Chapter 20

Visual Cognition in Baboons:

Attention to Global and Local Stimulus Properties

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The survival fitness of any visual animal, including primates, depends on its ability to properly recognize the objects surrounding it. This can be a complex task because objects do not always have fixed visual appearances. In the everyday life, objects are often partially masked by other objects and can be perceived at different distances and from different points of view. In addition, objects of interest are often moving and are, therefore, seen in front of a variety of backgrounds. Given such high variability in viewing conditions, the challenging task of object recognition necessarily implies the presence of efficient mechanisms by which the different parts of the objects are grouped into coherent perceptual units, distinct from their background. In the domain of comparative psychology, it is only recently that primatologists have started paying attention to such an important mechanism as perceptual grouping. Historically, attention on this topic suffered due to a natural inclination of comparative psychologists to study higher cognitive functions instead, such as concept formation, imitation, or the ability to solve complex problems. Interest in perceptual grouping also suffered due to early theoretical accounts considering vision as a bottom-up process, with species differences mostly reflecting variations in late (cognitive) rather than early (perceptual) mechanisms. However, vision should no longer be theorized as a strict bottom-up form of processing, given the strong evidence that top-down effects can influence the response of neurons as early as in area V1 (e.g., Li, Piëch, & Gilbert, 2004; see also Chapter 5, this volume). In addition, both human and nonhuman vision depends on expectation or early experience, further suggesting the involvement of top-down processes (Crist, Li, & Gilbert, 2001). Thus, top-down influences on perception suggest that species differences in perceptual grouping functions may exist between nonhuman primate species, or between nonhuman primates and humans.

Following that reasoning, we have conducted several studies that compared grouping mechanisms in two nonhuman primate species (chimpanzees and baboons) and in humans. This chapter will synthetically present our contribution in that domain, while also summarizing some of the recent related findings of the field.

The Framework: Navon’s Global Precedence Theory

The human visual system has an amazing capacity for grouping. We can recognize objects as wholes remarkably well, even when some of their parts are masked or deleted. We also have the ability to perceive a line from a series of dots, or shapes from discontinuous lines. These abilities demonstrate that the perception of unity does not imply perceptual continuity. The perception of objects as wholes from spatially discontinuous features has received significant attention since the pioneering work of Navon (1977). In this work, human subjects were presented with hierarchical stimuli structured in a clear two-level hierarchy, such as a large letter (for instance a large H) that was composed of smaller letters (for instance a small S). The participants were requested to identify the letter serving as features (local level), or the compound letter made by the small ones (global level). Navon (1977) reported converging evidence showing that the overall structure of the stimuli is, in general, perceived prior to their local structure. One the one hand, response times were shorter on average for identifying the letter at the global level than for identifying the letter at the local level. On the other hand, recognition of the local letters were faster when the global and local stimulus levels represent the same letter (consistent stimuli) than when they represent two different letters (inconsistent stimuli). Navon (1977) concluded from these two findings that perception generally proceeds from an analysis of the global structure of the forms toward a more fine-grained analysis. This hypothesis, coined the *global precedence hypothesis”*, has received a great deal of experimental support (e.g., Lamb & Robertson, 1988; Lamb, Robertson, & Knight, 1990) since Navon’s pioneering studies (1977).

There are reasons to believe that global precedence must have important adaptive value. According to Navon (1991), priority for attending to the global structure of the form may promote a prompt identification of the object by narrowing the number of possible identities. This first rough identification would then be refined by the analysis of those local object features that may be less unique than the global whole. Attention to the global dimension of the stimuli may also help to quickly estimate the behavior of an object more efficiently than if the attention was focused on its local dimensions. This might be of high value for estimating, for instance, if the object target of attention is moving or not, in order to adjust the behavior of the perceiver in response to this object. Although global precedence seems adaptive to humans and perhaps all predominately visual animals, it remained to be tested if global precedence also characterizes the perception of nonhuman primates. This was achieved in our research, as described below.

