSF grating bars, it is

possible that subjects were not switching the areal spread of attention across the LSF bias local condition. This latter claim is also consistent with the evidence of task switching costs. In humans it is well-known that when a task changes from trial  $n$  to trial  $n+1$  there is a cost in performance in comparison to when the task does not change, therefore, when the task in trial  $n$  and trial  $n+1$  are identical. This cost in performance consists of slower RTs and more errors in the task immediately after a task switch (Monsell, 2003). In the experiment of the present study, when the switch occurred from a SF matching task to a global-local matching task, certainly there was a task switch. However, the possibility that the areal spread of attention required to process both LSF patterns and local elements was very similar across the two tasks may highly attenuate the task switching costs. Thereby, this situation may lead to a performance not different from the control condition in the species which usually exhibits local bias, as monkeys do, or even an increased performance in the species that usually exhibits a global bias, as humans do. This interaction, together with the "zoom lens" hypothesis may contribute to explain why monkey performance decreased during the HSF condition. In fact, as mentioned above (see discussion to Experiment 2, Par. 5.3.3) the attentional "spread" necessary to process HSF and the local elements was different.

By contrast, in humans no effect during the HSF condition but faster performance on the local trial in the LSF condition were observed. As mentioned before, the lack of any effect during the HSF conditions may be due to the fact that the HSFs processing was relatively difficult for humans. For what concerns the LSFs, perhaps, the easing effect proposed above is even more evident in the level of processing that is usually processed worse by humans. Alternatively, the robustness of the global advantage in humans can probably explain why global trials were not affected by SF processing in any condition.

Comparing the results obtained with humans in Experiment 2 and 3, there are some parallels that are worth to highlight. In fact, whereas in Experiment 2 the trials processed faster and better (i.e., global trials) were not affected by the attentional biases, analogously in Experiment 3 the trials processed faster and better (i.e., LSF trials) were not affected by the attentional biases. These findings are compatible with the notion that in humans trials which develop an advantage (i.e., global and possibly LSF trials) might be less attention demanding (see also Deruelle & Fagot, 1998) and therefore, can be less affected by attentional manipulations (see also Chapter VI for a more detailed discussion).

In conclusion, the present study provides, for the first time, some information about capuchin monkey ability to process different spatial frequencies. Furthermore, it highlights some similarities but also some possible differences in capuchin monkey visual cognition in comparison with humans, as demonstrated by monkey bias toward high SFs which contrasts the human bias toward medium SFs. Furthermore, the results of the present study suggest that it is possible to influence the distribution of attention which leads to an effect on global-local trials even in condition when the main task is a completely unrelated task. Finally, coherently with that observed in the study on attention, this study confirmed that global trials are less affected by attentional conditions and, interestingly, this is true for both capuchins and humans.

## CHAPTER VI

### GENERAL DISCUSSION AND CONCLUSIONS

#### 6.1 GENERAL DISCUSSION

The present research is another attempt to understand the factors affecting the global-local processing in humans and capuchin monkeys. Within a comparative framework, given the high degree of similarities, and therefore possible homologies, shared by humans and non-human primates in their visual cognition, studies aimed at disentangling alternative explanations of the observed differences in their global–local processing could help in understanding the emergence and the evolution of the human cognitive system. Moreover, these kinds of comparative studies could help us in assessing the strengths and the weakness of the use of non-human primate species as model in medical research.

The discovery that several primate species, as opposed to humans, when processing hierarchically organised visual stimuli show a local advantage has attracted a substantial interest in comparative cognition (De Lillo *et al.*, 2005; Fagot & Deruelle, 1997; Lea, Goto, Osthaus, Ryan, 2006; Spinozzi *et al.* 2003). However, before this work, it has proved difficult to identify a key factor which can explain this difference across primate visual cognition (Fagot & Deruelle, 1997).

