Fagot, J., Barbet, I & Parron, C. (2012). Grouping and Segmentation in Human and Nonhuman Primates. In Wasserman, E. & Zental, T. The Oxford Handbook of Comparative Cognition (2nd edn). Page 12-24.

Grouping and Segmentation in human and nonhuman primates

Fagot Joël (1), Barbet Isabelle(2) & Parron Carole (1)

(1) CNRS,
Laboratoire de Psychologie Cognitive, UMR 6146
Bat 9, Case D, 3 Place Victor Hugo
13331 Marseille cedex 1, France

(2) CNAM,
Laboratoire Brigitte Frybourg, Malakoff, France

Grouping and Segmentation in human and nonhuman primates

This chapter focuses on the processing of visual information by nonhuman primates. Early students of primate cognition have mainly investigated the highest cognitive functions of nonhuman primates, such as imitation, theory of mind, tool use, or the ability to solve complex problems. It is only during the last two decades that comparative researchers have systematically examined more perceptual mechanisms. In both humans and animals, perception does not only depend on the characteristics of the sensory inputs. Perception is the product of a complex interaction of bottom-up and top-down processes, and therefore depends on factors such as attention, expectation, personal history, memory, and cognitive abilities, beyond the properties of the visual input per se. These intertwining effects of bottom up and top-down processes make it very unlikely that animals live in the same perceptual world as us and, in experimental contexts, necessary process the same dimensions of the stimuli as we (humans) do. What, then, are the main perceptual differences between humans and animals? What are their consequences? A complete answer to these questions is of course impossible in the context of this chapter, but we will at least approach these issues here.

Two main lines of researches from our group will be presented in this chapter to illustrate similarities and differences in the processing of visual information by baboons and humans. The first one will concern perceptual grouping, a highly adaptive process by which parts (for instance of objects) are put together into a whole. We will demonstrate that baboons are not as prompt as humans to group spatially separated elements into a single percept, and will report convergent findings on other animal species supporting that conclusion. The second one will concern the perception of depth cues, with the demonstration that baboons can perceive depth from pictorial depth cues, as humans do. However, we will highlight subtle human-baboon differences in their processing of occlusion cues as an indicator of depth, probably as a consequence of species variations in grouping mechanism. In conclusion, we will discuss the potential heuristic significance of these findings for accounting species differences in higher cognitive functions.

Species of interest and test procedure

We conduct our research on a small group of Guinea baboons (*Papio papio*) living in the CNRS animal facility in Marseille. Our interest in baboons is due to the baboons sharing of important properties with human vision. These primates have a visual spectral sensitivity very similar to humans (de Valois & de Valois, 1990), and approximately the same visual acuity (Fobes & King, 1982). In addition, as baboons originate from the savannah primates (Altman & Altman, 1970), and thus probably as a consequence of their living condition, they evolved a more elongated visual field than forest primate species (Kobayashi & Koshima, 2001) and a more elongated retina (Fischer & Kirby, 1991), facilitating the comparison with humans who a similarly elongated visual field.

The baboons involved in our research have been continuously tested with manual and then computerized operant conditioning tasks, since they arrived in the laboratory in 1987. These socially housed baboons are tested into an experimental booth (68 cm x 50 cm x 72 cm) facing an analogue joystick, a metal touch pad and a 14-inches color monitor driven by a Pentium IV personal computer (see Figure 1, for technical description see Vauclair & Fagot, 1994). An automatic dispenser is installed along the cage for the delivery of 190-mg food pellets into the enclosure, in accordance to the prevailing reinforcement contingencies.

Insert figure 1 about here

One interesting characteristic of the baboons is that they are highly active and manipulative animals, which is facilitated by a complete opposition between the thumb and the index (Napier & Napier, 1967). We take advantage of these manipulative skills when in our task the baboons delicately control a joystick to respond to the stimulus display. Most of the test procedures firstly involve the presentation of a fixation point on the computer screen. The animal responds to that display by an action on the joystick in order to a cursor on the fixation point. This aspect of the procedure ascertains that the subject pays attention to the screen at the beginning of each trial. Manipulation of the joystick induces isomorphic displacements of the cursor on the monitor. An early video recording of eye fixation confirmed that this procedure is highly effective to capture baboons' attention on the fixation stimulus (Wilde, Vauclair & Fagot, 1994).

Multiple procedures were developed and used with our baboons over years, they include the go-nogo task, the two-alternative forced-choice discrimination task (2AFC), the visual search task, and variations of identity and conditional matching tasks. These different procedures are commonly combined in our research projects. In addition, the research strategy often implies a comparison between humans and baboons, using human volunteers tested with the same joystick task as baboons.

Studies on Visual Attention to Global and Local Stimulus Levels

Global (or local) precedence ?

Objects have often a hierarchical structure. They are entities made of parts, subparts and so on. One first set of experiments assessed if the baboons decompose objects in whole and parts, and if they pay attention to the same component (s) of the objects, as we do. Navon (1977) proposed that the visual perception of objects implies a first analysis of the global level (i.e., whole) prior to the analysis of the details of this object (i.e., parts). This hypothesis is referred to in the human literature as the “global precedence hypothesis” (Navon, 1977). Experimental supports of global precedence are numerous in the human literature (e.g., Lamb & Roberston, 1988; Lamb, Robertson & Knight, 1990), at least when the stimuli are not overly large (Martin, 1979). They mostly derive from the use of stimuli, such as a large letter made of smaller ones, with a clear two-level hierarchy. Two main effects supporting the global precedence are commonly found in the human literature (Navon, 1977). First, response times are shorter for identification of the global letter compared to the local ones. This effect is referred to as a global advantage. Second, there is a global-to-local interference corresponding to faster identification of the local letters when the two stimulus levels represent the same (consistent stimuli) than different letters (inconsistent stimuli).