General Methods

Our experiments mostly involved baboons as subjects (Deruelle & Fagot, 1997, 1998; Fagot & Deruelle, 1997; Parron, Deruelle, & Fagot, 2007; Parron & Fagot, 2007), although some of our collaborative studies were also conducted on chimpanzees (Fagot & Tomonaga, 1999). Baboons are appropriate subjects for human–nonhuman comparative research because they belong to the Cercopithecidae superfamily that shares important properties of human vision. These primates have a visual spectral sensitivity very similar to that of humans (de Valois & de Valois, 1990), and they share with humans the ability to detect fine visual details (Fobes & King, 1982). Another interesting feature of baboons is that they are short-grass savannah primates (Altman & Altman, 1970) that rely on vision for daily activities and social communication. As an adaptation to their living conditions, baboons evolved a more elongated visual field than did forest primate species (Kobayashi & Koshima, 2001) and a more elongated retina (Fischer & Kirby, 1991), thus facilitating the comparison with humans who have similar visual properties. In addition, the exact functional properties of the chimpanzees' visual system remain to be determined. Nevertheless, assessments of color or form perception (e.g., Grether, 1940; Matsuno, Kawaï, & Matsuzawa, 2004) and visual acuity in chimpanzees (e.g., Matsuzawa, 1990) showed strong similarities with primates from the Old World family to which the baboons belong. These similarities suggest that that these functions evolved little between these Old World monkeys and apes (Fobes & King, 1982) and warrant direct comparison between baboons and chimpanzees.

Our experiments used a total of eight baboons, all trained in various operant conditioning computerized tasks. Figure 20.1 shows our setup. The baboons were tested individually in an experimental booth facing a color monitor (Figure 20.1; see Vauclair & Fagot, 1994, for technical description). The monitor served to present the stimuli. Response to the test displays implied selection of the positive stimulus when it appears on the screen. This was done by manipulating an analogue joystick that controlled the displacements of a cursor on the screen. The baboons were not food deprived, but received high-value food rewards (banana-flavored pellets) in case of correct responses. These reinforcements were delivered inside the experimental booth through an automatic food dispenser. In all our experiments, the test displays were systematically presented after a fixation stimulus. Video recording of eye fixation indicated an effective capture of the baboons' attention on the fixation stimulus (Wilde, Vauclair, & Fagot, 1994).

<Insert Figure 20.1>

Perception of Hierarchical Objects by Baboons

The degree to which animals perceive the global properties of the visual input in comparison to more featural ones has been an issue of concern in animal cognition for some time, but traditional studies were mostly conducted in the spatial domain (e.g., Cook, 2001; Spetch & Edwards, 1988). To our knowledge, the first primate study on global–local processing of hierarchical objects was conducted by Horel (1994). This author used cold to temporally inactivate the dorsal inferotemporal cortex of macaques by placing cryodes in the brain while macaques were engaged in a global–local discrimination tasks. The cooling procedure hampered the subject's ability to process the local level of the hierarchical forms, but had no such effect for the global level, suggesting that two distinct systems exist in the macaque brain for processing these two stimulus levels. Hopkins (1997) used a divided-field procedure to present hierarchically organized global–local stimuli to chimpanzees. A right visual field (i.e., left brain hemisphere) advantage was observed during the processing of the local stimulus level, although there was no significant advantage for the processing of the global level. He thus confirmed that two different neural systems are involved when viewing the global–local stimulus features. Our first series of research on this issue (Deruelle & Fagot, 1997; Fagot & Deruelle, 1997; Fagot, Tomonoga, & Deruelle, 2001) complemented these two studies.

Our comparative studies on global–local processing in humans and baboons did not use hierarchical stimuli made of letters, because letters have a special status for humans but not for baboons. We used instead hierarchical stimuli made of geometrical shapes, three examples of which are shown in Figure 20.2. The stimuli were large/global circle, square, diamond, and cross (4.7 × 4.7 degrees of visual angle), comprised from small/local circles, squares, diamond, and crosses (0.6 degrees of visual angle). In the first experiment, we employed a matching-to-sample procedure (Fagot & Deruelle, 1997). After eye fixation on the fixation point, the test trials began with the presentation of a hierarchical sample stimulus of 120 ms on the screen. Immediately after, the subjects viewed two different comparison stimuli. In local trials, the sample stimulus and the match to choose were identical at the local level but different at the global level, as illustrated in Figure 20.2A. In the global trials, the sample and the match had a common global shape but had different local features, as illustrated in Figure 20.2B. By way of joystick manipulation, the baboon had to select the comparison form matching the sample. To do so, it had to selectively attend the global stimulus level in the global trials, and local stimulus level in the local trials. For comparative purposes, we also tested 14 human subjects using the same procedure as for baboons. Interested readers can find more details about this experiment in Fagot and Deruelle (1997, Experiment 2).

