

Behavioural responses to photographs by pictorially naïve baboons (*Papio anubis*), gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*)

Carole Parron^a, Josep Call^b, Joël Fagot^{a,*}

^a CNRS-INCM, Marseille, France

^b Wolfgang Köhler Primate Research Center, Leipzig, Germany

Received 2 July 2007; received in revised form 7 January 2008; accepted 22 January 2008

Abstract

This study assessed how pictorially naïve nonhuman primates understand pictures. Fifty-five baboons with no prior exposure to pictures were trained to grasp a slice of banana presented against a pebble in a two alternative forced choice task. Post-training testing involved three stimulus pairs: (1) real banana slice vs. its picture, (2) the banana picture vs. a real pebble and (3) banana picture vs. a pebble picture which were presented twice. Preliminary data were also collected on naïve gorillas ($n=4$) and chimpanzees ($n=7$) using the same procedure. Baboons revealed a preference for the food picture in (2) and (3) and often ate this stimulus, but the food item and its picture were accurately discriminated in (1). These results suggest that baboons mistook the pictorial stimulus and its referent, but processed the banana pictures as poor exemplars of the real banana category. Among apes, only gorillas ate the banana pictures, suggesting that picture–object confusion may also occur in this species. Findings are discussed as pertaining to the general issue of representational abilities in nonhuman primates, and its evolution.

© 2008 Elsevier B.V. All rights reserved.

Keywords: Apes; Monkeys; Picture; Referential cognition

1. Introduction

Experimental use of pictures to study animal cognition started in 1964, when Herrnstein and Loveland (1964) trained pigeons to discriminate human from nonhuman slides in a categorization experiment. Since this pioneering study, pictures (i.e., slides, photographs or videographic pictures) have probably become the most predominant stimuli in the field. They are commonly used as convenient medium to investigate aspects of cognition, such as object recognition, categorization or spatial cognition, beyond picture processing. But pictures are also interesting stimuli in themselves because they are two-dimensional stimuli which give rise to a vicarious perception of objects and actions of the perceptual world. To understand pictures as pictures, it is necessary to mentally represent the concrete object itself (i.e., the picture) and its abstract relation to what it stands for (DeLoache, 2004). However, this understanding of pictures as referential stimuli is not mandatory and the perceiver might also simply mistake the real object and its depiction (Fagot et

al., 2000). The question thus arises of how animals understand pictures, and if they process them as real objects or referential stimuli. That question has been largely neglected so far (see Fagot, 2000; Bovet and Vauclair, 2000) although it is of direct relevance for the highly debated literature on the abstract and symbolic cognitive abilities in animals, and its evolution.

Several authors reported that monkeys often react emotionally to pictures as they normally do with the real objects. Perrett and Mistlin (1990) observed emotional responses in macaques, such as lip-smacking, consecutive to the presentation of pictorial faces. Young macaques reared in isolation presented more vocalizations and signs of disturbance when presented with threat pictures than with less emotional picture (Sackett, 1966). Wright (1989) observed fear gestures in macaques using pictures of highly emotional objects. Because these behaviours are perfectly appropriate in response to real objects but inappropriate in response to pictures, it is presumed that the monkeys in this research did not process the pictures as representations, but rather confused the real objects with their depictions.

There is by contrast a great deal of literature suggesting that pictures might also occasionally be processed as representations. Savage-Rumbaugh et al. (1980) taught language trained chimpanzees to associate real food and tool objects with two

* Corresponding author.

E-mail address: fagot@incm.cnrs-mrs.fr (J. Fagot).

lexigrams that serve to “label” these categories. After training, performance transferred from the real objects to pictorial depictions of tools and foods, suggesting that the chimpanzees processed picture expression and picture content as two independent dimensions, and classified the pictures considering their representational content, not their expression. Comparable results were reported on Ai, another language trained chimpanzee. Ai was firstly trained to “name” real humans, chimpanzees or one orangutan by way of lexigrams. After training, Ai could properly name the same individual when shown on pictures (Matsuzawa, 1990) and on more abstract drawings (Itakura, 1994). Because drawings were perceptually very different from the living models, confusion must be ruled out as an explanation for that performance. Note however that some evidence has been reported that apes may also mistake the picture and its referent. For instance, Viki, a chimpanzee raised as a child by humans, placed her ear to a picture of watch to “listen it” (Hayes, 1951). The significance of such anecdotic reports is unfortunately unclear and subject to interpretation.