Prior to our study, researchers had paid very little attention to this issue of global/local processing in the animal literature, probably because they implicitly embraced the idea that global precedence is such a general mechanism that it must also be present in the animal kingdom. In one preliminary study, Horel (1994) found that cooling the inferotemporal cortex of macaques selectively hampered local processing, but hat no clear effect global processing, suggesting that these two mechanisms are supported by different neural structures. Hopkins (1997) also reported a right visual field (i.e., left hemispheric) advantage in chimpanzees for local processing, but no significant advantage for global processing. In our laboratory, we run several experiments to test global/local processing in baboons. Some of these experiments are summarized below. More detailed information on these studies can be found in Fagot and Deruelle (1997), Deruelle and Fagot (1998) and Fagot, Tomonoga and Deruelle (2001).

Navon’s type two-level structured hierarchical stimuli were presented to a total of 8 baboons in the context of a matching-to-sample task (MTS, see Fagot & Deruelle, 1997, Exp. 2). The stimuli (see Figure 2a) were 4.7 x 4.7 degrees large circles, squares, diamonds and crosses constructed from smaller (.6 degrees) circles, squares, diamond and crosses. In each trial, the baboon firstly saw hierarchical sample stimulus after the eye fixation period. After a brief presentation of the sample during 120 ms, it was then presented with two comparison stimuli. One of them shared one stimulus level with the sample. The other one was completely different from it at both stimulus levels. To obtain a food reward, the baboon had to select the form sharing one stimulus level with the sample. Some of the test sessions involved local trials only, in which S+ shared the local stimulus level with the sample. The other test sessions involved global trials, in which similitude between the sample and S+ concerned the global level. A total of 14 humans were also tested in that task, to compare their performance to that of baboons. The human subjects were tested with the same procedure as for baboons, except that the monitor and joystick were laid on a table at which human subjects were seated.

Insert Figure 2 about here

Figure 2c illustrates the finding. The humans behaved differently from the baboons in that task. Considering either scores (see figure 2b) and response times (see Figure 2c), only humans showed a global advantage corresponding to better performance and shorter response times for global trials compared to local trials. Baboons had by contrast a higher performance and shorter response times for local trials, suggesting an advantage for these trials. In addition, only humans reveal an effect of stimulus consistency, corresponding to an enhanced performance for local trials when the global and local stimulus level illustrated the same shape. In other words, global precedence was only found in humans in our study, as baboons showed an advantage for local trials and no effect of stimulus consistency.

Baboons’s attentional processes

To verify the nature of the attentional mechanism recruited in the previous task, new experiments were conducted using a visual search task paradigm (Deruelle & Fagot, 1998). The procedure was inspired from Saarinen's (1994) and Enns and Kinstone's (1995) earlier studies on humans. In that new task, the displays could contain either 4, 8 or 12 stimuli, and there were two types of trials: the go- or the nogo trials. In nogo trials, all the stimuli of the display were identical, whatever the global or local stimulus level considered. They were either a large circle made up of 8 small squares, or a large square made up of 8 small circles. By contrast, one compound stimulus (the target) was different from the other stimuli (the distractors) in the go trials. For these latter trials, the difference between the target and the distractors either concerned the local (local-go trial) or global (global-go trial) stimulus level. To be rewarded, the baboons had to move the joystick as fast as possible when a target was detected in the go trial, and to refrain from moving it in case of a nogo trial. Again, a group of eight humans was also tested in the same conditions as for baboons, to assess species differences in attentional processes.

Response times for the go trials were analyzed considering the species, the stimulus level (global vs. local) and display size. We found that humans were faster on average for the global trials (mean = 421 ms) than for the local ones (mean = 470 ms). The global advantage was therefore again replicated for them. The findings also replicated the local advantage of the baboons, as they had shorter response times on average for the local trials (mean = 466 ms) than for the global trials (mean = 510 ms). Maybe more importantly, there was a significant interaction of the three considered factors. In baboons, response times increased linearly with display size in global trials (linearity accounted for 99% of the variance), but did not vary significantly with display size in the case of the local trials. In humans, display size exerted no reliable control of response times, which remain approximately stable regardless the number of distractors, and for both the global and local trials.

In the human literature, the visual search task is commonly employed to distinguish parallel- from serial-information processing. According to Treisman and Gelade (1980), flat search slope (i.e., when the response times are independent of display size) demonstrate a parallel processing of the information contained in the display. In that case, very little attentional resources would be required to recognize the target which “pops out”. By contrast, a linear increment of the response times with display size would demonstrate a serial search procedure, during which the subjects sequentially pay attention to the stimuli contained in the visual displays. Conclusions from our study are thus straightforward in the context of that theory. First, when they have to pay attention to the shape of the local stimulus features, the baboons would inspect the display in parallel, a process requiring minimal attentional ressources. By contrast, linear increments of response times in global trials suggest that the same animals employed a much more attention-demanding procedure (i.e., a serial search) when they have to pay attention to the global stimulus level to detect target. In humans, a parallel search strategy would be used in both the global and local trials. In sum, this study is a clear demonstration that humans and monkeys, tested with the same stimuli and the same experimental procedure, process the task in two very distinct ways.

Difficulty in perceptual grouping as a source of local precedence in baboons

One interesting aspect of the hierarchical stimuli used in our research is that only the local elements are continuous perceptual entities (such as small squares), while the global shape is made up with spatially disconnected local elements. In other words, the perception of the global structure of the compound forms implies that the local elements are grouped into a single percept in spite of their separation. In the global/local task described above, the baboons demonstrated a serial search strategy to detect the global target, while humans adopted a parallel search. This aspect of the results can be accounted for by the fact that baboons have a greater difficulty than humans to group the local elements into a coherent whole. This hypothesis - suggesting a global disadvantage in baboons rather than a local advantage per se - was tested in the next experiment.

Two novel factors were manipulated independently (Deruelle & Fagot, Exp 4, 1998), they were the overall size of the global shapes (2 or 4 degrees of visual angle), and their density (8 or 16 local elements). Combinations of these factors led to three independent test conditions of interest to assess the effect of density and stimulus size. They were the large dense condition (4 degrees, 16 local elements), the large sparse condition (4 degrees, 8 local elements) and the small dense condition (2 degrees, 8 local elements). The experiment was proposed to the same 8 baboons as before as well as 8 human subjects. Display size was set to 3, 6 or 9 stimuli.