Many studies have been carried out in order to find conditions under which capuchin monkey local advantage can be reversed and, by doing so, to find possible explanations that may account for it. However, it has been proved that such advantage cannot be accounted for by a preference in this species to process better stimuli of a particular size as capuchins display a local bias even when

dramatic changes in the stimulus size occurred (Spinozzi *et al.*, 2006). Further studies suggested that monkeys' local advantage cannot be accounted for an inability to process the internal spatial relationship between stimuli parts or to use grouping cues. In fact, as explained in the introduction, transformations of the arrangement of stimulus parts affect pattern recognition in both humans and capuchins (De Lillo *et al.*, 2007). Moreover, capuchin monkeys as well as humans are able to use some *Gestalt* rules like the proximity, the shape similarity and the orientation of local elements as visual perceptual grouping cues (Spinozzi *et al.*, 2009).

In the present work, across three comparative studies (each one featuring numerous experiments in both species) the effects of several factors that can potentially affect global-local processing of capuchin monkeys in comparison to that of humans were analysed.

The aim of the first study was to analyse the effect of pattern redundancy, as defined by Garner (1974), on global-local processing. This was done using dot-patterns derived from those described by Garner but arranged to form hierarchical stimuli.

The aim of the second study was to analyse the effect of selective attention to different level of hierarchical stimuli on global-local processing. This was done by using a procedure which has been demonstrated effective in human studies (Kinchla *et al.*, 1983; Lamb & Robertson, 1987).

Finally, the aim of the last study was to analyse the effect of selective attention to different spatial frequencies on global-local processing following the paradigm proposed by Shulman *et al.* (1987). This was done by using the same procedure of the previous study but applied to non-hierarchical stimuli.

Overall, global advantage in humans and local advantage in monkeys seem to be very robust features of these species as they occur under many conditions and following several different experimental manipulations (Kinchla & Wolfe, 1979; Lamb &

Robertson, 1988; Spinozzi *et al.* 2003; 2005). Also the results from the present work support this idea, as, overall, humans revealed their typical global advantage whereas monkeys revealed their typical local advantage in many conditions. Some manipulations, like for instance the visual angle (see the Study on Redundancy), coherently with what documented in previous literature (Kinchla & Wolfe, 1979; Lamb & Robertson, 1988) did affect human global bias but not monkey local bias.

The first study was addressed to understand whether or not redundant hierarchical stimuli can facilitate the global-local processing in comparison with non-redundant ones in both species. In addition, the study aimed at evaluating the degree of the local advantage using different types of stimuli, changing in the perceived visual angle and in the degree of grouping required to process them.

With few exceptions, possibly related to some confounds and/or some internal stimulus properties already discussed in Chapter III, overall, the results of this study indicate that tufted capuchin monkeys can benefit from stimulus redundancy with hierarchical patterns in their global-local processing. Nevertheless, this benefit happened under different conditions across the five experiments. In fact, the effect from stimulus redundancy emerged mostly during Experiment 2, 3 and 5 (inconsistent set) which featured the use of patterns all derived by the same Garner's dot-patterns (see also discussion on study on redundancy), whereas in the other experiments the effect was less pronounced. This consistency within the group of experiments featuring similar shapes, reinforce the strength of the present results and indicate that capuchin monkeys can truly benefit from stimulus redundancy. Sensitivity to symmetry has an adaptive value as it help animals in face recognition and it is important for the kin-selection. In fact, asymmetrical faces or bodies may relate to anatomical dysfunctions and thus do not represent desirable features to select in a partner (see, for example, Jones,

Little, Tiddeman, Burt, Perrett, 2001). Therefore, the ability to detect symmetry should represent an adaptive trait in animal visual cognition. A previous study carried out on capuchin monkeys demonstrated a preference in this species for symmetrical shapes as opposed to asymmetrical shapes (Anderson *et al.*, 2005). However, that study did not clarify whether or not capuchin monkeys can benefit from stimulus symmetry in order to facilitate visual encoding. Whereas this question has been widely addressed in humans (Garner, 1974; 1970), the relation between redundancy and global-local processing has not been well established yet even in human studies. In fact, it has to be emphasized that some of the stimuli used in the literature in this domain often use symmetrical, thus redundant, patterns at the global level. Therefore, within a comparative framework, if it was found that only humans were able to process the redundancy, this could have represented a possible explanation for the interspecies differences observed so far. Conversely, the finding that also capuchin monkeys can benefit from stimulus redundancy allows us rule out that this factor may account for the observed interspecies differences between humans and monkeys in their global-local processing.