The above literature suggests differences between monkeys and apes in picture comprehension, but firm conclusions would remain hazardous mostly because studies on apes often involve apes much more familiar with pictures than monkey studies. Cross-cultural studies have underlined the role of expertise on picture comprehension. Humans with no experience with pictorial displays are often unable to recognize the objects depicted by the image (e.g., Barley, 1986) and their understanding of iconic drawings is also different from that of western people much more familiar with pictorial displays (Deregowski, 2000). Developmental studies confirmed the role of experience on picture comprehension. Nine-month-old infants manually investigate two-dimensional depictions of three-dimensional objects, which suggest that they mistake these two objects at this age (DeLoache et al., 1998). It is only by the age of 2.5 years, after they had much experience with iconic stimuli, that children from our western culture process pictures as representations (e.g., DeLoache, 2004).

Assessment of picture processing in nonhuman primates may follow two different approaches. One may develop designs demonstrating differentiation between picture expression and picture content. The main difficulty of this approach is that proper procedures usually involve a long and effortful training with pictures which seriously complicates the control of practice effects, especially if different species are used. An alternative strategy is to test if the participants adopt a confusion mode of processing, considering that such demonstration of picture–object confusion rules out the use of pictorial stimuli as representations. The current research favored this second strategy. One strength of the current research is to provide comprehensive data on picture understanding obtained in a group of 55 baboons. This is to our knowledge the first time that picture comprehension was assessed in such a large group of nonhuman primates. The second main strength of our study is that expertise with pictures was strictly equated by focusing our attention on pictorially naïve participants. Finally, preliminary comparative data on gorillas and chimpanzees are also offered in this

research, to provide some first inputs on possible evolutionary trends in picture understanding.

2. Materials and methods

2.1. Participants

They were 26 male and 29 female baboons (*Papio anubis*, $N=55$, mean age 6.9 years, S.D. = 4.6 years) from the CNRS Rousset-sur-Arc Primate Center (France), 3 male and 4 female chimpanzees (*Pan troglodytes*, mean age 9.75 years, S.D. = 7.3 years) from the Wolfgang Kohler Primate Research Center of the Leipzig Zoo, and 1 male and 3 female gorillas ($N=4$, *Gorilla gorilla*, age 24.5 years, S.D. = 11.15 years) from the zoos of Leipzig or Nuremberg (Germany). All participants were selected at purpose from their social groups because they have no known exposure to videos, still pictures, or drawings. In that context, the reduced sample size for gorillas and chimpanzees reflects our difficulty to find pictorially naïve apes. Participants received their daily food ration after completion of experiments. Water was available *ad libitum*. Baboons were identified by numbers on neck collars. Apes were identified by visual appearance.

2.2. Apparatus

It consisted in a horizontal wooden board (80 cm × 22 cm) fitted with two panels (17 cm × 19 cm) that served as supports for the presentation of real objects or pictures (see Fig. 1). The two panels were separated by 35 cm, and subtended an angle of 45° with the horizontal board in order to facilitate full perception of the stimuli. The apparatus was systematically placed outside the living quarter of the animals at approximately 15 cm from their enclosure, offering a hand access to the stimuli through the fence or wire-mesh. A large carton board (100 cm × 100 cm) served as a screen for preventing the animals to view the apparatus during the baiting process. The screen was placed and removed manually. The apparatus was presented directly on the floor for baboons testing and on a table (84 cm × 32 cm × 52 cm) for gorillas and chimpanzees. Behavioural sequences and comments by the experimenter were recorded online during the test using a Sony DCR-HC39E DV camera recorder.