The analysis of response times (RTs) was impossible in that task, due to the baboons' very poor performance in the large sparse condition. Inspection of the scores obtained by the baboons indicated a significantly poorer performance on average in the large sparse trials (mean = 58% correct) than in the large dense (mean = 94.5%) and small dense (mean = 91.2%) trials, with no reliable statistical difference between the latter two conditions. Similar scores in the large dense and small dense conditions suggest that variations in global size did not affect the processing. For the large sparse trials, there was also a linear relation in baboons between the number of errors and display size (linearity accounted for 99% of the variance). The number of errors was by contrast independent of the display size in the small dense and large dense test conditions. In humans, the scores reached a very high level (>99% correct on average) that precluded an analysis of accuracy. However, RTs were analyzed and showed significant longer RTs on the average for the large sparse (M = 432 msec) than for the large dense condition (M = 387 msec), but no significant difference between the large sparse and the small dense condition. In addition, RTs were found to be faster for the global (M = 397 msec) than for the local condition (M = 427 msec). Altogether, these findings suggest that baboons are much more sensitive than humans to the separation of the local elements, and in comparable test situations, are not as proficient as humans in overcoming spatial separation between the elemental features of the stimuli in order to perceive a coherent whole.

Perception of the global stimulus structure in an implicit task

The previous experiments have all implied judgements on the global level and/or local level of hierarchical stimuli. We also assessed perceptual grouping in baboons, when the task involved an implicit perception of the global form of the stimuli. This new study (Parron & Fagot, 2007) used the Ebbinghaus (also named Titchener) illusory figures to study implicit perceptual grouping in baboons. The Ebbinghaus illusory figure consists of a central target shape surrounded by large or small shapes (Figure 3). With that stimuli, humans usually perceive the central figure as being larger when it is surrounded by smaller shapes (called inducers) than when it is surrounded by larger inducers (e.g., Massaro & Anderson, 1971). The strength of the illusion is in humans partly controlled by the distance between the target and the inducers, with smaller distance leading to stronger illusion (Roberts, Harris, & Yates, 2005). This effect of stimulus distance suggests that grouping factors contribute to illusory perception. Assuming, as argued above, that the baboons have reduced abilities for perceptual grouping, we hypothesized that baboons would not experience the Ebbinghaus illusion (or would have reduced illusory effects) in comparison to humans. Indeed, the illusion should be attenuated in baboon as a consequence of a local mode of processing allowing consideration of the central target independently of the surrounding distractors.

Insert figure 3 about here

Eight baboons and 8 humans were tested with displays such as illustrated in Figure 3. The illusory figure with small inducers systematically contained a central target circle of 19 mm diameter (referred to as the “constant” target). The other configuration contained a central target varying from 14 mm to 24 mm, by 1 mm steps (“variable” target). In some trials, the constant target was therefore smaller than the variable target. The opposite was true in some other trials. The task for the subject was to select the compound display containing the largest central target (for procedural details, see the original article).

The most informative test conditions was when the two central targets were of the same size (0 mm condition), or when the constant target was larger than the variable target (+1, +2, +3, +4 and +5 mm). The humans exhibited a reliable bias for selecting the constant target for target size differences of 0, +1, +2 and +3 mm. This bias unambiguously demonstrates that humans experienced the Ebbinghaus illusion. However, this bias was not replicated in baboons, suggesting species differences in the illusion.

To further assess species differences in this task, we computed the condition of target size leading to 50% correct. That condition is referred to as the point of subjective equivalence (PSE). The PSE were significantly larger on average for humans (22.1 mm) than for baboons (18.3 mm). They were moreover different from 19 mm (veridical equality) only for the group of humans. Clearly, only humans experienced the illusion in that task. We propose that the baboon’s local mode of stimulus processing allowed a restricted attention to the ‘to-be-judged’ central shape without misperception.

Convergent and divergent findings

The issue of perceptual grouping has gained importance in the animal literature, since our first demonstration of a local mode of processing in baboons (Fagot & Deruelle, 1997). Several papers are now available on this issue in pigeons (Fremouw, Herbranson & Shimp, 1998; Cavoto & Cook 2001), capuchin monkeys (Spinozzi, De Lillo, & Truppa, 2003; De Lillo, Spinozzi, Truppa & Naylor, 2005; Spinozzi, De Lillo, & Salvi, 2006), tamarins (Neiworth, Gleichman, Olinick & Lamp, 2006), macaques (Tanaka & Fujita, 2000; Hopkins & Washburn, 2002) and chimpanzees (Hopkins & Washburn, 2002, Fagot & Tomonaga, 1998; Fagot et al., 2001). Considered together, these publications confirmed that animals can successfully process the two levels of hierarchical stimuli, but do not all consistently reveal a local precedence effect.

Findings convergent with a local processing advantage in baboons have been published in several animal species. In one such study, Cavoto and Cook (2001) trained pigeons to recognize global or local shapes of hierarchical stimuli made with letters. The learning curves showed that the pigeons acquired the discrimination faster in the local relevant condition than in the global relevant condition. Spinozzi and collaborators have conducted studies on capuchin monkeys (*Cebus apella*), (Spinozzi et al., 2003; De Lillo et al., 2005; Spinozzi et al. , 2006). Their first study (Spinozzi et al., 2003) replicated with capuchins Fagot and Deruelle's (1997) study on baboons using a matching to sample procedure, in which the sample stimulus shared the two stimulus levels with the positive matching stimulus, and the negative comparison had no dimension in common with the sample. Not unlike baboons, the findings revealed a greater performance in the local (94.8% correct on average) than in the global trials (70.8%). Demonstration that the increment of the inter-element distance has a stronger effect in nonhuman primates than in humans (Deruelle & Fagot, 1998, Exp 4) was also replicated with the capuchins (Spinozzi et al., 2003, Exp. 3; De Lillo et al., 2005; Spinozzi et al., 2006).

In one collaborative research with Japanese colleagues (Fagot & Tomonaga, 1998; Fagot et al., 2001), we could also replicate a local advantage in chimpanzees, a more closely human related species. This study, using geometrical shapes made up with smaller shapes, such as large circles made up of squares. In this study, the chimpanzees showed a stronger local bias than humans tested under the same conditions. Note however that this effect of local precedence was weaker than previously found on baboons, as it disappeared with very dense stimuli and turned into a global-to-local advantage when the local elements were connected by small lines (Fagot & Tomonaga, 1999).