To my knowledge, this is the first research which demonstrated that a monkey species can benefit of stimulus redundancy during the visual processing. In fact, the only other study carried out on stump-tailed monkeys using a similar paradigm did not provide any evidence that this species could detect stimulus redundancy (Schrier *et al.* 1979). The present study and that one carried out by Schrier *et al.* (1979) share some similarities but they are also different under a few aspects. Whereas both studies adopted stimuli derived from Garner's work, Schrier *et al.* (1979) used a binary discrimination task rather than a MTS task and the dot-patterns were not arranged to form hierarchical patterns. These differences make some kind of interspecies comparisons not completely reliable as it cannot be ruled

out that, if tested under the same conditions featured in the present study, stump-tailed macaques may also show a benefit from stimulus redundancy in global-local processing. Further experiments carried out on other primate species using the same paradigm may be extremely helpful in assessing the universality of these findings and therefore would be extremely important to better characterise the evolution of human cognitive system. With regard to the level of processing, overall monkeys displayed a local bias in every experiment, even in the first two experiments where there was a requirement to group dots at local level. This is a very important finding given the fact that these kinds of studies on monkeys have been always carried out using hierarchical stimuli based on Navon's paradigm featuring whole shapes as local elements. In fact, it has been suggested the monkey local bias may depend on a relative difficulty in grouping local elements (Fagot & Barbet, 2006), and testing monkeys with stimuli featuring solid shape as local elements did not rule out this possibility.

The differences between humans and monkeys in their global-local processing may be explained in terms of resources required to group elements by proximity. This justification has been proposed also to explain the lack of sensitivity to the *Ebbinghaus* illusion observed in baboons (Parron & Fagot, 2007) and the fact that the distance between visual elements can affect monkey ability to process them conjointly (Fagot & Parron, 2010).

Therefore, it could be argued that in Experiment 1 and 2 of the first study, even if grouping was required at both levels, the local advantage in monkeys could be explained by the requirement to group twice. However, the paired sample comparisons between trials featuring either global or local matches across the experiments featuring similar shapes but different global-local organisation (i.e., Exp. 1 vs. Exp. 4 and Exp. 2 vs. Exp. 3, see Chapter III, par. 3.7) did not reveal any significant difference. In fact, monkey local bias

occurred *with* and *without* the requirement of grouping twice. This finding suggests that grouping requirements cannot entirely justify the local advantage displayed by monkeys in the present study.

For what concerns humans, they displayed a varied pattern of results. In fact, no advantage emerged in Experiments 1 and 2, whereas a local advantage emerged in Experiments 3 and 4, finally, in Experiment 5, in the many-elements condition, human typical global bias emerged. Therefore, the global advantage emerged again in humans when the visual angle was reduced and the number of local elements was increased. These results suggest that the salience of local elements has a significant impact in human global-local processing supporting what was already documented before in humans (Kimchi, 1992; Kinchla & Wolfe, 1979; Lamb & Robertson, 1988).

In the present study, some experiments showed that the effect of stimulus redundancy can occur regardless of the level of processing. However, other experiments proved this beneficial effect only at the level of processing typically processed better by each species. Furthermore, the second study demonstrated that monkeys can shift their attention from different levels of stimulus structure (see also below). Therefore, it is possible to envisage that sensitivity to redundancy in monkeys occur mostly when they have to pay their attention to the level of stimulus structure where they spontaneously tend to direct their attention (i.e., the local level). Analogously, humans may be more sensitive to the stimulus redundancy when it is featured by the level of processing typically processed faster and better by them.

In sum, the study on redundancy provided a first demonstration that capuchin monkeys can benefit from stimulus redundancy. This result supports other findings which suggest that capuchin monkeys share with humans a number of high cognitive skills such as the perception of some visual illusions, the ability to use similar *Gestalt*

principles as grouping cues and the reliance to the correct spatial arrangement of the stimulus parts in order to recognise it (De Lillo *et al.*, 2007; Spinozzi *et al.* 2009; Suganuma *et al.* 2007).

Furthermore, this study highlighted that capuchin monkeys' local advantage persists even when they have to process hierarchical stimuli that require grouping at both levels of processing. This result indicates that monkeys' local advantage does not depend on a possible difficulty, displayed by this species, to group elements into a whole, as previously suggested (Fagot & Barbet, 2006).

