

Comparison of Grouping Abilities in Humans (*Homo sapiens*) and Baboons (*Papio papio*) With the Ebbinghaus Illusion

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This research comparatively assessed grouping mechanisms of humans ($n = 8$) and baboons ($n = 8$) in an illusory task that employs configurations of target and surrounding circles arranged to induce the Ebbinghaus (Titchener) illusion. Analyses of response behaviors and points of subjective equality demonstrated that only humans misjudged the central target size under the influence of the Ebbinghaus illusion, whereas baboons expressed a more veridical perception of target sizes. It is argued that humans adopted a global mode of stimulus processing of the illusory figure in our task that has favored the illusion. By contrast, a strong local mode of stimulus processing with attention restricted to the target must have prevented illusory effects in baboons. These findings suggest that monkeys and humans have evolved modes of object recognition that do not similarly rely on the same gestalt principles.

Keywords: baboon, Ebbinghaus illusion, Titchener illusion, global-local precedence, visual cognition

Comparative psychology attempts to identify similarities and differences between animal species or between animals and humans. An interesting aspect of human/animal comparative researches concerns visual illusions. Although there are not as many studies on illusory perception in animals than there are in humans, several papers have reported that animals share some visual illusions with us. Thus, animals experience the horizontal-vertical illusion (several monkey species: Dominguez, 1954), the Zöllner illusion (baboons: Benhar & Samuel, 1982), the corridor illusion (baboons: Barbet & Fagot, 2002), stereokinetic illusions (chicks: Clara, Regolin, Zanforlin, & Vallortigara, 2006; marmosets: Clara, Regolin, Vallortigara, & Rogers, 2007) and the Ponzo illusion (pigeons: Fujita, Blough, & Blough, 1991; horses: Timney & Keil, 1996; macaques: Bayne & Davis, 1993; chimpanzees: Fujita, 1997). Demonstration of such functional similarities between the human and animal provides direct information on fundamental aspects of vision and on the evolution of visual systems.

The current research tested the susceptibility of a nonhuman primate species, the baboon, to the Ebbinghaus illusion (also called the Titchener illusion). That illusion is induced by displays consisting in a central circle target enclosed in a series of circle inducers (see Figure 1). With such illusory displays, humans typically perceive the central target circle larger when it is surrounded by the smaller inducers (e.g., Massaro & Anderson, 1971). We considered that a test of this illusion in monkeys would be particularly important and timely for at least two reasons. First, considering that this illusion has never been tested in animals, such

a test would add to the debate on the similarities and differences between human and animal vision. This kind of information is critical, in particular for the growing body of studies using non-human primates as experimental models of human vision. Second, although all the sources of the Ebbinghaus illusion and their interactions have not been clearly identified, there are strong indications that this illusion reflects the involvement of grouping mechanisms, as revealed by a direct relation between the strength of the illusion and the absolute distance separating the target and the inducers (Roberts, Harris, & Yates, 2005). The study of the Ebbinghaus illusion is therefore of strong heuristic value for the current debate on the similarities and differences in perceptual grouping abilities in humans and animals, as discussed hereafter.

The ability to group elemental visual features into coherent objects is one fundamental characteristic of vision that was best demonstrated by Navon (1977). In Navon's research (Navon, 1977) human participants had to judge the global or local shape of compound stimuli made of small letters arranged to form larger letters. Grouping processes appeared so powerful in this context that the global shapes were perceived faster than the shape of the local elements, despite a physical discontinuity between the local elements. This phenomenon, referred to as an effect of "global precedence," has been found in a large number of test situations involving humans (e.g., Kimchi, 1992). As for the Ebbinghaus illusion, global precedence also depends on the distance between the local elements (e.g., Martin, 1979), and thus, among other factors, on grouping mechanisms.