By contrast, a global precedence effect was reported in several studies involving pigeons (Goto, Wills & Lea, 2004), tamarins (Neiworth et al., 2006), macaques (Tanaka & Fujita, 2000) and chimpanzees (Hopkins & Washburn, 2002). Goto et al. (2004) reported that pigeons process the global forms of hierarchical stimuli in priority. In our view, this result has a limitation due to stimuli that strongly minimized the need for perceptual grouping as a consequence of a very close proximity between the local elements. It remains unknown in this study if global precedence would resist when the gap separating the local elements is enlarged (and we suspect it would not). The same limitation applies to another divergent study, by Hopkins and Washburn (2002), which also used very dense stimuli for discrimination. As for Goto et al. (2004), we assume that global precedence has been permitted in this research by the reduced need for grouping associated to short inter-element distances. Neiworth et al. (2006) more recently tested global processing in a species of New World monkeys, the tamarin (*Saguinus Oedipus*). Two different stimulus densities were used in their research, and the findings revealed a global mode of processing for the densest stimuli. As the dense stimuli had the same visual appearance as the stimuli in Deruelle and Fagot (1998), we are unable to reconciliate the different outcomes. We note however that global bias disappeared in the tamarins in the condition of lowest density, which confirms that the expansion of the gap separating the local feature exerts a strong control on the ability to perceive the global structure of the stimuli. Finally, another instance of global processing is also reported by Tanaka and Fujita (2000) who worked with macaques. The task was a highly difficult one for the macaques, as it involved the discrimination of stimuli that were mirror images of each other at both the global and local stimulus level. In our view, the fact that the macaques made very little discrimination errors (less than 5%) in this difficult task suggest that they have been over-trained prior to the test. Unfortunately, the authors provide no information on the training, which limits the significance of their findings.

Which conclusion should finally be drawn for these divergent findings? We propose that these studies have the advantage to demonstrate that the predilection for local processing is not an all-or-none effect. In spite of inconsistencies with regard to the direction (global or local) of precedence effects, the existing literature demonstrates that when a local advantage emerges in animal, this effect lies on perceptual grouping deficiencies. In support of this conclusion, Spinozzi et al. (2003) reported a local advantage in capuchins which was mostly evident when large sparse stimuli were used (for similar results, see Spinozzi, de Lillo, & Castelli, 2004, De Lillo et al. 2005, Spinozzi et al. 2006; De Lillo, Spinozzi & Truppa, 2007). We also reported that chimpanzees exhibit a reliable local advantage for the processing of hierarchical stimuli (Fagot & Tomonaga, 1999). This advantage turned into a global advantage when the local features were connected by line segments. It is likely that these segments have helped the grouping of the local features into a coherent whole. In brief, although more studies would remain useful to guaranty the generality of the phenomenon, the conclusion derived from our studies that a variety of animals have difficulties to overcome gap barriers seems valid and applicable to a wide range of animal species (for complementary convergent findings on rats or sea lions, see Kurylo, Van Nest & Knepper, 1997; and Burke, Everingham, Rogers, Hinton & Hall-Aspand, 2001).

Insert figure 4 about here

Perception of pictorial depth

The next section of this chapter will focus on the processing of depth cues available in pictorial representations. We will report below several lines of evidence suggesting that the processing of these cues may occasionally differ between animals and humans.

Our visual system has the highly adaptive ability to perceive and process depth. For comparative psychologists, one interesting situation of depth perception is obtained when the subjects (animals or humans) perceive pictorial representations of 3-dimensional scenes or objects. Consider what a 2-dimensional image is. Two of the three dimensions of the visual world are explicitly available in images, they are the width and the height, but information on the third dimension, the depth, is highly ambiguous and contradictory on images. On the one hand, images are flat objects. Reflection of the surface of the image, as well as motion, accomodation and stereoscopic cues suggest that this image is flat. On the other hand, depth is depicted on images by the so-called monocular pictorial depth cues, such as gradient, shading, or occlusion cues, which are similarly available in the natural life as well as when we look at picture (but see Palmer, 1999). For instance, if an object is partly masked by another object in the image, the picture suggests that the occluded object is more distant from the observer than the occluding objects. Images are thus ambiguous stimuli, they are flat objects suggesting depth. Considering these attributes of pictorial representations, the question arises of how animals process depth information available on the images, and if they perceive them as we, humans, do.

This important question of depth perception was studied in two complementary ways in our laboratory. We firstly verified if baboons experience the corridor illusion, a special case of size illusion induced in humans by the perception of pictorial depth cues. We then verified the role of occlusion cues as an indicator of depth perception in baboons. The reader is referred to Barbet and Fagot (2002), Deruelle, Barbet, Dépy and Fagot (2000) and Fagot, Barbet, Parron and Deruelle (2006) for more detailed descriptions of the experimental conditions and findings.

The corridor illusion

Have a quick look at Figure 5. Which of the two persons depicted on the pictures is taller than the other one? Like most of the human observers, you probably perceive the person in the back taller than that on the front. This is an illusion as the two persons are exactly of the same size, which can be confirmed by measuring them. This illusion is named the “corridor illusion”. It is an interesting illusion for our purpose because it is induced by the various depth cues contained by the hallway background. Indeed removing the background stops the illusion and the two persons now appear of similar size. Theoreticians of visual perception generally consider that the illusory image deceives the size constancy system. In the case of the corridor illusion, our visual system would assume that the background person is the largest one, because the two persons have the same visual size but appear at different distances.

Insert figure 5 about here

In our laboratory, we tested the corridor illusion in baboons using a procedure based on the go-nogo paradigm (Barbet & Fagot, 2002). Our stimuli are illustrated in Figure 5. In each trial, the baboons perceived an image containing two persons or either equal or different veridical sizes. To receive a food pellet, they were requested to either move the joystick during a response period of 3 seconds when the size of the two persons was different, or to refrain from moving it when the two persons on the pictures were of identical sizes.