2.3. Stimuli

They consisted of pebbles or slices of banana which were presented as real 3D objects or as photographic pictures. All pebbles had approximately the same size (i.e., 6 cm × 3 cm × 3 cm), the same oval shape and the same colour because they were made with the same geological material (i.e., grey lime stones). Slices of bananas were approximately 3.5 cm in diameter and 2 cm thick. Pictorial representations of the pebbles and banana slices were in colour and subtended the same size as the real objects. They were shown on a white 8 cm × 8 cm background and were printed on a mat photographic paper preventing surface reflectance.



Fig. 1. Illustration of one sequence coded as “EAT”. The upper part of the figure shows the setup on which the two pictures are shown, one representing a banana slice and the other representing the pebble. In that bout, the baboon chose the picture of the banana (a), grasped it (b and c), and smelled it (d) before eating the part of the photograph containing the depiction of the banana (e and f).

2.4. Procedure

2.4.1. General procedure

Monkeys and apes were either tested in groups or isolated, depending on the specificity of their living quarters. Their participation was always voluntary. A two-alternative forced choice procedure was used. A trial started when the experimenter placed the screen along the wire-mesh of the enclosure to prevent the participant from viewing the baiting process. Two stimuli were then placed on the apparatus, one on each panel. Great care was taken during baiting to avoid visual or auditory cues that could inform the subject of the real nature of the stimuli. The left-right location of the stimuli was counterbalanced. The test began when the experimenter removed the screen to provide free access to the two stimuli. The task was then to reach one of the two stimuli through the mesh. Only one choice was allowed. Once a stimulus had been chosen, the screen was placed again along the mesh to prevent the participant from reaching the second stimulus. The trial was aborted if the participant expressed no interest in the task during the two minutes following stimulus presentation.

2.4.2. Training

Training trials were offered prior to testing. They consisted in the simultaneous presentation of a real pebble and a real

slice of banana. These trials were repeated until a clear preference for the banana slice emerged. Baboons, gorillas and chimpanzees respectively received 7.3 (S.D. = 2.1), 10 (S.D. = 0) and 10.4 (S.D. = 1.1) such training trials on average. All participants promptly preferred the slice of banana in these trials, which could be eaten once reached.

2.4.3. Test procedure

The experiment consisted of four test trials per participant using different pictures. Test trial 1 assessed the discrimination of a real slice of banana from a banana slice picture, when these stimuli were shown simultaneously on the board. Test trial 2 assessed the attractiveness of the three-dimensional real objects in comparison to pictures. It involved a picture of a banana slice and a real pebble as stimuli. In test trials 1 and 2, the reach was systematically aborted by the experimenter who placed the screen along the mesh prior to hand contact with the stimulus. Because participants were completely naïve with pictures at this stage of the experiment, stimulus choices could only be given considering visual cues. Test trial 3 consisted in the simultaneous presentation of two pictures, one showing a banana slice, the other one showing a pebble. This test assessed if preference for the banana slice established in training would transfer when these two objects are now presented as pictures. In that trial, the participant could freely reach and manipulate the selected stim-

ulus. It was its very first manipulation of a picture. Test trial 4 replicated test trial 3 to assess if stimulus choices would change with repeated exposure. Test trials 1–4 were run sequentially for all participants. Three training trials with real objects were systematically presented between two test trials in order to maintain motivation. Participants received test trials 1–4 within a single session which lasted approximately half an hour.