The issue of global-local processing has been recently introduced in comparative animal psychology after a great deal of human research. Results from this animal literature show that global precedence does not necessarily characterize the vision of animal or even that of nonhuman primates. Thus, a local rather than a global precedence was found in pigeons (Cavoto & Cook, 2001), capuchins (Spinozzi, De Lillo, & Truppa, 2003), baboons (Fagot & Deruelle, 1997; Deruelle & Fagot, 1998), macaques (Hopkins & Washburn, 2002) as well as in chimpanzees (Fagot &

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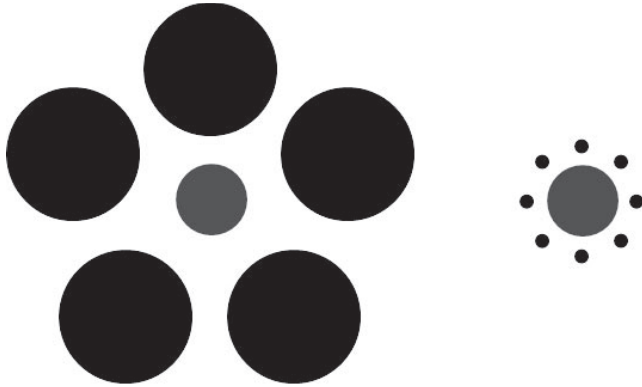


Figure 1. Illustration of the Ebbinghaus illusion and stimulus configurations used in the test. The central target surrounded by the small inducers appears the larger one to normal vision. Note that in the actual testing, the central target (in light gray in the figure) was displayed in yellow and the surrounding inducers (in black in the figure) were displayed in blue.

Tomonaga, 1999, see their large-sparse condition) using a matching-to-sample procedure with Navon's types of hierarchical visual stimulus. To account for such discrepancies between animal and human findings, authors have suggested that proximity grouping mechanisms in nonhuman species might not be as efficient or as readily recruited as for humans (e.g., Deruelle & Fagot, 1998; Fagot & Deruelle, 1997; Spinozzi, De Lillo, & Truppa, 2003). Several results support this conclusion. Thus, rats showed lower proximity grouping efficiency than humans in a task implying bistable arrays of dots (Kurylo, Van Nest & Knepper, 1997). In capuchins (e.g., Spinozzi, De Lillo, & Salvi, 2006; Spinozzi, De Lillo, & Truppa, 2003), baboons (Deruelle & Fagot, 1998) as well as chimpanzees (Fagot & Tomonaga, 1999), the strength of the local precedence effect is similarly reduced for greater stimulus densities. The comparative use of a visual search task (Deruelle & Fagot, 1998) furthermore showed qualitatively different modes of processing of the global stimulus level in monkeys and humans, baboons demonstrating an attentional-serial search strategy to discriminate global shapes whereas humans demonstrating nonattentional-parallel search.

However, contradictory results exist in this animal literature because global precedence was reported in pigeons (Goto, Wills, & Lea, 2004), macaques (Tanaka & Fujita, 2000), and chimpanzees (Hopkins & Washburn, 2002). Interestingly, the density of the stimuli appears usually greater in these three studies than in the other animal studies reported above, which might have facilitated grouping by proximity, and thus perception of the global shape. In support of this hypothesis, cotton-top tamarins showed a global bias with dense hierarchical displays but no clear-cut global or local biases with sparse displays (Neiworth, Gleichman, Olinick, & Lamp, 2006). Another important characteristic of the animal literature on global/local precedence is that it systematically required some training to attend the relevant stimulus dimension, namely the shape of the global or local stimulus levels. Differences in training procedures might therefore also partly account for variations in experimental findings.

The current research used the Ebbinghaus illusion as a natural vehicle to pursue the comparative analysis of perceptual grouping

of monkeys and humans. One main interest of this illusion in this context is that (in humans at least) it emerges in situations in which the perceiver has to judge the size of the target in absence of explicit request to process the inducers per se. In that sense, perception of the illusion demonstrates that grouping mechanisms may be recruited independently of training. In our research, we surmised that if baboons have a higher propensity than humans to attend the local feature of the illusory figures; as they do with other hierarchical visual objects (e.g., Fagot & Deruelle, 1997), such a focal attention should minimize interference of the inducers on the processing of the central target, and should thus weaken the illusion in comparison to humans. By contrast, demonstration of a human-like illusion in baboons, with similar strength as for humans, would contradict the hypothesis of reduced grouping abilities in monkeys.

Method

Subjects

Participants were five males (B03, B07, B09, B11, and B15) and three females (B04, B06, and B08) 20-year-old Guinea baboons (*Papio papio*) of the primate facility of the C.N.R.S (Marseille). The baboons were already highly familiar with the joystick apparatus and conditional matching-to-sample procedure used in that experiment (e.g., Fagot & Deruelle, 1997). Baboons were not food deprived but received their food ration after daily training or testing sessions. Four men and four women (age range 23–46 years old) were also tested. They were laboratory staff or student volunteers unaware of the purpose of the experiment.