The first training phase systematically implied backgrounds containing no pictorial depth cues, such as textured flat surfaces or wallpapers. After the baboons met a training criterion of 80% correct or more in training sessions with flat backgrounds, we introduced 4 new kinds of backgrounds in the test phase. They were (1) photographic images of real corridors and (2) their control scrambled version. Note that the scrambling procedure removed depth cues. The other types of backgrounds were (3) novel pictures of 2D surfaces, such as new wallpapers and (4) their corresponding control scrambled images. Two blocks of trials were run in this task.

If baboons perceive the corridor illusion, they should provide more go responses (i.e., “different” responses) with the corridor backgrounds than with the other three kinds of background when the two persons have the same veridical size on the images. This effect was found in the results. In the first block of test trials, the frequency of “go” was reliably higher for the illusory corridor pictures (45%) than for the three other kinds of backgrounds (corridor scramble = 21.2%; 2D background = 17.5%; scramble of the 2D background = 8.8%). The same finding was replicated in the second block of test trials (corridor = 56.2%; corridor scramble = 8.7%; 2D background = 18.7%; scramble of the 2D background = 12.5%), suggesting the reliability of the effect.

To confirm the illusory perception in baboons, we also inspected if presentation of a corridor background facilitates detection of size differences in go trials, when the largest person is shown behind the smallest one. This effect was found in the analysis of response times. Thus, the baboons responded faster with the corridor backgrounds (mean = 796 ms) than with their scrambled images (mean = 935 ms, $p < .05$). There were by contrast no reliable differences in response time between the 2D background-trials and the 2D-scrambled controls. Findings therefore converge to demonstrate that the use of 3D-backgrounds altered size-judgments in our baboons. Demonstration of the corridor illusion in baboons indicates that in these animals, and presumably in other animals too, depth information can be derived from the sole presentation of pictorial depth cues. This conclusion has been recently confirmed in two experiments (Imura, Tomonaga, & Yagi, 2008; Imura & Tomonaga, 2009) showing that chimpanzees also exhibited the corridor illusion with backgrounds containing linear perspective cues.

Occlusion cues indicators of depth

Occlusion is one of the pictorial cues suggesting depth (Palmer, 1999). The contribution of occlusion as a cue to depth is illustrated in Figure 6. That figure shows a display that can either be perceived as a square adjacent to a 3-quarter-circle or as a square partly covering a complete circle. Most of the people perceive depth from that display, and therefore interpret it as showing a square above a circle (e.g., Rensik & Enns, 1998). In that situation, depth is inferred because the visible junctions between the two objects are coherent with what would be seen if a square occludes one part of a circle.

There are contradictory results on animals' abilities to perceive occluded shapes as complete (i.e., amodal completion), some studies suggesting that animals can complete invisible objects (Kanizsa, Renzi, Compostela & Guerani, 1993; Lea, Slater & Ryan, 1996; Forkman, 1998; Forkman & Vallortigara, 1999; DiPietro, Wasserman, Young, 2002; Fujita & Giersh, 2005, Nagasaka, Hori, & Osada, 2005) while others provide more negative results (Cerella, 1980; Fujita, 2000, Sekuler; Lee & Shettelworth, 1996, Ushitani & Fujita, 2005; Fujita & Ushitani, 2005). These discrepancies can be accounted for by the test of very different species, mice, pigeons, chicks and hens, monkeys, which may have evolved their own mode of processing. However, they might also be due to the use of stimuli containing different kinds of pictorial depth cues. The stimuli used in Sekuler et al. (1996), for instance, only contained junction cues as cues depth, while those of Forkman and Vallortigara (1999) contained both junction cues and background perspectives depth cues. Finally, another possible source of divergence is the prior experience of the subjects with pictorial displays. It is possible that previous training has also affected the ability to recognize partly occluded objects (DiPietro et al., 2002; Lazareva, Wasserman & Biederman, 2007; Nagasaka, Lazareva & Wasserman, 2007).

Our research group has conducted several experiments on visual completion in baboons. Here, we only report a synthesis of the most critical ones published as Deruelle et al. (2000, Experiment 5) and Fagot et al. (2006, Experiment 1). In one experiment, baboons were initially trained to select one circle on the screen and to avoid selecting a three-quarter circle (named here after the amputated stimulus). The circle and the amputated stimuli were presented side by side with a randomization of their left/right location on the computer screen. After the baboons had been trained to select the full circle in more than 80% of the trials, they were presented with the two compound stimuli shown in Figure 7. One of these stimuli can be interpreted as a circle partially occluded by a square. This is the occluded test stimulus. The other stimulus represented the amputated circle shown adjacent to a square. This stimulus will be referred as the amputated test stimulus. Our rationale in this experiment was that the baboons should indicate a reliable preference for the occluded circle, rather than a random choice, if they experience amodal completion and therefore interpret the occluded stimulus as a circle behind a square. Results disconfirmed our hypothesis. There was no reliable preference for the occluded stimulus in the test trials, suggesting that the baboons did not experience amodal completion in our task. Note that these negative findings were found in several experiments, using occluded shaped only defined by junction cues, but a go-nogo instead of a two alternative forced-choice procedure (see Deruelle et al., 2000).

Insert Figure 6 and 7 about here

In these latter baboons studies, depth was only indicated by junction cues. In their study on hens, Forkman (1998) and Forkman and Vallortigara (1999) found that hens complete visual occluded objects when the stimuli contain contextual information suggesting depth, in addition to the junction cues. In line with these authors, we then tested if baboons would show amodal completion when contextual background containing cue to depth were added to the amputated and occluded stimuli. Four baboons were thus retested with the same two alternative forced-choice procedure as before, but with the stimuli shown on Figure 8. The findings revealed that the use of the depth background altered their judgment. All baboons now more readily selected the occluded stimulus (in 67.5 % of the trials on average). Preference for the occluded stimulus was significant in three of the four baboons (chi-square tests, $p < .05$). We thus conclude from these experiments that perception of the corridor background alters the processing of the to-be-completed stimulus, and promotes completion of that stimulus.