These findings, together with previous literature on capuchins (De Lillo *et al.* 2007; Spinozzi *et al.* 2003; 2006; 2009), suggest that monkey local advantage does not depend on lower perceptual mechanisms. Therefore, the search for the conditions under which monkeys' local advantage can occur points toward higher cognitive mechanism such as attention. For this reason, a second and a third study, both focused on the visual attention, were carried out.

The second study was specifically aimed at assessing the effect of attentional biases toward each level of hierarchical stimuli, while the third study was aimed at assessing the effect of attentional biases toward either high or low spatial frequency patterns.

It is well established that, in humans, the relative efficiency of global and local processing can be modulated by attention as selective attention to either level of hierarchical visual stimuli can increase the performance when processing that particular level (Kinchla *et al.*, 1983; Lamb & Robertson, 1987, 1988; Miller, 1981; Robertson *et al.*, 1982). Moreover, some studies suggest that attention also plays a relevant role in certain animals. For example, when pigeons are biased to focus their attention to only one level of hierarchical stimulus structure, they are able to shift their visual attention from one to the other level of stimulus structure (Fremouw *et al.*, 1998; 2002).

In the second study, the attention toward either level of hierarchical stimuli was manipulated by administering sessions in which the proportion of each trial varied across sessions. In the global bias condition there were 85.7% trials featuring global trials and only 14.3% featuring local trials, the situation was reversed in the local-bias condition. Following these manipulations, it was possible to create an attentional bias which was effective in creating a switch in performance across conditions in both species. In fact, in the second study, monkeys displayed a local advantage in the local-bias condition but, for the first time, a global advantage when they were biased to pay their attention toward the global level of stimulus structure. This was the first evidence of a possibility to reverse the local advantage so often observed in tufted capuchin monkey. Interestingly, whereas in the local-bias condition the local advantage emerged as increased performance in local trials in comparison to global trials, in the global-bias condition global advantage emerged as decreased performance of local trials rather than improved performance in global trials. In fact, overall performance on global trials was very stable across conditions and the observed significant differences in each bias condition were due mostly to a fluctuation of performance on local trials. Nevertheless, the analysis of the performance along the time revealed that this trend was a function of task practice. In fact, when the performance across two separate session blocks was analysed, it was found a pattern consistent with the general experiment but only in the first session block, whereas in the second session block, the switch along the biases condition was complete. Interestingly, even if humans displayed an overall different pattern, global trials were less affected by attentional biases also in this species.

There is evidence that in condition of selective attention, the local advantage so often reported in children with autism can be reversed (Plaisted *et al.*, 1999). This shift of dominance was observed

in parallel with clear effects of interference in conditions featuring inconsistent stimuli. In particular, children with autism showed a change from local-to-global interference in a divided attention task (i.e., when children were not instructed about the level of processing that they must attend) to a global-to-local interference in a selective attention task (i.e., when children were instructed to attend to either level of processing). Authors suggested that in conditions of selective attention the priming at the global level would increase the ability to inhibit the influence of the irrelevant local level (Plaisted *et al.*, 1999). There are some similarities between that study of Plaisted *et al.* (1999) and the present study as both demonstrate that the local advantage can be reversed under appropriate attentional conditions. The weak central coherence theory (Frith, 1980) claims that the local advantage so often observed in autistic children does not represent an actual deficit as observed, for example, in neuropsychological conditions such as agnosia (Behrmann & Kimchi, 2003) or simultagnosia (Huberle, Driver, Karnath, 2010). By contrast, it is described as a different style of cognitive processing (Happè, 1999). Analogously, the interspecies differences between humans and monkeys should not be interpreted as a deficit in processing the global shapes of visual stimuli. In fact, the present experiments demonstrate that monkeys can successfully process the global aspect of a visual scene, and this result is very robust as it has been observed in the present work as well as in previous literature (see also below). Therefore, the local bias so repeatedly observed in monkeys may be interpreted as a different style of cognitive processing mediated by the visual attention.