Apparatus

Baboons were tested inside an experimental booth (68 cm × 50 cm × 72 cm), comprising a food dispenser, a view port, two hand ports providing free access to an analogue joystick, and a starting panel located 25 cm in front of the cage. Manipulation of the joystick controlled the displacements of a cursor on a 17-inch color monitor located 49 cm from the view port. The food dispenser delivered 190-mg banana-flavored food pellets inside the enclosure in accordance with the prevailing reinforcement contingencies. Humans were tested in similar conditions. They sat in front of a 17-inch color monitor screen located 49 cm from the eyes and had to manipulate a joystick to displace the cursor on the screen. Note that at such viewing distance, one centimeter on the screen corresponds approximately to one degree of visual angle.

Stimuli

They comprised a central yellow circle target (luminance = 30.4 cd/m²) surrounded by several large (32 mm in diameter) or small (3 mm) blue inducing circles (luminance = 32.2 cd/m², see Figure 1). The center-to-center distance between the target and each inducer was 43 mm for the large inducers and 15 mm for the small inducers. Use of different colors to display the targets and the inducers was aimed to promote attention to the yellow central target. Test displays involved the simultaneous presentation of one configuration with the small inducers along with another configuration using the large inducers (15 cm separated the center-to-center distance between the two central targets). The configuration

with small inducers systematically contained a target circle of 19 mm diameter. It will be hereafter named “the constant stimulus.” The configuration with large inducers contained a target varying from 14 mm to 24 mm, with 1 mm steps. It will be named “the variable stimulus.” Thus, there were five conditions in which the constant target (with small inducers) was smaller than the variable target (with large inducers), and one condition (19 mm) in which they were equal and five conditions in which the constant target was the largest one.

General Procedure

At the beginning of each trial, the participants of both species had to move the joystick to place and maintain the cursor on a fixation point. Then, two Ebbinghaus configurations were shown in a randomized left-right location. By manipulating the joystick, participants had to bring the cursor in contact with the Ebbinghaus stimulus containing the largest central target of the two. Contacts of the cursor with either the inducers or the central targets were recorded as a response. For both species, incorrect responses were followed by a 3 sec timeout during which the screen turned green. This green screen did not appear in the case of correct trial, therefore providing a feedback on the accuracy of the response. To promote motivation, baboons also received a food reward in case of correct response. Irrespective of the trial outcome, the screen systematically turned black by the end of each trial during an intertrial time interval of 6 seconds.

Test Procedure

The experiment contained a balanced number of trials in which the constant (i.e., 19 mm) target was objectively the larger or smaller one. To that end, each baboon received two consecutive test blocks of 8 sessions each. Baseline and probe trials in both test blocks systematically involved illusory figures containing a central target surrounded by inducers. In block 1, the test sessions comprised 96 baseline trials using illusory figures containing the 25 mm and 16 mm targets, intermixed with 16 probe trials. The variable target in probe trials could measure 17, 18, 19, 20, 21, 22, 23, or 24 mm (two trials per condition of size), but the constant target systematically measured 19 mm in diameter. In block 2, sessions comprised the same 96 baseline trials as in block 1, which were now intermixed with 12 probe trials in which the variable target size could measure 14, 15, 16, 22, 23, and 24 mm (two trials per condition). Use of the 22, 23, and 24 mm variable targets served to counterbalance trials in which the variable target was smaller than the constant one (i.e., 19 mm), and trials in which it was larger. Considering that these latter three conditions were already presented in block 1, trials of block 2 involving variable targets of 22, 23, and 24 mm were omitted for the analysis of the data set. Therefore, Block 2 adds to Block 1 the test of three novel conditions in which the size of the variable target ranged from 14 to 16 mm. Humans received a lower number of sessions than baboons to avoid loss of attention or boredom. They received three test sessions per test block. In addition, probe trials in these sessions were intermixed with 20 rather than 96 baseline trials. The number of probe trials per block was otherwise identical to baboons. For both humans and baboons, feedbacks in baseline trials were provided considering the accuracy of the response. Trial

feedbacks in probe trials were by contrast delivered irrespective of the participant’s behavior to prevent the intervening effect of reinforcement contingencies on the illusion. In these latter trials, positive feedbacks (reward and reduced time-out) were randomly delivered at a rate of 80% equivalent to that obtained by participants by the end of the training phase (see hereafter).