2.4.4. Coding scheme and statistical analyses

For test trials 1 and 2, we only coded the identity of the stimulus that the participant tried to reach. These trials were coded as a no reaching attempt (i.e., NRA) trial when no choice was expressed within the 2 min of the test. The same coding scheme was applied to test trials 3 and 4. However, because the participants could grasp the chosen stimulus in these trials, the coding scheme also considered the behaviour expressed toward that stimulus. A hierarchical coding scheme of four behavioural categories was used. Behaviours were defined as follows: (1) TOUCH/GRASP: The participant touches or grasps the stimulus which is released after the grasp. (2) SMELL: The participant grasps the stimulus, may perform different actions on it, and smells it, but the stimulus is never brought to the mouth. (3) BRING TO MOUTH: The participant grasps the stimulus, may smell, lick or bite it, and brings it to the mouth without ingesting it. (4) EAT: The participant eats the stimulus either partially or entirely. Only the behaviour of the highest category was coded. Occurrences of behaviours were scored, not their duration. Coding was performed online, during the behavioural sequence (audio recording), but later confirmed by viewing the video tapes. All statistical tests were nonparametric and two-tailed.

Sixty-three behavioural sequences were scored by two independent observers. The proportion of inter-observer agreement was equal to 89% (Kappa-Cohen coefficient = .86). Intra-coder reliability was also assessed by having the main coder coding the same behavioural sequence twice. Agreement was similarly high (percentage of agreement: 98.4%; Kappa-Cohen coefficient = .98) which assures the reliability of our coding procedure.

3. Results

3.1. Test trials 1 and 2

There was no NRA behaviour in the test trial 1. In these trials, 75% of the baboons preferred the banana (Binomial test, $p < .05$). Chimpanzees revealed a similar bias for the real banana (71%), with 5 chimpanzees preferring the real banana and 2 preferring the banana picture, but this bias was not significant (Binomial test, $p > .05$). The small sample size of the gorillas ($N=4$) prevented us from analyzing group biases, but note that three of them chose the picture, and one chose the real piece of banana. An analysis of the response choices as a function of age indicated that baboons who reached for the real banana did not differ in terms of age from those who reached for the banana picture (Mann-Whitney U test, 40 vs. 14, $U = 323$, $p > .05$). Comparable analyses were not conducted for gorillas and chimpanzees due to the small sample sizes.

The number of NRA trials increased from test trial 1 to test trial 2. Nine baboons, one chimpanzee and one gorilla did not reach at all in this test. Eighty-five percent of the baboons who reached one stimulus preferred the banana picture (Binomial test, $p < .05$) but only 50% of the chimpanzees showed that preference. Two of the gorillas chose the banana picture and one chose the pebble. Considering the effect of age, baboons who selected the banana picture were older on average (mean age = 7.7 years, S.D. = 4.8) than those who selected the pebble (mean age = 3.8 years, S.D. = 2.6, Mann-Whitney U test, 39 vs. 7, $U = 204$, $p < .05$). However, there was no reliable age difference between the baboons who made a reaching attempt (mean age = 6.5 years, S.D. = 3.8) and the other baboons (mean age = 7.1, S.D. = 4.7, Mann-Whitney U test, 46 vs. 8, $U = 211$, $p > .05$).

3.2. Test trials 3 and 4

3.2.1. Stimulus choices

The number of NRA trials continued to increase. In test trial 3, a total of 16 NRA responses was observed in baboons, 0 in chimpanzees, and 1 in gorillas. In test trial 4, there were 26 NRA responses in baboons, 3 in chimpanzees and 1 in gorillas. Baboons showed a significant banana picture preference in both tests (Binomial test, $p < .05$ in both cases). In contrast, chimpanzees showed no preference for either picture in test trial 3 (Binomial test, $p > .05$). In test trial 4, three of the four chimpanzees who chose one stimulus selected the banana picture. Similarly, the three gorillas who expressed a choice selected the banana picture in both test trials 3 and 4.

Although participants could freely reach and manipulate one stimulus in test trials 3 and 4, some of them only seized this opportunity in test trial 4. We thus combined the results of these two test trials to obtain data on the participants' first stimulus manipulations. Eighty-three percent of the baboons who reached one stimulus (43 out of 52, binomial test, $p < .05$) and 100% of the gorillas (3 out of 3) selected the banana picture. The distribution was more symmetrical for chimpanzees, with four preferring the banana picture and three preferring the pebble picture. There was no age difference between the baboons exhibiting a preference for the pebble or the banana pictures in test trials 3 and 4, or between those who reached and did not reach in these trials (Mann-Whitney U test, all $ps > .05$).