Before the present work, many studies have been carried out in order to understand the reasons behind monkey local advantage. Each study, step by step, discarded the role of many factors that potentially could have been involved in it, though leaving the main question unanswered. The study on attention provided, for the first

time, indicating that the key mechanism involved in monkey local bias could be based on visual attention. This represents a very crucial finding, as it highlights the importance of high cognitive mechanisms also in non-human primate species, supporting, once again, the notion that capuchin monkeys and humans share a large amount of similarities in their visual system and cognition. However, the study on attention did not clarify exactly on which components of the stimuli the attention bias operates. One possibility is that it operates through priming of spatial frequency channels responsible for the detection of high and low spatial frequency. In fact, whereas a huge body of literature on humans proved that there is a strong relationship between the global-local processing and the spatial frequency processing (see, for example, Shulman *et al.*, 1986; Shulman & Wilson, 1987) the mechanism underlying this relation is still the object of debate. It is certainly well-known that the global aspect contains mostly low spatial frequencies whereas the local aspect contains mostly high spatial frequencies. However, the way by which the visual system access to these information has not completely characterized. Some investigators claim that the visual channels responsible for encoding HSF or LSF are transmitted at different speed rates, with LSF transmitted faster than HSF, and this would account for the global advantage as the global level contain mostly LSF (Breitmeyer, 1975; Lupp *et al.*, 1976). Others claim that there is an overlap between the brain areas involved in processing each level of hierarchical stimuli and different spatial frequencies respectively, which leads to a correlation between LSF and global processing and HSF and local processing (Fink *et al.*, 1996; Han, Weaver, Murray, Kang, Yund, 2002; Hübner, 1997; Hübner & Volberg, 2005; Robertson & Lamb, 1991). As an alternative, or in addition to, these sensory mechanisms, it has been suggested that the link between spatial frequencies processing and global-local processing can be seen in terms of post-perceptual phenomena

related to attentional mechanisms (Boer & Keuss, 1982; Flevaris *et al.*, 2009, 2011; Kinchla *et al.*, 1983; Miller, 1981; Shulman & Wilson, 1987). As suggested also by Shulman and Wilson (1987), one possible explanation is that in humans sensitivity to particular spatial frequencies might be controlled by the attentional window to local or global information whose changing in size can affect spatial frequencies recognition. In the present work, the goal was to assess this claim by running a study in which the attention set was manipulated toward different spatial frequency patterns (either high or low). However, whereas Shulman and Wilson (1987) assessed the effect of global-local processing on spatial frequencies processing, in the main experiment (Exp. 2) of the last study, the effect of spatial frequencies processing on global-local processing was assessed. Nevertheless, in the third experiment (carried out on humans only) the experimental set-up was reversed making the conditions more similar to those proposed by Schulman and Wilson (1987). In both experiments, a similar procedure to the one on attention was adopted, but the attentional bias was induced using spatial frequencies patterns instead of hierarchical patterns (Exp. 2) and vice versa (Exp. 3). Therefore, after assessing which spatial frequencies were processed well by capuchins (Exp. 1), another experiment was carried out in both species. This experiment featured session in which the majority of trials (85.7%) consisted of spatial frequencies trials (either high or low) and a minority of trials (14.3%) consisted of global-local trials (either global or local). The experiment rested on the rationale that a large proportion of trials requiring the processing of particular spatial frequencies would form an attention set towards those particular frequencies. The formation of such attention set would, in turn, affect global and local processing, if the latter is mediated by attention towards particular spatial frequencies in monkeys and humans.

This study demonstrated that directing visual attention toward a particular spatial frequency can affect the processing of hierarchical patterns. The statistical analysis revealed that the interaction between SF processing and global-local processing was significant in both species. Furthermore, in both cases, this interaction was in an unexpected direction, drawing a complex final picture. In fact, on the basis of previous literature on humans (see for example Shulman & Wilson 1987; Lamb & Yund, 1993; 1996), it could possibly be expected that the HSF bias would *positively* affect local processing whereas the LSF bias would *positively* affect global processing. By contrast, it was found that monkeys performed worse in the local trials under the HSF condition, while humans performed faster in the local trials under the LSF condition. Moreover, in both species, the global trials were not affected by any SF condition.