<Insert Figure 20.2>

This experiment revealed an amazing species difference in global–local processing. Thus, computation of a species (human, baboon) by matching condition (global, local) analysis of variance (ANOVA) on scores indicated a significant interaction between these two factors. Human participants exhibited a global advantage, whereas baboons showed their greatest performance in the local matching condition (Figure 20.3A). The analysis of correct median response times confirmed this first observation on scores. A significant species-by-matching condition interaction showed faster correct response times in the global condition in humans, but a reverse effect in baboons (Figure 20.3B). Put in a different way, humans' accuracy and response time results indicated a clear global precedence in this task. Global precedence did not emerge at all in baboons, which rather demonstrated a mode of processing characterized by local precedence. That was, to our knowledge, the first time that local precedence was demonstrated in nonhuman primates. At this stage, our study remained limited because it provided no cues on the possible origins of differences between humans and baboons in global–local processing. Identification of the source of this difference was made possible by our use of a go/no-go visual search task in a subsequent experiment (Deruelle & Fagot, 1998).

<Insert Figure 20.3>

In the typical visual search task, the subjects are required to detect a target presented among a variable number of distractors. Inspection of the response times as a function of distractor set size may reveal either longer response times with increasing set size or stable response times with increasing set size. Treisman and Gelade (1980) proposed that flat response time slopes (i.e., stable response times) demonstrate that the displays are processed in parallel, with very little recruitment of attentional resources. By contrast, a linear increment of response times with set size indicates the use of a serial, rather than parallel search strategy, during which the participant sequentially scans the various stimuli composing the display. Following this reasoning, we considered the visual search task to be an appropriate task for investigating whether attentional factors account for the difference between humans and baboons in the processing of hierarchical stimuli.

Our visual search task used the same eight baboons as before. In that experiment, they perceived a display containing four, eight, or 12 hierarchical stimuli. Half of the trials were no-go trials. The displays in these trials consisted of either a large circle made of eight small squares, or a large square made of eight small circles (Figure 20.4). To obtain a food reward, baboons had to refrain from moving the joystick in these no-go trials. On the go trials, corresponding to the other half of the trials, one stimulus (the target) was different from the other stimuli (the distractors). We arranged two types of go trials, the global and the local trials. On the global go trials, the target and the distractors were made up of the same local elements but differed in global shapes. For instance, the target could consist of a large square made of small circles, and the distractors could consist of large circles made of smaller circles. By contrast, on the local go trials, the target and the distractors differed in local shape but shared the same global properties. For instance, the target could be a large circle made up of small squares, and the distractors could be large circles made up of small circles. In local and global go trials, the baboons received a reward when they moved the joystick within 3 s after the onset of a display. Again, humans were also tested using the same monitor, joystick, and visual search procedure as for baboons.

<Insert Figure 20.4>

Response times revealed highly interesting results (Figure 20.5). Humans behaved very differently from the baboons in this task. Humans were faster to respond on global go trials than on local go trials, thus confirming Navon's (1977) global precedence hypothesis. We also found that the manipulation of the stable display sizes did not affect response times in these global go trials. These stable response times suggest that stimuli were processed in a parallel fashion. In contrast, baboons were faster to respond on local go trials than on global go trials, demonstrating local advantage instead of global advantage. In addition, baboons' response times increased with display size for the global go, but not for local go trials. In sum, the findings suggest that human participants processed the global and local dimensions of the stimuli in an attention-free parallel fashion. By contrast, baboons used two distinct modes of processing on global go and local go trials. Like humans, they employed parallel search on the local trials but used a more attention-demanding serial search on global trials. This implies that perceiving the global dimension of our hierarchical stimuli is a challenging problem for baboons, one that requires a great deal of attention resources (see Deruelle & Fagot, 1998).

<Insert Figure 20.5>

Difficulties in Perceptual Grouping Account for the Local Advantage in Baboons

The hierarchical stimuli we have used so far were made of spatially distinct local features composing a global shape of a higher order. Consequently, perceiving the global shape requires at least two steps. First, the viewer must be able to expand his perceptual/attentional field so as to process the entire stimulus. Second, the viewer must perform some operations of grouping to bind the local elements into a higher global shape. Under these considerations, it is possible that the local advantage shown by baboons reflects some limitations in attentional shifting, perceptual grouping, or both.