3.2.2. Manipulative behaviours

The analysis of the behavioural sequences was conducted separately for the first and second sequence of stimulus manipulation, irrespective of whether these behaviours were observed in test trials 3 or 4. Fig. 2 reports the distribution of the different actions performed during the first bout of manipulation of the banana picture. Recall that our monkeys and apes were fully naïve with pictures at this stage of the research, and that they have had no prior opportunity to manipulate pictorial displays. EAT was one of the most frequently observed behaviours both in baboons (39.5% of the participants) and gorillas (100%). Interestingly, the baboons who ate the picture in the first bout of manipulation were younger on average (mean age = 5.1 years,

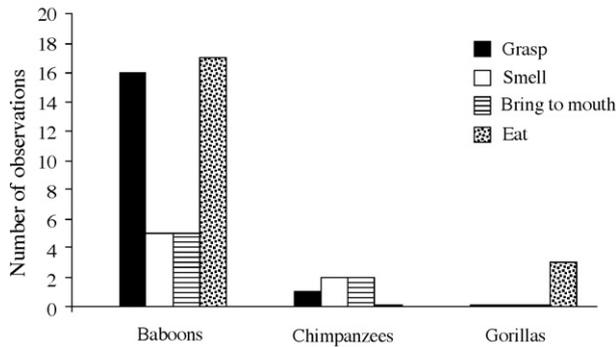


Fig. 2. Frequencies of each action obtained in baboons, gorillas and chimpanzees during the first bout of picture manipulation.

S.D. = 3.3) than the baboons who did not eat it (mean age = 9.6, S.D. = 5.1, Mann-Whitney U test, 17 vs. 24, $U = 346$, $p < .01$). For the banana pictures, EAT was never observed in chimpanzees, even though there was a larger number of chimpanzees than gorillas.

Fig. 3 reports the distribution of actions directed towards the banana picture in the second manipulation bout. All gorillas and 44% of the baboons who grasped the banana picture ate it. The baboons expressing these behaviours were younger on average (mean age = 4.7 years, S.D. = 3.8) than the baboons who manipulated but did not eat the picture (mean age = 8.5, S.D. = 5.2, two-tailed Mann-Whitney U test, 11 vs. 14, $U = 118$, $p < .05$). None of the chimpanzees showed this behaviour. Note also that a substantial number of baboons (10 out of 17) and all gorillas ate the picture in both bouts. This finding demonstrates that a single exposure to the picture does not necessarily alter their mode of processing.

The responses elicited by the pebble picture differed substantially from those observed with the banana picture. Nine baboons took the picture of the pebble in test trials 3 or 4 (never twice). Their behaviours were coded as TOUCH/GRASP ($N = 4$), SMELL ($N = 3$) and BRING TO MOUTH ($N = 2$). EAT was never observed in these baboons. This finding should be contrasted with the large number of baboons (17/43) who ate the banana picture in the first manipulation bout. In fact, baboons ate the banana picture significantly more often than the pebble picture (Fisher's test, $p = 0.024$). Three chimpanzees selected

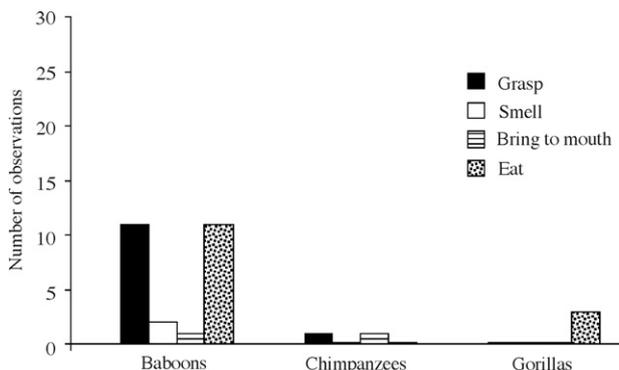


Fig. 3. Frequencies of each action obtained in baboons, gorillas and chimpanzees during the second bout of picture manipulation.

the pebble picture once during test trial 3 or 4. They revealed a SMELL, BRING TO MOUTH, or EAT behaviour. None of the gorillas took the pebble picture in these trials, confirming that gorillas expressed much less interest in the pebble pictures than in the banana pictures. In sum, 35 eating behaviours were observed during this experiment and all of them, except one, was observed when the participants manipulated a picture of the banana.