In Chapter V, the possible reasons which may have lead to these results were discussed. Perhaps, HSF patterns induced a contraction in the attentional window which led in turn to worse performances in subsequent global-local trials, both featuring shapes wider than the HSF bars. Conversely, during the LSF condition, the bars featuring LSF patterns were roughly of the same size of local elements, leading to no effect or even a possible increment in the processing of local trials, as it was found in humans. Therefore, the size of the attentional window can account for the observed pattern of results (see Chapter V, Par. 5.3.3).

However, analysing the entire research work and comparing the second study on attention with the third study on spatial frequencies some interesting similarities can be observed. Both studies revealed that global trials were less affected by attentional manipulations and, interestingly, this pattern was found in both species. In the study on attention, attention biases towards different levels of hierarchical stimuli determined a shift in global-local performance in capuchin monkeys which resulted in a global advantage when a global

attention bias was induced. However, the global bias was accounted mostly for a reduced performance in local trials during the global-bias condition rather than an increased performance in global trials as performance in global trials was unvaried across conditions. Similarly, in the last study on SF, biasing the attention towards different SF determined a change in global-local performance in capuchin monkeys. Nevertheless, this was evident only on local trials (HSF condition) as global performance was very consistent across conditions. Additional comparisons with previous studies confirm this tendency in monkeys. Across four different studies carried out on subjects belonging to the same colony and with the same procedure and stimuli, the overall performance recorded on global trials using Navon-like stimuli ranges between 70.8% and 75.2% (performance on global trials recorded in Spinozzi *et al.* 2003, Exp. 1,  $M = 70.8\%$ ; Spinozzi *et al.*, 2006, Exp. 1,  $M = 75.2\%$ ; study on attention mean combined for the two bias condition,  $M = 74.9\%$ ; Spatial frequencies study mean combined for two SF bias conditions,  $M = 71.2\%$ ). Therefore, several different studies seem to confirm a very consistent pattern in monkeys global processing, regardless of the procedure adopted. This finding suggests that, although not dominant, monkeys global processing, as opposed to local processing, is much less sensitive to attentional biases.

For what concerns humans, the pattern of results on global processing is relatively similar to that one recorded with the monkeys. In the study on attention human accuracy performance on global trials did not change across conditions and also the reaction times revealed a lower sensitivity to the bias condition for the global trials (as demonstrated by the very similar latencies recorded in global and local trials in the local-bias condition). Likewise, in the study on spatial frequencies, global trials, in contrast to local ones, were not affected by any attentional conditions.

Overall, several comparative studies on humans and capuchin monkeys seem to suggest that human global advantage and capuchin local advantage depends on high cognitive mechanism like the visual attention. Furthermore, the present work suggests that in both, capuchin monkeys and humans, global processing is less sensitive to attentional biases regardless of the procedure adopted to induce the biases. Within a comparative framework, this finding represents an additional similarity between capuchin monkeys and humans in their visual processing. However, the reasons beyond these results are less clear.

A possible explanation refers to the costs of switching attention. In humans, an asymmetrical effect has been demonstrated from zooming 'down-up' (i.e., from local-to-global level) and 'up-down' (i.e., from global-to-local level). In fact, there is evidence suggesting that shifting attention in an 'up-down' direction requires extra time than shifting attention in 'down-up' direction (Stoffer, 1993, 1994). The difference in the latencies between global and local trials recorded with humans may depend on the time required to switch attention from an involuntary focusing at the global level to a voluntary focusing at the local level (Stoffer, 1993, 1994). Perhaps, monkeys share with humans a similar effect, with zooming 'up-down' more difficult than zooming 'down-up'. This would possibly explain why, in the second study, only local trials were affected by the bias conditions. In fact, in the global-bias condition monkeys were induced to engage their attention at the global level and would find it difficult to disengage it when the occasional local trials were presented, thus causing a decrement in their performance in these latter trials. However, the pattern of results observed in Chapter V would be more compatible with the idea that switching 'down-up' is more difficult than switching 'up-down' and not vice versa as suggested below. In fact, in the study on SF, which always featured a switching in 'down-up' direction (see Chapter V), if the switch cost was like the one

described in humans, during global-local processing unlikely any deteriorating effect would be found. By contrast, the pattern of results observed in the study on spatial frequencies seems to be more compatible with the idea that switching 'down-up' is more difficult than 'up-down'. Therefore, this interpretative scenario may not fully account for the observed pattern of results across the two studies.