Further tests conducted in our laboratory have shown that baboons can efficiently discriminate continuous circles and squares, as large as the global shapes of the hierarchical stimuli (Deruelle & Fagot, 1998, Experiment 2). This finding shows that their difficulty in global trials is not due to an inability to process large stimuli, but seems rather due to a deficit in perceptual grouping. Confirmation that the baboons are deficient in perceptual grouping, relative to humans, also derives from another experiment. In this new experiment (Deruelle & Fagot, 1998, Experiment 4), a visual search task procedure was adopted with hierarchical global–local stimuli varying in global size and density. Three conditions were tested: the large sparse, large dense, and small dense (Figure 20.6). Display sizes were set at three, six, or nine items.

<Insert Figure 20.6>

This research again showed important differences between humans and baboons. Humans could achieve a very high performance in this task, whatever the stimulus considered. By contrast, density had an important effect on baboons’ performance. Their performance was high in the two densest conditions, but it declined drastically in the large sparse condition. There was no reliable difference between the large dense and small dense conditions. The performance of the baboons was thus size independent, but it depended strongly on the stimulus density. Even more interesting findings were obtained when the display size was introduced as a factor in the analyses. This revealed a linear relation between the number of errors and the display size for the large sparse trials achieved by baboons. By contrast, linearity did not account for a significant portion of the variance in the other test conditions (small dense and large dense stimuli). We therefore concluded from our findings that baboons group the local elements with much more difficulties than do humans. That finding explains perfectly well why these animals are so poor in global trials, in comparison to the local ones.

Implicit Versus Explicit Grouping: Test of the Ebbinghaus Illusion in Baboons

The above experiments all used an instrumental procedure involving an explicit discrimination of hierarchical stimuli. Our next experiments went one step further, testing whether baboons could efficiently group the local elements into higher-order figures, but would be unable to use that information when the task involved an implicit perception of the global form of the stimuli.

We used Ebbinghaus (or Ebbinhaus-Titchener) illusory figures as natural tools to assess this hypothesis. Ebbinghaus illusory figures consist of a central target shape surrounded by large or small shapes (Figure 20.7). Humans usually perceive the central figure to be larger when it is surrounded by smaller shapes (called *inducers*), than when it is surrounded by larger inducers (e.g., Massaro & Anderson, 1971). In humans, the strength of the illusion directly depends on the distance between the target and the inducers, with smaller distance leading to stronger illusion (Roberts, Harris, & Yates, 2005), suggesting that grouping factors contribute to illusory perception.

<Insert Figure 20.7>

We hypothesized that baboons would not experience the Ebbinghaus illusion, or would at least have reduced illusory effects in comparison to humans tested in the same conditions as baboons. Our rationale was that the illusion should be attenuated by the processing of the central target independently from the distractors, as a consequence of a local mode of processing.

In this study, the subjects (eight baboons and eight humans) perceived a display composed of two illusory figures. One of these figures was made with small inducers, whereas the other one involved larger inducers (see Figure 20.7). The configuration with small inducers always contained a central target circle of 19 mm diameter (“constant” target). The configuration with large inducers contained a target varying from 14 mm to 24 mm, by 1 mm steps ("variable" target). Hence, there were trials in which the constant target was smaller than the variable target, trials in which it was larger, and trials in which two targets had the same size. In each trial, the human or baboon subjects had to point with the cursor to the compound display containing the largest central target (for procedural details, see Parron & Fagot, 2007).

The most informative test conditions were those in which the constant target had the same size as the variable target (0 mm condition) and those in which the constant target was larger than the variable target (+1, +2, +3, +4, and +5 mm). Only in these conditions should the illusion lead to erroneous size judgments. As Figure 20.8 illustrates, all 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. There was no such evidence for the baboons.

<Insert Figure 20.8>

To assess species differences in this task, we computed the points of subjective equality (PSE) for the two species. The PSE corresponds to the condition of size leading to 50% correct. Confirming the above findings, the PSE were significantly larger on average for humans (22.1 mm) than for baboons (18.3 mm), and were different from 19 mm (veridical equality) only for the group of humans. It is therefore clear that only humans experienced the illusion in this task. We propose that the baboons' failure to experience the Ebbinghaus illusion reflects a reduced integration of the inducers as a consequence of a local mode of processing, thus allowing restricted attention to the "to-be-judged" central shape without misperception. Together with our research using Navon's hierarchical figures (Navon, 1977), this research further confirms that, in the same viewing conditions, reliable perceptual differences emerge between humans and closely related nonhuman primates (see also Chapter 7, this volume).