4. Discussion

Our data suggest that baboons did not process the pictures as representations, but rather mistook the real piece of banana and their depiction. The fact that a large number of baboons ate the banana pictures in test trials 3 and 4, while none of them ate the pebble pictures supports that hypothesis. A picture/object confusion mode of processing explains perfectly why baboons preferred the banana picture when it was presented in test trial 2 against a real pebble. Moreover, it accounts for the baboons' preference for the banana picture in test trials 3 and 4, when this picture was presented against the pebble picture. However in test trial 1, baboons reliably preferred the real banana over the pictorial suggesting they process these two stimuli as distinct. This behaviour might appear in contradiction with the idea that the baboons mistook the real banana and its picture, but we believe that it is not. Pictorial displays are not perfect duplicates of the real objects. They lack a series of perceptual cues (such as stereoscopic cues) normally available for the real three-dimensional objects. Given these differences between the real piece of banana and their photographs, we suspect that the baboons processed the pictorial banana as a poor, less attractive but nevertheless real exemplar of the banana category, and in test trial 1 preferred for that reason the real food over its depiction. In the next test trials, this poor typicality did not prevent preference for the picture of the banana when that stimulus was presented against a pictorial or real pebble. Interestingly, the baboons expressed several other behaviours suggesting that they mistook the pictures and its referent. They often tried to grasp the pictorial banana instead of the more graspable border of the photograph (see Fig. 4). In the sequence shown in Fig. 4, a baboon maintained the picture with one hand while trying to remove the pictorial banana from its support.

The current demonstration of picture-object confusion is in perfect line with previous observations on other pictorially naïve monkeys (e.g., Sackett, 1966; Wright, 1989) but with a larger sample size. It is also in agreement with studies showing that picture-object confusion may also be found in naïve birds (e.g., Looney and Cohen, 1974, for a review see also Fagot, 2000). These convergent findings suggest that these animals can properly recognize objects on pictures, and thus that pictures are appropriate stimuli to study object recognition, at least as far as pictorially naïve participants are involved.

Our study showed that young baboons ate the banana picture in test trials 3 and 4 more than the older baboons. Although human infants tend to confuse the real objects and their pictures more than older children (DeLoache et al., 1998), this effect cannot account for the current finding. Indeed, the hypothesis