In 1998 Deruelle & Fagot tested baboons, in comparison with humans, in a visual search task in order to find out possible justifications for baboon local bias. Baboons' RTs revealed a positive correlation with the stimulus size, and this was more evident during global processing. Moreover, also variations in the density of local elements affected their global processing. Conversely, RTs in humans resulted independent of all these manipulations. These results were considered consistent with the idea that perceptual grouping operations required to process hierarchical stimuli are more attention demanding for baboons than for humans (Deruelle & Fagot, 1998). Even if the effect on global trials recorded with baboons is different from that one recorded with capuchins in the present study, the underlying reason might be similar. If global processing is particularly attention demanding for capuchins, in the study on attention, the global-bias condition, which consisted of a large number of global trials, may have taken away a consistent amount of attentional resources from the task, affecting in this way the local trials. Conversely, the local-bias condition, where the majority of trials required processing at local level, may have not depleted attentional resources to the same extent and thus failed to negatively affect performance on the few global trials present there. Whereas this hypothesis shows some strengths and can represent a constructive explanation for the results observed in the study on attention, it does not fully account for the varied pattern of results observed in the last

study, where an asymmetrical effect was found in the global-local processing by spatial frequency processing.

Another possible interpretation is that monkey global processing may be *less* attention demanding and therefore performance on global trials is less affected by attentional conditions because it does not depend on particular attentional sets. This claim can potentially explain why performance on global trials was so stable. It is important to highlight that capuchin monkeys, whereas displaying a local advantage, always performed global trials above the chance level, showing a good ability to process the global aspect of hierarchical stimuli (Spinozzi *et al.*, 2003; 2006). Therefore, in this interpretative scenario, global processing was less attention demanding than local processing and therefore, it was less affected by attentional biases. This suggestion fits quite well with the results of both, attention and spatial frequencies, studies where none attentional bias was effective in affecting global performance. Furthermore, it is consistent with the Deruelle and Fagot (1998) interpretation where the trials considered more attention demanding were those affected the most, rather than the less, from attentional biases. Deruelle and Fagot (1998) found that in humans, the processing of the global aspect of the visual scene requires less attentional resources than processing the local one, but the same pattern of results was not found in baboons. However, this feature may still be shared with other primate species. Therefore, it is possible to envisage that, even though the global processing is less attention demanding than local processing, during capuchin evolution, local processing instead of global processing, developed as more advantageous in this species.

It should be pointed out how the ability to process faster and better the global aspect of the visual scene represents an advantage for the majority of animal species since it allows the utilization of low resolution, the economy of processing resources and the fast

disambiguation of unclear details of information (Navon, 1977). Since visual information is often very dynamic, there might not be time for a complete analysis of the constantly changing visual input, then, having an approximate idea of the general structure of the visual scene is often more important than spotting few isolated details (Navon, 1977). Therefore, this feature represents an asset for the survival of most animal species. Given the remarkable value of the global advantage, this may be a feature more widespread among the animal kingdom than it was thought originally. In fact, whereas several bird species such as pigeons and chicks display a local advantage (Chiandetti, Pecchia, Patt, Vallortigara, 2014; Cavoto & Cook, 2001), a growing amount of literature reveals that other non-primate species, even positioned in an early stage of evolution, show a global advantage. For example, the redbill splitfin fish (*Xenotoca eiseni*) shows a global preference when tested with hierarchical stimuli regardless of the density and size of the stimuli (Truppa, Sovrano, Spinozzi, Bisazza, 2010). Even some insects like honey bees (*Apis mellifera*) seem capable of integrating local features and their spatial relationships into global representations to appropriately categorise global images (Stach, Bernard, Giurfa, 2004; Avarguès-Weber, Portelli, Benard, Dyer, Giurfa, 2010). Therefore, the ability to process faster the global aspect of a visual scene, far from representing an exclusive trait of humans, might have developed in an early stage in the animal evolution and may be quite common among the animal kingdom. The literature in this domain is not enough to support this claim; therefore, the following should be considered just like a theoretical speculation. However, if a particular feature is shared by several species, in general, this means that such feature may provide some advantage in terms of adaptation and evolution. Then, as the economy of resources is a common denominator of animal evolution, being able to show and use such feature using lesser resources as possible, represents a benefit.