The decade consecutive to the publication of our first global–local experiment (Fagot & Deruelle, 1997) has given rise to a great deal of experimental research on the processing of hierarchical stimuli by animals. Some of them converge with our findings, whereas others do not. Convergent and divergent studies will be briefly reviewed below.

Convergent Findings

Findings convergent with our demonstration of an advantage for processing local features in baboons have been published for several other animal species. Evidence for a local-to-global mode of processing in animals was found by Cavoto and Cook's (2001) study on pigeons. Their pigeons were trained to associate four hierarchical stimuli made of letters X, N, H, and T, with a specific choice key (four alternative choices). Examples of their hierarchical stimuli are shown on Figure 20.9. Each hierarchical stimulus depicted an X, N, H, or T letter, at the global (Global relevant) or local (Local relevant) stimulus levels. The irrelevant level was represented by the letter O. Control trials were also run with a continuous presentation of the letters X, N, H, and T that were the same size as the local (local equivalent) or global (global equivalent) size of the hierarchical stimuli.

<Insert Figure 20.9>

Cook and Cavoto (2001) showed that the pigeons acquired the discrimination faster in the local-relevant condition than in the global-relevant condition. Moreover, their accuracy with the size-matched global equivalent condition using solid letters was superior to that with the global-relevant condition. These results indicate that the observed local advantage during acquisition was not due to the larger visual angle and size of the global-relevant stimuli. Additional tests using “conflicting” stimuli representing the target letters at both levels further confirmed this conclusion. It is therefore clear from this study that pigeons processed the local stimulus dimension more easily than they did the global ones, not unlike baboons. This similarity is interesting as the visual system of pigeons is largely different from that of primates (for instance, considering the size of their visual field, their number of photosensitive receptors, and their visual acuity; Lea & Dittrich, 2001).

Spinozzi and collaborators have conducted studies on the processing of global–local hierarchical stimuli on a New World primate species, the capuchin monkey (*Cebus apella*) (De Lillo, Spinozzi, Truppa, & Naylor, 2005; Spinozzi, De Lillo, & Salvi, 2006; Spinozzi, De Lillo & Truppa, 2003). Their first study (Spinozzi et al., 2003) used capuchins to replicate our previous experiments with baboons involving a matching-to-sample task (Fagot & Deruelle, 1997). Instead of using a computerized task, they used cards mounted on sliding lids to present the stimuli. In each trial, a reward was placed behind the lid showing the correct match. In the global trials, the positive matching stimulus (S+) was identical to the sample, and the negative stimulus (S-) differed from the sample only at its global level. For instance, if the sample was a circle made up of small circles, S+ was a circle made up of small circles, whereas S- was a square made up of small circles. In the local trials, S+ was identical to the sample, and S- differed from the sample only by its local elements. Findings revealed a clear local advantage: Matching performance was greater on local trials (94.8% correct on average) than on global trials (70.8%). Another similarity between the results of capuchins and baboons concerned the effects of stimulus density on global–local processing. Remember that global processing in baboons is hampered by a low stimulus density. This effect of density on global processing was replicated in several experiments with capuchins (De Lillo et al., 2005; De Lillo, Spinozzi, & Truppa, 2007; Spinozzi et al., 2003, 2006; Spinozzi & Castelli, 2004).

We have conducted collaborative research with Japanese colleagues based at the Primate Research Institute of Kyoto University. Our collaboration used hierarchical stimuli presented on a touch screen to chimpanzees in the context of a visual search task (Fagot & Tomonaga, 1999; Fagot et al., 2001). This research showed that chimpanzees had a stronger propensity to discriminate forms on the basis of their local properties than did humans tested under the same conditions. However, a strict comparison with the data obtained on baboons suggests that this effect was weaker in chimpanzees than in 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).

The hypothesis that animals have more difficulties than humans for perceptual grouping also finds some support from studies using compound stimuli for which the global stimulus structure has to be judged. One good example is a study by Kurylo, van Nest, and Knepper (1997) using rats. Their rats had to discriminate horizontal alignments of dots from vertical ones. As stimuli, they used matrixes of dots that varied in horizontal and vertical inter-dot distances (Figure 20.10). Their results revealed that the rats diminished capacity to use proximity and alignment cues for perceptual grouping, in comparison to humans. Similar conclusions were also obtained from the study of Australian sea lion (Burke, Everingham, Rogers, Hinton, & Hall-Aspand, 2001). Finally, other reports also show that animals may have difficulties processing the overall shapes of dot configurations (e.g., pigeon: Watanabe, 1988; baboon: Parron et al., 2007). Clearly, the baboons' deficiencies in perceptual grouping is not an isolated phenomenon.