Preliminary Training

Participants received training before testing. For both species, training proceeded in three phases using the stimuli shown in Figures 2a-c. In training Phase I, the displays only contained two yellow circles of different sizes, in absence of inducers (see Figure 2a). Stimuli used early in training Phase I consisted in 29 and 15 mm in diameter circles, and participants had to point with the cursor the largest of the two stimuli. Monkeys and humans were trained with these two stimuli until they achieved more than 80% correct in two consecutive sessions. Once done, the size difference between the two circles was reduced by 2 mm, and trials were repeated until the criterion of 80% correct was reached twice again. That stepwise procedure, consisting in a progressive reduc-

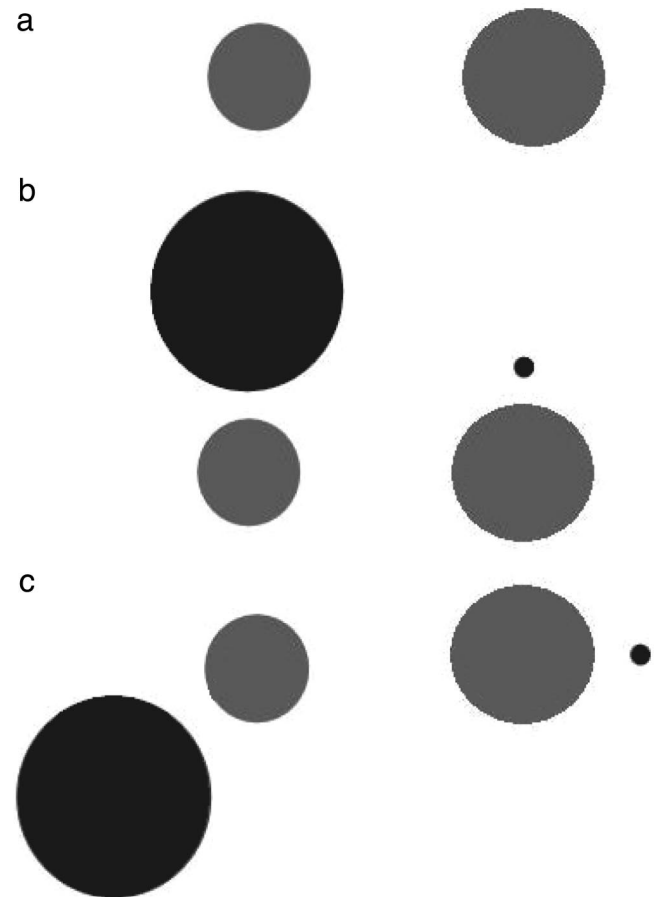


Figure 2. Illustration of the displays used in training Phase I (Figure 2a), training Phase II (Figure 2b), and training Phase III (Figure 2c). The actual colors of the stimuli were as reported for Figure 1. In training Phases II and III, each training display contained two targets (shown in light gray); each target was presented nearby a single inducer (shown in black in the figure).

tion of size differences between the two targets was pursued until participants could accurately discriminate circles differing by only 2 mm. Training Phase II started immediately after Phase I. In that second phase, humans or baboons had to continue to pay attention to the size of the targets but the target circles were now embedded in multielement displays (see Figure 2b). In that phase, the displays systematically contained the 29 and 15 mm in diameter yellow circles, and two blue inducers of either 3 or 32 mm always displayed at the same vertical location above the targets. All combinations of target and inducer sizes were presented in a counterbalanced order within a session. The center-to-center distance between the targets and inducers were as described in the stimulus section. The main innovation of training Phase III, in comparison to training Phase II, was that the two inducers were no more showed in a fixed vertical position but could be displayed in eight possible locations around each target (see Figure 2c). Again, the target-inducer distance was as described in the stimulus section. In all training phases, training sessions consisted in 10 (for humans) or 100 (for baboons) counterbalanced trial. All participants required 2 to 3 sessions to reach criterion per condition of training. Test sessions with the Ebbinghaus figures (as in Figure 1) proceeded immediately after completion of these three training phases.