Insert Figure 8 about here

A comparison with humans

The contour of the occluded object typically forms intersections known as T junctions, when an object is occluded by another object (e.g., Rubin, 2001). The continuous contour (the horizontal bar of the T) delineates the border of the object whose surface occludes the other edge (the stem of the T). It has been repeatedly demonstrated that T junctions exert the greatest control on amodal completion, when the edges leading to discontinuities can be connected with minimally curved line segments (Kellman and Shipley, 1991; Palmer, 1999).

It remains uncertain why baboons did not complete our stimuli in absence of depth background. One first possible explanation is that the T junctions available in the display were not properly treated as indicators of depth, thus hampering amodal completion. This hypothesis leads to the prediction that the baboons should remain incapable to complete the visual form with the corridor backgrounds, and this is not what we have observed. Another explanation could be that our baboons had a too focal attention in our task to process the whole scene, and therefore to interpret it as showing an object occluded by another one. In that context, the use of the corridor backgrounds might have induced greater attention to the global aspects of the stimuli, and therefore promoted an interpretation of the T junctions as cues to depth. We are currently planning experiments to test this hypothesis.

From the processing of shapes to the processing of more abstract relations

This chapter has treated two aspects of visual information processing in baboons: global/local precedence and depth perception. Regarding the issue of global/local precedence, we have reported a local precedence in baboons during the processing of hierarchical stimuli, which contrasts with global precedence in humans. We have also proposed that the local precedence in baboons can be explained by their difficulty to overcome the separation between the local elements, a necessary process for perceiving the whole. Regarding depth perception, we have demonstrated that baboons perceive the corridor illusion and therefore that they gain depth information from the pictorial cues available in the image background. Baboons however failed to process occluded objects as complete ones, when the objects are shown on a black background devoid of depth cues. When a corridor background was added to the to-be-completed form, presence of depth cues in the background likely induces attention to the global aspects of the forms, with the direct consequence of promoting completion of the occluded objects. We therefore for these studies conclude that a series of perceptual difference between baboons and humans (and presumably other animals too, e.g., Kurylo et al., 1997; Burke et al., 2001) affects the interpretation and understanding of pictorial displays.

The above studies have clearly established perceptual differences between humans and baboons, but the boundaries of these differences remain unclear at this point. It is in particular unclear if local precedence in baboons generalizes to other stimuli, possibly to more naturalistic stimuli, for which the global and local dimensions are rarely as well defined as for the hierarchical stimuli made with letters or shapes. We argue that propensity to process the local dimension of the stimuli depends on the parameters of the task, and the type of the stimuli it implies.

One recent study from ours has investigated the processing of biological motion point-light displays in baboons (Parron, Deruelle & Fagot, 2007). Point-light displays are created by placing lights on the joints of a human or an animal in action, and displaying these point-lights on a black background. In humans, point-light displays allow recognition of animal or human models (for instance its species), and even more impressively of the action performed by the model (e.g., Johansson, 1973). Use of such stimuli in our study has suggested that the baboons grouped subsets of point-light available in the displays, and based their responses on the configuration of these sub-parts of the displays. Motion cues, therefore, likely promote grouping in that context. Note however that motion cues were insufficient for the processing of the whole configuration of dots, and therefore for the recognition of the depicted actions, which confirms the baboons tendency to attend the local rather than global features.

In complementary perspective, one may wonder if the local processing would also persist in baboons when the stimuli are pictures of objects, rather than hierarchical stimuli “à la Navon” (1977). Because objects in the real life are continuous coherent objects, in contrast with the hierarchical stimuli that are composed with spatially discontinuous local features, it is not guaranteed that attraction to the local feature generalize to these more naturalistic stimuli. In fact, in other experiments not reported in details here, we found that the baboons discriminate realistic faces considering the facial contours rather than the inner-facial features (Martin-Malivel & Fagot, 2001). In another study, the baboons discriminated chimeric faces considering configurations of facial features, suggesting that the facial features were processed considering their context in this research (Parron & Fagot, 2007). Configural processing was also found with greeble stimuli (Parron & Fagot, in revision), which are artificial photorealistic stimuli sharing configural cues with faces (e.g., Gauthier & Tarr, 1997).

Although local processing might not systematically characterize the processing of objects encountered in the real life, a focal attention on the objects (or their features), as demonstrated in this chapter, might affect the perception of the abstract relations among objects. Spatial relations such as the above/below, near/far or in/our relations, are one first set of relations potientially affected by a focal attention. Animals can process such relations (e.g., above/below: Dépy, Fagot & Vauclair, 1999; in/out: Herrnstein, Vaughan, Mumford & Kosslyn, 1989), but this is notoriously difficult for them, and far from being spontaneous and immediate. A focal attention (focused on either the objects or their constituting feature), might account for such difficulties. A second set of relations potentially affected by a focal attention are the non-spatial abstract relations of sameness or differentness. In one recent study (Fagot & Parron, in press), we could demonstrate that baboons can discriminate pairs of stimuli considering the same or different relation they illustrate, but that this processing was facilitated when the elements of the pairs were in close spatial proximity. In sum, experiments such as those reported in the context of this chapter are critical to understand the perceptual world of animals, to delineate how it differs from that of humans, and the perceptual origins of their cognitive limitations.

References

Altman, S.A. & Altman, J. (1970). Baboon ecology. Chicago: The University of Chicago Press.

Barbet, I. & Fagot, J. (2002). Perception of the corridor illusion by baboons. Behavioural Brain Research, 132, 111-115.

Burke, D., Everingham, P., Rogers, T., Hinton, M., Hall-Aspland, S. (2001). Perceptual grouping in two visually reliant species: Humans (*Homo sapiens*) and Australian sea lions (*Neophoca cinerea*). Perception, 30, 1093-1106.

Cavoto, K.K., & Cook R.G. (2001). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. Journal of Experimental Psychology: Animal Behavior Processes, 27, 3–16.

Cerella, J. (1980). The pigeons analysis of pictures. Pattern Recognition, 12, 1-6.

De Lillo, C., Spinozzi, G., & Truppa, V. (2007). Pattern recognition in tufted capuchin monkeys (*Cebus apella*): the role of the spatial organisation of stimulus parts. Behavioural Brain Research, 181, 96-109.