<Insert Figure 20.10>

Diverging Evidence

Other evidence suggests that nonhuman animals may also prioritize processing of the global aspects of hierarchical patterns, at least under some circumstances. Among the earliest of such evidence is provided by the study of Tanaka and colleagues, who published two papers on this issue. Their first paper (Tanaka & Fujita, 2000) presents behavioral data on rhesus macaques, a species phylogenetically close to baboons. Their second paper presents neurophysiological positron emission tomography (PET) scan data on the same subjects (Tanaka, Onoe, Tsukada, & Fujita, 2001). In both experiments, macaques were required to discriminate the global (or local) form of visual patterns. Visual stimuli were in the form of hierarchically organized letters made of small letters (N, Z) and nontarget letters (reversed N, reversed Z; Figure 20.11). These two studies report a global advantage in two macaques.

However, some aspects of this research need to be more closely examined. First, the positive and negative stimuli at both the global and local stimulus levels were mirror images of each other. Discriminating mirror images is a notoriously difficult problem for monkeys, which might have required a great deal of training to be solved. Second, performance in this task was very high in both global and local trials, much higher than in any other study reported so far (<5% of errors). These two important considerations lead us to believe that the animals had probably been overtrained in this task. Unfortunately, neither Tanaka and Fujita (2000) nor Tanaka et al. (2001) report individual learning curves, therefore leaving uncertain whether their global advantage is a consequence of this specific training or reflects a natural propensity of macaques to prioritize processing of the global dimension. With much less training, Hopkins and Washburn's (2002) report a local (although not significant) advantage in the processing of hierarchical letters by macaques, contrary to Tanaka et al. (2001).

<Insert Figure 20.11>

The second study of this section considered pigeons as subjects (Goto, Wills, & Lea, 2004). These authors reported that pigeons prioritize the processing of the global forms of hierarchical stimuli, but their study had a limitation. As shown in Figure 20.12, it used stimuli that strongly minimized the need for perceptual grouping because the local elements were very close to each other. We thus take Goto et al. (2004) as demonstrating that the advantage for local processing is not an all-or-none effect. When the need for grouping is high, for instance due to a large interelement distance, animals' performance deteriorates more than does that of humans (e.g., Deruelle & Fagot, 1998; Spinozzi et al., 2006), but this difference disappears when the local stimuli are close together, promoting a global mode of processing (as in Fagot & Tomonaga, 1999; Goto et al., 2004).

<Insert Figure 20.12>

More recently Neiworth, Gleichman, Olinick, and Lamp (2006) used a species of New World monkeys, the tamarin (*Saguinus oedipus*), as subjects. After training to discriminate two compound hierarchical stimuli, tamarins were presented with novel pairs of stimuli that shared only one stimulus level with the training stimulus. The authors used two different stimulus densities in their research. Their results revealed a global mode of processing for the densest stimuli. Because the dense stimuli had about the same appearance as the stimuli that revealed a local advantage in Deruelle and Fagot (1998), we are unable to reconciliate different outcomes. However, this global bias disappeared for the low-density stimuli, which confirms our earlier suggestion that the expansion of the interelement distances has strong effects on grouping abilities in animals.

Fremouw, Herbranson, and Shimp (1998) used a two-alternative choice task in which the pigeons had to report forms or letters presented at either the global or local level. The experimenters manipulated the relative probabilities of a locally relevant or globally relevant display within a session. The results showed that their pigeons responded faster to the more frequently tested level, irrespective of whether this level was the local or global one. According to Fremouw et al. (1998), this priming indicates that pigeons can flexibly shift their attention between the different levels of hierarchical stimuli in a human-like way.