Results

Preliminary analyses investigated accuracy scores to ascertain that all participants made a real attempt to select the largest central target. For that purpose, we looked at how often the veridically largest target was selected by each participant, and for both blocks, irrespective of whether this target was the constant or the variable one, and calculated the overall accuracy scores of each participant. Trials in which the two targets were identical were excluded from this analysis because there was no correct answer in these probe trials. Findings indicated that the two species performed reliably above chance on average in both baseline (baboon: 96.6% correct on average, range 91.7-99.9%, $t(7) = 42.5$, $p < .001$; humans: 98.3%, range 93.3-100%, $t(7) = 55.1$, $p < .001$) and test trials

(baboon: 72.9%, range 59.4-86.7%, $t(7) = 7.69$, $p < .001$; humans: 77.7%, range 65.6-87.5% $t(7) = 9.01$, $p < .001$), confirming that they behaved properly in the task.

To more directly investigate the illusion, we considered response choices as a function of size differences between the variable and constant targets. For this analysis, size differences were calculated by subtracting the size of the constant target (i.e., 19 mm) to that of the variable one (ranging from -14 mm to +29 mm), resulting in a -5 mm to +5 mm size difference scale. Considering that variable of size difference, baboons' or humans' susceptibility to the illusion should be revealed by an enhanced tendency to select the constant target (and thus a reduced tendency to select the variable target) at least in some of the conditions involving positive size differences, because the constant target should be perceived larger than reality because of the presence of the small surrounding inducers. To statistically investigate this hypothesis, we introduced the proportion of choosing the variable target in a two-way Species (human vs. baboon) \times size difference (-5 mm, -4 mm, -3 mm, -2 mm, -1 mm, 0 mm, +1 mm, +2 mm, +3 mm, +4 mm, +5 mm) analysis of variance (ANOVA). It appeared very clearly that the two species behaved differently in the task (see Figure 3). Thus, the effect of species was reliable, $F(1, 14) = 28.2$, $p < .001$, humans having a reduced bias to select the variable target (20.8% of the trials) compared to baboons (51.4%). The main effect of size difference was also reliable, $F(10, 140) = 54.9$, $p < .001$, but as was also the target size \times species interaction, $F(10, 140) = 10.7$, $p < .001$. Post hoc analyses of this interaction focused on the 0 and positive size difference conditions (+1, +2, +3, +4, and +5 mm), because only in these conditions responses the illusion should lead to erroneous size judgments. The two species behaved differently with target size differences of 0, 1, and +2 mm (Tukey's tests, $p < .05$). Without any exception, all humans exhibited a reliable bias (binomial test, $p < .05$) for selecting the constant target for target size differences of 0, +1, +2, and +3 mm. Thus, this preference was reliable at the group level (binomial test, $p < .05$). Hence, in the 0 condition, humans judged the constant target as being the largest of the two targets

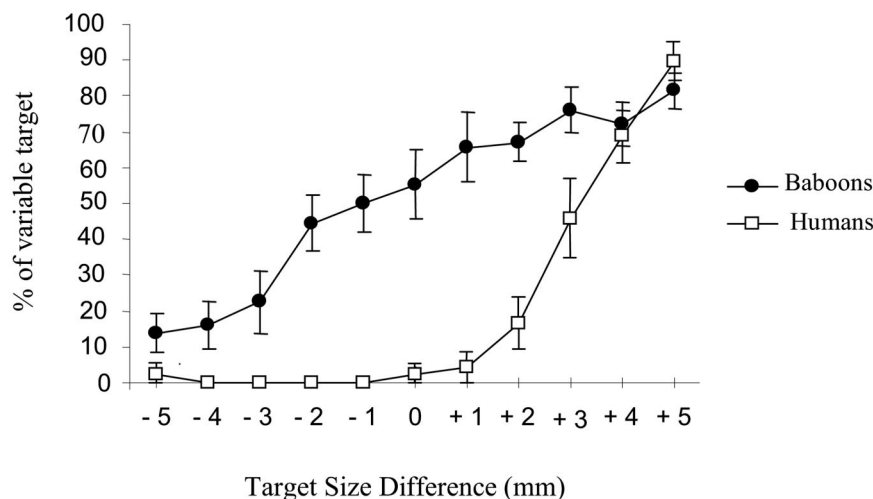


Figure 3. Mean percentage of variable target choices for each species as a function of target size differences.

despite veridical equality. This bias to judge the constant target as being the largest one also emerged for size differences of +1 and +2 mm, although that target had the smallest veridical size in these trials. We take these findings as strong evidences that humans experienced the Ebbinghaus illusion in our test conditions.