De Lillo, C., Spinozzi, G., Truppa, V., & Naylor, D.N. (2005). A comparative analysis of global and local processing of hierarchical visual stimuli in young children and monkeys (*Cebus apella*). Journal of Comparative Psychology, 119, 2, 155-165.

de Valois, R. L., & de Valois, K.K. (1990). Spatial vision. Oxford: Oxford University Press.

Dépy, D., Fagot, J. & Vauclair, J. (1999). Processing of above-below categorical spatial relations by baboons (*Papio papio*). Behavioral Processes, 48, 1-9

Deruelle, C. & Fagot, J. (1997). Hemispheric lateralization and global precedence effects in the processing of visual stimuli by humans and baboons. Laterality, 2, 233-246.

Deruelle, C. & Fagot, J. (1998). Visual search task for global/local stimulus features in humans and baboons. Psychonomic Bulletin Review, 5, 476-481.

Deruelle, C., Barbet, I., Dépy, D. and Fagot, J. (2000). Perception of partly occluded figures by baboons (*Papio papio*). Perception, 29, 1483-1497.

DiPietro, N.T., Wasserman, E., & Young, M.E. (2002). Effects of occlusion on pigeons' visual object recognition. Perception, 11, 1299-1312.

Enns, J.T., & Kingstone, A. (1995). Access to global and local properties in visual search four compound stimuli. Psychological Science, 6, 283-291.

Fagot J & Parron C. (in press). Relational Matching in baboons with reduced grouping requirements. Journal of Experimental Psychology: Animal Behavior Processes.

Fagot, J. & Tomonaga, M. (1999). Comparative assessment of global-local processing in humans (*Homo sapiens*) and Chimpanzees (*Pan troglodytes*): Use of a visual search task with compound stimuli. Journal of Comparative Psychology, 113, 3-12.

Fagot J., & Deruelle, C. (1997). Processing of global and local visual information and hemispheric specialization in humans (*Homo sapiens*) and baboons (*Papio papio*). Journal of Experimental Psychology: Human Perception and Performance, 23, 429-442.

Fagot, J., Barbet, I., Parron, C., & Deruelle, C. (2006). Amodal completion by baboons (*Papio papio*): contribution of background depth cues. Primates, 47: 145-150

Fagot, J., Tomonaga, M. & Deruelle, C. (2001). Processing of the glocal and local dimensions of visual hierarchical stimuli by humans (*Homo sapiens*), Chimpanzees (*Pan troglodytes*) and baboons (*Papio-papio*). In Matsuzawa, T. (Ed.) Primate Origins of Human Cognition and Behavior (pp. 87-103). Tokyo: Springer.

Fischer, Q.S. & Kirby, M.A. (1991). Number and distribution of retinal ganglion cells in anubis baboons. Brain Behaviour and Evolution, 37, 189-203.

Fobes, J.L., & King, J.E. (1982). Vision: The dominant primate modality. In J.L. Fobes, & J.E. King (Eds.), Primate behavior (pp. 219-243). New York : Academic Press.

Forkman, B. 1998. Hens use occlusion to judge depth in a two-dimensional picture. Perception, 27, 861-867.

Forkman, B. and Vallortigara, G. (1999). Minimization of modal contours: an essential cross-species strategy in disambiguating relative depth. Animal Cognition, 2**,** 181-185.

Fremouw, T., Herbranson, W.T. & Shimp, C.P. (1998). Priming of attention to local and global levels of visual analysis. Journal of Experimental Psychology: Animal Behavior Processes, 24, 278-290.

Fujita, K. (2000). What you see is different from what I see: Species differences in visual perception. In: Matsuzawa, T. (Ed.), Primate Origin of Human Cognition and Behavior, Springer: Tokyo (pp. 28-54).

Fujita, K. & Ushitani, T. (2005). Better living by not completing: a wonderful peculiarity of pigeon vision? Behavioural Processes, 69, 59-66.

Fujita, K., & Giersh, A. (2005). What perceptual rules do Capuchin Monkeys (*Cebus Apella*) follow in completing partly occluded figures? Journal of Experimental Psychology: Animal Behavior Processes, 31, 387-398.

Gauthier, I, & Tarr, M. J. (1997). Becoming a “greeble“ expert: exploring mechanisms for face recognition. Vision Research, 37, 1673-1682.

Goto, K,Wills, A.J., Lea, S.E.G. (2004). Global-feature classification can be acquired more rapidly than local-feature classification in both humans and pigeons. Animal Cognition, 2, 109-113.

Herrnstein, R.J., Vaughan, Jr. W., Mumford, D.B. & Kosslyn, S.M. (1989). Teaching pigeons an abstract relational rule: insideness. Perception & Psychophysics, 46, 56-64.

Hopkins, W.D. (1997) Hemispheric specialization for local and global processing of hierarchical visual stimuli in chimpanzees (*Pan troglodytes*). Neuropsychologia, 35, 343-348.

Hopkins, W.D., & Washburn, D. (2002). Matching visual stimuli on the basis of global and local features by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca Mulatta*). Animal Cognition, 5, 27-31.

Horel, J.A. (1994). Local and global perception examined by reversible suppression of temporal cortex with cold. Behavioural Brain Research, 65, 157-164.

Imura T., & Tomonaga, M. (2009). Moving shadows contribute to the corridor illusion in a chimpanzee (*Pan troglodytes*). Journal of Comparative Psychology. 123, 280-286.

Imura T., Tomonaga M., & Yagi A. (2008). The effects of linear perspective on relative size discrimination in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). Behavioural Processes, 77, 306-312

Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. Perception & Psychophysics, 14, 201–211.

Kanizsa, G., Renzi, P., Conte, S., Compostela, C. and Guerani, L. (1993). Amodal completion in mouse vision. Perception, 22, 713-721.

Kellman, P.J., & Shipley, T.F. (1991). A theory of visual interpolation in object perception. Cognitive Psychology, 23, 141-221.

Kobayashi, H. & Koshima, S. (2001). Evolution of the human eye as a device for communication. In Matsuzawa, T. (Ed.) Primate Origins of Human Cognition and Behavior (pp. 383-401). Tokyo: Springer.