Individual Variations in Human Global–Local Processing

We have stated before that a prioritization of the global dimension of hierarchical stimuli characterizes human perception. Although this conclusion seems broadly applicable in the populations tested so far, some variations exist across human groups. Adopting a cross-cultural perspective, Nisbett and Miyamoto (2005) showed that in perceptual tasks, Westerners tend to engage in context-independent and analytic perceptual processes by focusing on a salient object of the scene independently of its context, whereas Asians tend to engage in context-dependent and holistic perceptual processes. This observation suggests that cross-cultural variations may exist in global–local processing. To confirm such variations, we have conducted a cross-cultural study on the Himba (Davidoff, Fonteneau, & Fagot, 2008). Himba are isolated, seminomadic people living in Namibia. This study revealed a local bias for the Himba participants stronger than that previously observed in any other nonclinical human population. Moreover, the local mode of processing in the Himba was confirmed in another study using the Ebbinghaus illusory figures (de Fockert, Davidoff, Fagot, Parron, & Goldstein, 2007). Results revealed that the Himba group was much less sensitive to the Ebbinghaus illusion than were Westerners tested in the same conditions as the Himba. Overall, we take these results as an evidence that cultural factors may, at least in part, interfere with the processing of the global–local dimension of the stimuli.

Similarly revealing results were obtained with studies conducted on people with autism. Autism is a developmental disorder in which, among other things, specific deficits are found in tasks that demand the processing of wholes. In contrast, a person with autism performs rather well at tasks that demand the processing of details. Several lines of evidence support the idea that people with autism excel in processing local features in comparison to global features. For instance, individuals with autism exhibit superior performance compared to controls in perceptual tasks involving a local analysis of the stimuli (e.g., Joliffe & Baron-Cohen, 1997) or the detection of a target feature embedded in a set of distractors (Plaisted, O'Riordan, & Baron-Cohen, 1998). In addition, children with autism often fail to perceive visual illusions, such as the Ebbinghaus illusion and the Poggendorf illusion (Happé, 1996). According to Happé, failure to experience these illusions reflects the fact that participants do not integrate the surrounding context of the figures, thus allowing focalization on the "'to-be-judged'" shapes without misperception. Use of Navon's type of hierarchical stimuli with autistic people revealed mixed findings. Some papers report a local advantage (e.g., Wang, Mottron, Peng, Berthiaume, & Dawson, 2007), whereas others report a global advantage (e.g., Mottron, Burack, Iarocci, Belleville, & Enns, 2003). Clearly, however, the reported global precedence is not as pronounced as it is in people without autistic disorder. All these results can in part be explained by a relative deficit in perceptual grouping in children with autism (Brosnan, Scott, Fox, & Pye, 2004). They might be accounted for as well by a more general deficit in processing of the configural properties of the stimuli, leading to a focal attention on local features (Deruelle, Rondan, Gepner, & Fagot, 2006). Deficits of processing wholes, relative to details, in people with autism have been claimed to reflect abnormalities of information integration caused by a reduced connectivity between specialized networks in the brain (Brock, Brown, Boucher, & Rippon, 2002). The fact that local precedence has also been reported in clinical groups other than people with autism, such as people with schizophrenia (Chen, Nakayama, Levy, Matthysse, & Holzman, 2003) gives credence to this hypothesis.

Overall, these cross-cultural and clinical studies demonstrate that perception in global–local tasks is not an all-or-none phenomenon, and that it might be influenced by experiential and other subject-related factors. It is possible that such factors also account for the divergence obtained in the animal literature (see section on divergent findings).

Conclusion

At the beginning of this research program on the processing of the global and local properties of visual objects, we wanted to verify if global precedence (as described by Navon, 1977) can be replicated in nonhuman primates. We were surprised to discover a local advantage, rather than a global advantage characterized by the processing of hierarchical stimuli in baboons. We tested humans using the same conditions that were used for baboons and confirmed a global mode of processing for this population. Our detailed investigation of local advantage in baboons further revealed that (1) local precedence can be accounted for by a reduced proximity grouping, and (2) a local mode of stimulus processing was also evident in the perception of the Ebbinghaus illusion (Parron & Fagot, 2007), for which there was no explicit training to process the global stimulus structure. Similar studies of global–local precedence were conducted in other primate species and in birds. With a few exceptions (e.g., Goto et al., 2004), these comparative studies confirmed that the local processing mode is not restricted to baboons, but also characterizes the perception of chimpanzees (Fagot & Tomonaga, 1999), macaques (Hopkins & Washburn, 2002), capuchins (e.g., De Lillo et al., 2005), and even pigeons (Cavoto & Cook, 2001).