Of the most interest, these effects did not replicate in baboons, suggesting that they did not experience the illusion. In practice, only a subset of baboons indicated a reliable (binomial test, $p < .05$) preference for any target in Test Conditions 0 ($n = 4$), +1 ($n = 5$), and +2 ($n = 5$), but these biases were inconsistently in favor of the variable or constant target. There were therefore no reliable response biases at the group level (binomial test, $p > .5$)

Points of subjective equality (PSE) were also considered to confirm species differences in the Ebbinghaus illusion. The PSE values, corresponding to 50% of choice of the variable target, were inferred by linear extrapolation for each animal and compared across species. PSEs were significantly larger on average for humans (22.1 mm, corresponding to a mean size difference of +3.1 mm) than for baboons (18.3 mm corresponding to a mean size difference of $-.68$ mm, two-tailed t test for independent samples, $t(14) = 4.17$, $p < .05$). In addition, only for humans was the mean PSE different from 19 (i.e., veridical equality; two-tailed t test, $t(7) = 11.4$, $p < .05$). In brief, the analysis of PSEs confirmed that only humans experienced the Ebbinghaus illusion in this task.

Discussion

Several explanations can be advanced to explain why only humans experienced the Ebbinghaus illusion in our task. One hypothesis would be to propose that the greater number of sessions received by baboons ($n = 8$) in comparison to humans ($n = 3$) have masked illusory effects. To investigate this hypothesis, we compared the behavioral profiles of baboons and humans considering only the first three test sessions. This analysis (species \times size difference ANOVA) provided the same reliable main effects and interactions as before. In addition, it appeared that species differences already emerged when the very first trial was considered. Hence, in the 0 mm condition, humans already exhibited a reliable preference at the group level for the constant target (binomial test, $p < .05$), that preference being absent in baboons (binomial test, $p > .05$). Thus, it is very clear that interspecies differences were unrelated to the number of test sessions proposed to each species.

Another possible account for the lack of illusory effect in baboons might consider the properties of the stimuli, especially color differences between the target and inducers. Use of different colors to display the target and inducers reduces the magnitude of the Ebbinghaus illusion in humans (Rabin & Adams, 1993). Although such effects could account for an overall reduced illusory strength in both species, it is of no help to explain why humans continued to demonstrate the illusion with our stimuli whereas baboons did not.

It could also be proposed that the behavioral differences observed between humans and baboons reflect some differences in visual processing, for instance in terms of color wavelength discrimination functions, visual acuity or contrast sensitivity functions. This hypothesis also appears unlikely, although we acknowledge that it cannot be definitively ruled out. Psychophysical examinations of perceptual visual abilities of cercopithecinae species, the subfamily of the old-world monkeys to which baboons

belong, have systematically suggested that these animals have perceptual abilities comparable to humans (see Fobes & King, 1982; De Valois & De Valois, 1988). Taken together, it seems that the differences observed between baboons and humans can hardly be accounted by such factors.

Our results might be better explained by species differences in grouping abilities. We propose that two possible sources of influence may have hampered grouping processes in baboons, in comparison to humans, for a reduction of the illusory effect. The first one might be that baboons perceived the inducers and the targets as strongly dissimilar stimuli, because they differed in color and size. Considering that enhanced dissimilarity reduces the strength of the illusion in humans (e.g., Choplin & Medin, 1999) it can be assumed that perception of the target and inducers as completely different stimuli might have masked illusory effects in baboons. The second source of variation might be that baboons had a very strong attentional focus on the target circles, which might have limited the influence of the inducers on target size judgments. A similar reduction in the Ebbinghaus illusion has been shown in patients with autism (Happé, 1996, but see Ropar & Mitchell, 1999) known to favor a featural mode of processing, as well as in seminomadic Himba people who have expressed a similar bias for local processing (de Fockert, Davidoff, Fagot, Parron, & Goldstein, in press). The baboons' failure to experience the Ebbinghaus illusion in our testing may very well reflect a reduced integration of the inducers as a consequence of a featural mode of processing (see Fagot & Deruelle, 1997), thus allowing attention to the 'to-be-judged' forms without misperceptions.