Kurylo, D.D., van Nest, J., & Knepper, B. (1997). Characteristics of perceptual grouping in rats. Journal of Comparative Psychology, 111, 126-134.

Lamb, M.R. & Robertson, L.C. (1988). The processing of hierarchical stimuli: Effects of retinal locus, locational uncertainty and stimulus identity. Perception and Psychophysics, 44, 172-181.

Lamb, M.R., Roberston, L.C., & Knight, R.T. (1990). Component mechanisms underlying the processing of hierarchically organized patterns: Inferences from patients with unilateral cortical lesions. Journal of Experimental Psychology: Learning, Memory and Cognition, 16, 471-483.

Lazareva, O.F., Wasserman, E., & Biederman,I. (2007). Pigeons' recognition of partially occluded objects depends on specific training experience. Perception, 36, 33-48.

Lea, S.E.G., Slater, A.M. and Ryan, C.M.E. (1996). Perception of object unity in chicks: A comparison with the human infant. Infant Behavior and Development, 19, 501-504.

Martin, M. (1979). Local and global Processing: The role of sparsity. Memory and Cognition, 7, 476-484.

Martin-Malivel J., and Fagot, J. (2001). Perception of pictorial human faces by baboons: effects of stimulus orientation on discrimination performance**.** Animal learning and behavior, *29*, 10-20.

Massaro, D.W. & Anderson, N.H. (1971). Judgmental model of the Ebbinghaus illusion. Journal of Experimental Psychology, 89, 147-151.

Nagasaka, Y., Hori, K., & Osada, Y. (2005). Perceptual grouping in pigeons. Perception, 34, 625-632.

Nagasaka, Y., Lazareva, O.F., & Wasserman, E. (2007). Prior experience affects amodal completion in pigeons. Perception & Psychophysics, 69, 596-605.

Napier, J.R. & Napier, P.H. (1967). A Handbook of Living Primates. New York: Academic Press.

Navon, D. (1977). Forest before the tree: The precedence of global feature in visual perception. Cognitive Psychology, 9, 353-383.

Neiworth, J.J, Gleichman, A.J, Olinick, A.S, & Lamp, K.E. (2006). Global and local processing in adult humans (*Homo sapiens*), 5-year-old children (*Homo sapiens*), and adult cotton-top tamarins (*Saguinus oedipus*). Journal of Comparative Psychology, 120, 4, 323-330.

Palmer, S.E. (1999). Vision Science : Photons to Phenomenology. MIT Press: Cambridge.

Parron, C., & Fagot, J. (2007). Comparative assessment of grouping abilities in Humans (*Homo sapiens*) and Baboons (*Papio papio*) with the Ebbinghaus illusion. Journal of Comparative Psychology, 121: 405-411.

Parron, C., & Fagot, J. First- and second-order configural sensitivity for greeble stimuli in baboons. Learning & Behavior (*in revision).*

Parron, C., Deruelle, C., & Fagot, J. (2007). Processing of biological motion point-light displays by baboons (*Papio papio*). Journal of Experimental Psychology: Animal Behavior Processes, 33: 381-391.

Rensik, R.A. & Enns, J.T. (1998). Early completion of occluded objects. Vision Research, 38, 2489-2505.

Robert, B., Harris, M.G., & Yates, T.A. (2005). The roles of inducer size and distance in the Ebbinghaus illusion (Titchener circles). Perception, 34, 847-856.

Rubin, N. (2001). The role of junctions in surface completion and contour matching. Perception, 30,339-366.

Saarinen, J. (1994). Visual search for global and local stimulus features. Perception, 23, 237-243.

Sekuler, A.B., Lee, J.A.J. and Shettleworth, S.J. (1996). Pigeons do not complete partly occluded figures. Perception, 25, 1109-1120.

Spinozzi, G., de Lillo, C. & Truppa, V. (2003). Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). Journal of Comparative Psychology, 117, 15-23.

Spinozzi, G., De Lillo, C., & Castelli, S. (2004). Detection of "grouped" and "ungrouped" parts in visual patterns by tufted capuchin monkeys (*Cebus apella*) and humans (*Homo sapiens*). Journal of Comparative Psychology, 118, 297-308.

Spinozzi, G., De Lillo, C., & Salvi, V. (2006). Local advantage in the visual processing of hierarchical stimuli following manipulations of stimulus size and element numerosity in monkeys (*Cebus apella*). Behavioural Brain Research, 166, 45-54.

Tanaka, H. & Fujita, I. (2000). Global and local processing of visual patterns in macaque monkeys. Neuroreport, 11, 2881-2884.

Treisman, A., & Gelade, G. (1980). A feature integration theory of attention. Cognitive Psychology, 12, 97-136.

Ushitani, T, & Fujita, K. (2005). Pigeons do not perceptually complete partly occluded photos of food: an ecological approach to the “pigeon problem”. Behavioural Processes, 69, 67-78.

Vauclair, J. & Fagot, J. (1994). A joystick system for the study of hemispheric asymmetries in nonhuman primates. In Anderson, J.R., Roeder, J.J., Thierry, B., & Herrenschmidt, N. (Eds.) Current Primatology: Behavioral Neuroscience, Physiology and Reproduction (pp 69-75). Strasbourg: Presses de l'Université Louis Pasteur.

Wilde, J., Vauclair, J., & Fagot, J. (1994). Eye movements in baboons performing a matching-to-sample task presented in a divided-field format. Behavioural Brain Research, 63, 61-70.

Figure captions

Figure 1. View of a baboon manipulating a joystick

Figure 2. a) Examples of compound stimuli used with baboons; b) Average scores achieved by humans and baboons in global and local trials; c) Average correct response times of humans and baboons in global and local trials

Figure 3. Illustration of the stimuli used to assess the corridor illusion in baboons. The two persons in this figure have the same veridical size.

Figure 4. Occluded and amputated test stimuli used with baboons

Figure 5. Percentage of "go" (i.e, "Different") responses achieved by each individual tested for amodal completion. All baboons provided more go responses when the stimuli were shown on a 3D background than when they were on a uniform 2D background

Footnotes

[1] The test procedure ascertained that completion with the corridor background was not a consequence of training, due to test order, see Fagot, Barbet, Parron & Deruelle (2006).