These findings have important theoretical and practical implications. Demonstration of local precedence in several animal species confirms that global precedence is not as general as could have been conceived prior to these human–animal comparative studies. Some authors have proposed that global precedence reflects the functional properties of the visual system: global visual information would be processed faster by the magnocellular pathway than by the parvocellular pathway (e.g., Hughes, Fendrich, & Reuter-Lorenz, 1990). Considering that humans and monkeys share very similar magnocellular and parvocellular pathways (e.g., Milner & Goodale, 1993), comparative studies revealing a local precedence in perception of hierarchical objects do not support this kind of physiological explanation. Instead, they suggest that proximity grouping, and consequently, the ability to process global-level hierarchical stimuli, is strongly affected by top-down information deriving from the past experience or training. Recent findings from clinical and cross-cultural studies in humans have largely confirmed that global precedence is not characteristic of the entire human population.

Our studies also have important practical implications for researchers using visual stimuli as tools to investigate animal perception and cognition, or the substrate underlying these processes. For instance, our research has confirmed that monkeys and humans tested in similar conditions and with identical stimuli do not necessarily pay attention to the same stimulus dimensions, and therefore call for caution in the use of “to-be-grouped” stimuli in experimental designs. A novel challenge is now to clarify the range of perceptual differences between humans and animals, beyond grouping processes, and to understand their origins and consequences.

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Figure 20.1 A baboon in front of the computerized test system.

Figure 20.2 Matching procedure used in global–local testing. **A**: Illustration of a local trial. In this trial, the sample (upper hierarchical stimulus) shares its local level with the lower right comparison stimulus. **B**: Illustration of a global trial. In that case, the sample (upper stimulus) shares its global level with the lower right comparison stimulus.

Figure 20.3 Results of local–global processing in humans and baboons. **A**: Mean percentage of correct responses in humans and in baboons for global and local trials. **B**: Response times in humans and in baboons for global and local trials. The stars indicate reliable statistical differences at p <0.05.

Figure 20.4 Illustration of the target–distractors differences in the visual search task. All the forms contained in the displays were identical in the no-go trials, as shown in the panel. The go trials used one target different from its surrounding distractors, and the target–distractors differences could concern either the global (*middle panel*) or local (*right panel*) stimulus levels. Note that the stimuli were arranged randomly on the screen and therefore were not necessarily aligned, as in this example.

Figure 20.5 Baboons' and humans' response times as a function of display size in the local go and global go trials of the visual search task.

Figure 20.6 Examples of hierarchical stimuli in global go trials and local go trials used in the three testing conditions varying in global size and density. In the large sparse condition, stimuli subtended 4 degrees of visual angle and contained eight local elements of .6 degrees. In the large dense condition, stimuli subtended 4 degrees of visual angle, and contained 16 local elements of .6 degrees. In the small dense condition, stimuli subtended 2 degrees of visual angle, and contained eight local elements of .6 degrees. Note that the interelement distances remained identical in the large dense and small dense conditions.

Figure 20.7 Illustration of the Ebbinghaus (Titchener) illusion. Humans typically judge the central circle larger when it is surrounded by the small circles (inducers).

Figure 20.8 Comparative findings on the Ebbinghaus illusion in humans and baboons. This figure shows the mean percentage of variable target choices for each species, as a function of target size differences. From 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. Reprinted with permission.

Figure 20.9 Examples of hierarchical stimuli used by Cavoto and Cook (2001). From 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. Reprinted with permission.

Figure 20.10 Examples of vertical and horizontal alignment of matrixes of dots. In **A** (proximity), the perception of vertical lines is induced by a reduced vertical inter-dot distance. In **B** (alignment), the proximity of elements is equivalent for the two orientations (vertical and horizontal), and thus grouping is established by the vertical alignment of elements. In **C** (proximity and alignment), grouping is established by greater proximity, as well as alignments that are concurrently applied to the same orientation (in this example, the vertical). From Kurylo, D. D., van Nest, J., & Knepper, B.

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Figure 20.11 Stimuli used in Tanaka, Onoe, Tsukada, and Fujita (2001). These authors used the letters N or Z, or their left–right mirror images, at the global and local level. From Tanaka, H., & Fujita, I. (2000). Global and local processing of visual patterns in macaque monkeys. *Neuroreport*, *11*, 2881–2884. Reprinted with permission.

Figure 20.12 Stimuli used in Goto, Wills, and Lea (2004). Each global stimulus consists of six local elements. In each pair of stimuli A, B and C, D, the local elements are similar, whereas the global shape is different. Note that these stimuli minimized the need for grouping, because the local features were close from each other. From Goto, K., Wills, A. J., & Lea, S. E. (2004). Global-feature classification can be acquired more rapidly than local-feature classification in both humans and pigeons. *Animal Cognition*, *7*, 109–113. Reprinted with permission.