Applying this idea to the global advantage, the ability to process faster and better the global aspect of the visual scene may be usually accompanied by a lower requirement of attentional resources. In other words, whereas the global processing still requires attentional (Ben-Av, Sagi, Braun, 1992), these resources would be less than those required to process the local elements of a visual scene. Furthermore, this attentional feature may be shared by many other species, perhaps even in those who display a local advantage. If this was the case, how could it be explained that several monkey species, which are taxonomically more related to humans than fish and insects, typically display a local advantage? A possible interpretation is that, in some animal species, the local bias developed as *secondary adaptation* from the global advantage. Animal evolution shows plenty of examples of secondary adaptations. The secondary adaptation of some tetrapods to life in water, typical of dolphins, whales and other sea mammals, is just one example among many. Therefore, it is possible to conjecture that, among the animal kingdom, the global advantage is the original feature, as such is less attention demanding, whereas the local advantage is the secondary adaptation of just a few species and therefore, although showing an advantage, is more attention demanding. In this respect, it could be possible to envisage that the evolution of social grooming (fur cleaning), in which subjects have to focus their attention on the smallest visible particles partly hidden in the fur, can account for this tendency in processing better the local elements of visual scene even if this requires more attentional resources.

The above mentioned interpretative scenarios represent only an attempt to explain the findings reported here and it is not known yet if any of them can, fully or just partly, account for the results observed across the two studies. For this reason, carrying-out further experiment specifically aimed at assessing the susceptibility of global processing to different type of attentional biases in several monkeys

species may provide useful information for the characterization of perceptual grouping among the animal kingdom and ultimately may help in clarifying the emergence of the human cognitive visual system.

## 6.2 CONCLUSIONS

In conclusion, overall several important findings come from the current work. Capuchin monkeys seem to be highly sensitive to some stimulus features like the proximity, the similarity and the orientation of local elements or the internal spatial relationship of a stimulus (Spinozzi *et al.*, 2009; De Lillo *et al.*, 2007). Furthermore, they seem to perceive some visual illusions like the *Müller-Lyer* illusion (Sagunama *et al.* 2007) and potentially the *Solitaire* illusion (Agrillo *et al.*, 2014b). These findings, suggest that monkeys can perceive the local elements of a visual scene and integrate them into a coherent whole. The present work provided evidence that monkeys can also benefit of stimulus redundancy in their visual processing. These findings, taken together, underline a high degree of similarity between human and capuchin monkey visual cognition, demonstrating that monkeys share with humans a wide number of high cognitive skills. Monkeys' local advantage persisted even when grouping was necessary at both levels of processing and when the visual angle of the stimuli was reduced or the numerosity of local elements was increased. These findings support the idea that monkey local bias does not depend on lower perceptual mechanisms such as the requirement to group elements at the global level. Therefore, they point out the notion that higher cognitive mechanisms may be involved in monkey local bias. In fact, biasing attention toward each level of hierarchical stimuli proved effective in reversing monkey typical local advantage and, for the first time, a global advantage

under selective attention conditions was found. Whereas the second study proved that attention can play an important role in monkey visual processing, the last study possibly clarified at least one component on which the attention may act, suggesting that the attentional window can be a key factor involved in it. The evidence that monkey local processing can be affected by attentional biases produced by administering non-hierarchical stimuli and the direction of this effect (with HSF impairing monkeys local processing and LSF facilitating human local processing) are consistent with this claim.

Finally, the present work revealed that monkey and human global processing are less affected by attentional biases and even if the reason of this tendency has still to be clarified, this important finding represents a starting point for future researches.

In conclusion, the findings of the present work highlight that monkey global-local processing is a flexible mechanism which can be modulated by visual attention and it is part of a high sophisticated system which shares many similarities with the human visual system. Therefore, some observed differences could be interpreted more as different cognitive styles driven by visual attention and perhaps associated with other behaviours typical of these species.

Albeit these results, on their own, may not fully account for the origin of the global-local biases exhibited by the two species studied here, they suggest that differences in attentional biases can explain some of the observed interspecies differences also in terms of evolutionary adaptations. Therefore, they point out that attention processes may have a prominent role in the characterization of important interspecies differences in primate visual processing and are worthy of further investigation.

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