It is noteworthy that several illusions demonstrated so far in animals involved illusory figures made of spatially connected, rather than disconnected local elements. This is clearly the case of the horizontal-vertical illusion (Dominguez, 1954; Harris, 1968), the Corridor illusion (Barbet & Fagot, 2002) and the stereokinetic illusions (e.g., Clara et al., 2006). In these researches, we suspect that connectedness favored attention to the illusory figures as wholes, and thus enhanced a greater sensitivity to these illusions. Demonstration of Zöllner illusion in baboons (Benhar & Samuel, 1982) and of the Ponzo illusion in pigeons (Fujita et al., 1991), macaques (Bayne & Davis, 1993), and chimpanzees (Fujita, 1997) appears to be counter examples in that respect, however, because these illusions involve discontinuous figures. Remember that in the Zöllner illusion, two parallel bars appear nonparallel because of oblique transverse lines, and that in the Ponzo illusion, a bar is judged larger when displayed toward the apex rather than the bottom inner part of the inverted V. Noticeably, however, these illusions have in common to contain expansion lines (i.e., the inverted V or the transverse oblique lines) that may enlarge the attentional field of the perceiver (Pressey & Epp, 1992). Thus, the hypothesis can be made that these two illusions were made possible by a simultaneous sampling of the illusory target and the inducers within the attentional field. The alternative hypothesis can also be proposed that the baboons did not experience the Ebbinghaus illusion in our research because the illusory figures lacked expansion fins that contribute to enlarge the attentional field, resulting in a sequential sampling of the target and inducers.

In fact, there are many similarities between the current testing and one control condition proposed by Fujita's (1997; Experiments 3 and 4) study on Ponzo illusion. In that condition, participants had to judge the size of a horizontal bar with two dots or two vertical

bars serving as context inducers, in absence of expansion fins. The illusion was much stronger in humans than in chimpanzees, and was moreover virtually absent in monkeys with these contextual elements (Fujita, 1997). We take this finding as a supporting evidence for grouping deficits in monkeys, relative to humans, at least when the displays are made of discontinuous elemental figures. Of course, our findings do not imply that the baboon would never experience the Ebbinghaus illusion if a different procedure was used. In humans (Martin, 1979) as well as in animals (e.g., Deruelle & Fagot, 1998; Fagot & Tomonaga, 1999; Spinozzi, De Lillo, & Salvi, 2006), the strength of the local bias is reduced when interelement distances is shorter. In baboons, therefore, reduction of the target-inducer distance is likely to promote perception of the illusion, as it does in humans (Roberts et al., 2005). The present investigators are planning further works to test this hypothesis. In this context, the main contribution of the current research is thus to nicely confirm that reliable perceptual differences emerge between humans and their closely nonhuman relatives in the same viewing conditions, and to pinpoint the size of their attentional focus as a source of this difference. This finding is of strong empirical implication for the use of animals, monkeys in particular, as experimental models of human vision.

Visual illusions are not isolated curiosities. They betray the fundamental operating characteristics of the sensory systems. Thus, when different species respond in accord with such illusory perception, we gain confidence in the basis nature of visual processing. By contrast, when two relatively distant species diverge in their processing of illusory displays, as demonstrated here, we gain information on the evolution of visual mechanisms. Following this line of thinking, the current research makes strongly suggest that the visual processes supporting the Ebbinghaus illusion must have recently evolved within the primate lineage. Of course, the behavioral and cognitive implications of these evolutionary changes remain uncertain at this point, considering that visual illusion can hardly be tested in more natural situations. Note however that baboons expressed more accurate size judgments than humans in our research, because they did not experience the illusion. Being able to accurately judge the size of natural living or nonliving objects is critical for behavioral adaptation and survival fitness. In this context, our research also reveals that processes involved in size perception are more hardly deceived in monkeys than in humans, which must have adaptive consequences for monkeys.

An apparent paradox must be alleviated, in closing. If baboons are so poor in our and related research to make objects from features, how can they so efficiently recognize important objects, such as food or predators, in nature? To address this puzzling question, it should be noted that object recognition is a rich and complex phenomenon potentially supported by a variety of mechanisms other than proximity grouping, as pinpointed by pioneer Gestalt psychologists (e.g., Koffka, 1935). In that respect, our research suggests that baboons and humans have both evolved highly adapted but different modes of stimulus processing, and that monkeys rely more strongly than humans on principles of perceptual organization other than proximity grouping, such as grouping by good continuation or common fate, which now need to be identified by further works. It is our firm conviction that delineating the perceptual world of animals is one major avenue to understand the richness and complexity of covert mechanisms controlling their behavior in nature.

References

- Barbet, I., & Fagot, J. (2002). Perception of the corridor illusion by baboons (*Papio papio*). *Behavioural Brain Research*, *132*, 111–115.
- Bayne, K., & Davis, R. (1993). Susceptibility of rhesus monkeys (*Macaca mulatta*) to the Ponzo illusion. *Bulletin of the Psychonomic Society*, *21*, 476–478.
- Benhar, E., & Samuel, D. (1982). Visual illusions in the baboon (*Papio anubis*). *Animal Learning and Behaviour*, *10*, 115–118.
- Cavoto, K. K., & Cook, R. G. (2001). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behaviour Processes*, *27*, 3–16.
- Choplin, J. M., & Medin, D. L. (1999). Similarity of the perimeters in the Ebbinghaus illusion. *Perception and Psychophysics*, *61*, 3–12.
- Clara, E., Regolin, L., Vallortigara, G., & Rogers, L. (2007). Perception of the stereokinetic illusion by the common marmoset (*Callithrix jacchus*). *Animal Cognition*, *33*, 135–140.
- Clara, E., Regolin, L., Zanforlin, M., & Vallortigara, G. (2006). Domestic chicks perceive stereokinetic illusions. *Perception*, *35*, 983–992.
- de Fockert, J., Davidoff, J., Fagot, J., Parron, C., & Goldstein, J. (2007). More accurate size contrast judgments in the Ebbinghaus illusion by a remote culture. *Journal of Experimental Psychology: Human Perception and Performance*, *33*, 738–742.
- Deruelle, C., & Fagot, J. (1998). Visual search for global/local stimulus features in humans and baboons. *Psychonomic Bulletin and Review*, *5*, 476–481.
- De Valois, R., & De Valois, K. (1988). *Spatial vision*. New York: Oxford University Press.
- Dominguez, K. E. (1954). A study of visual illusions in the monkey. *Journal of Genetic and Psychology*, *85*, 105–127.
- 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., & Tomonaga, M. (1999). Global and 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.
- 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.
- Fujita, K. (1997). Perception of the Ponzo illusion by rhesus monkeys, chimpanzees, and humans: Similarity and difference in the three primate species. *Perception & Psychophysics*, *59*, 284–292.
- Fujita, K., Blough, D., & Blough, P. M. (1991). Pigeons see the Ponzo illusion. *Learning and Behavior*, *19*, 283–293.
- Goto, K., Wills, A. J., & Lea, S. G. (2004). Global-feature classification can be acquired more rapidly than local-feature classification in both humans and pigeons. *Animal Cognition*, *7*, 109–113.
- Happé, F. (1996). Studying weak central coherence at low levels: Children with autism do not succumb to visual illusions. A research note. *Journal of Child Psychology and Psychiatry*, *37*, 873–877.
- Harris, A. V. (1968). Perception of the horizontal-vertical illusion in stump-tail monkeys. *Radford Review*, *22*, 61–72.
- Hopkins, W. D., & Washburn, D. A. (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.
- Kimchi, R. (1992). Primacy of wholistic processing and global-local paradigm: A critical review. *Psychological Bulletin*, *112*, 24–38.
- Koffka, K. A. (1935). *Principles of gestalt psychology*. New York: Harcourt, Brace & World.
- Kurylo, D. D., Van Nest, J., & Knepper, B. (1997). Characteristics of perceptual grouping in rats. *Journal of Comparative Psychology*, *111*, 126–134.

- Martin, M. (1979). Local and global processing: The role of sparsity. *Memory & Cognition*, 7, 476–484.
- Massaro, D. W., & Anderson, N. H. (1971). Judgmental model of the Ebbinghaus illusion. *Journal of Experimental Psychology*, 89, 147–151.
- Navon, D. (1977). Forest before trees: The precedence of global features 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, 323–330.
- Pressey, A. W., & Epp, D. (1992). Spatial attention in Ponzo-like patterns. *Perception & Psychophysics*, 52, 211–221.
- Rabin, J., & Adams, A. J. (1993). Size induction transcends the cardinal directions of color space. *Perception*, 22, 841–845.
- Roberts, 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.
- Ropar, D., & Mitchell, P. (1999). Are individuals with autism and Asperger's syndrome susceptible to visual illusion. *Journal of Child Psychology and Psychiatry*, 40, 1283–1293.
- 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 paella*). *Behavioural Brain Research*, 166, 45–54.
- 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.
- Tanaka, H. K., & Fujita, I. (2000). Global and local processing of visual patterns in macaque monkeys. *Neuroreport*, 13, 2881–2884.
- Timney, B., & Keil, K. (1996). Horses are sensitive to pictorial depth cues. *Perception*, 25, 1121–1128.

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