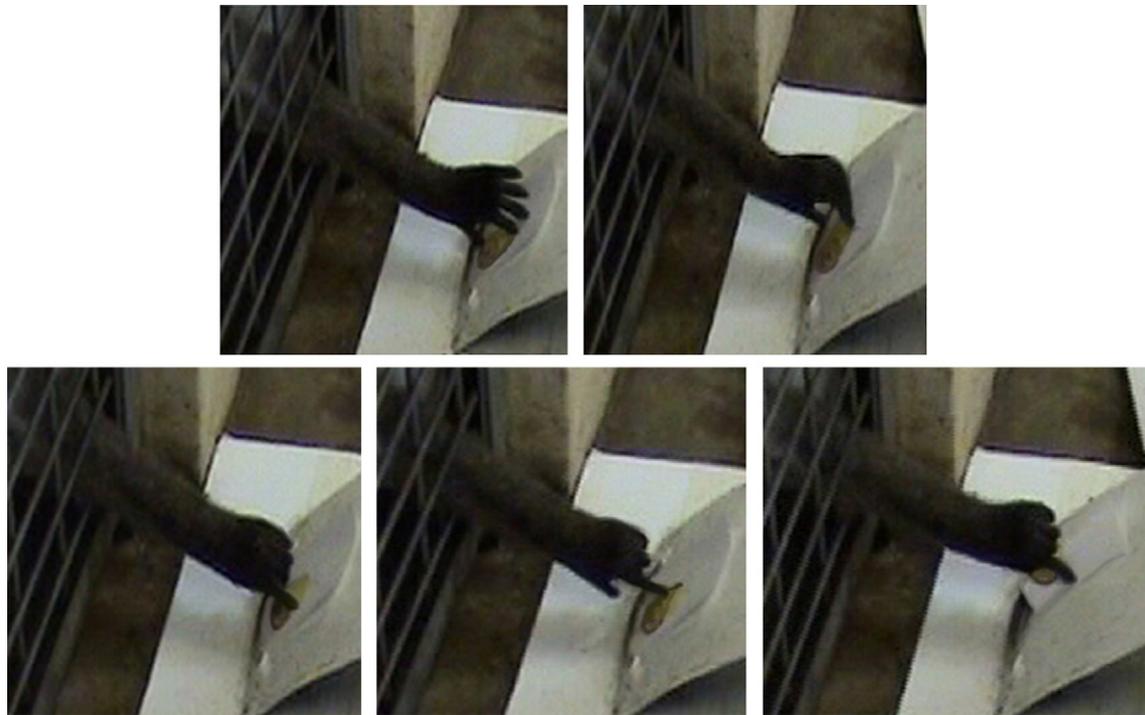


Fig. 4. Illustration of a behavioural sequence during which a baboon attempted to reach the pictorial banana. Because grasping failed, this baboon delineated the contour of the pictorial banana slice with its index finger as if it wanted to figure out if the picture was a flat object or not. It is only after this sequence that the animal grasped the photograph by its border.

of greater confusion in young baboons leads to the prediction of a stronger preference for the banana picture for the youngest baboons in test trial 2, and this result was not found. Young baboons have a higher level of activity than the old ones, especially when hand manipulations are considered (e.g., Vauclair and Fagot, 1987). They are also under greater social pressure (e.g., Altmann, 1980) in particular when they compete for food as in this research. Adults often steal food items from juveniles or sub-adults. We therefore presume that the young baboons alleviated social pressure in our task by quickly eating what they considered as being an attractive food object for others, namely the picture of the banana, therefore promoting the frequency of EAT responses. In a different perspective, it is noticeable that gorillas expressed the same preference for the banana picture as baboons, when in test trials 3 and 4 that picture was presented against the pebble picture. In addition, the three gorillas that reached and manipulated the picture of the banana in test trials 3 and 4 systematically ate it. This finding demonstrates that a confusion mode of processing is not restricted to pictorially naïve monkeys, but might also generalize to at least the pictorially naïve gorillas tested in our research. Another interesting finding is that chimpanzees behaved differently from baboons and gorillas in our task. On one hand, chimpanzees expressed no clear-cut preference at the group level for either stimulus in test trials 1–4, suggesting that the banana and pebble pictures were similarly attractive to them. On the other hand, none of the chimpanzees ate the banana picture, in spite of a larger sample size for chimpanzees ($N = 7$) than gorillas ($N = 4$). These findings suggest that the chimpanzees did not mistake the banana piece with its pic-

ture. Of course, this conclusion does not imply that chimpanzees processed our pictures as referential stimuli. Earlier studies have suggested that chimpanzees can use pictures to identify their referents (e.g., Savage-Rumbaugh et al., 1980), but other studies have shown that naïve apes do not spontaneously use pictures or objects in a referential fashion (Hermann et al., 2006; Tomasello et al., 1997). Although the lack of apparent picture/object confusion leaves open the possibility that the chimpanzees processed them as referential stimuli, further experiments will be needed to ascertain that hypothesis, in addition to a greater number of subjects. If a referential use of pictures can be demonstrated in such naïve animals, the hypothesis will have to be made that species differences in picture processing reflect variations in the use of stimuli as referential signs.

In closing, we would like to emphasize that studies on picture understanding have direct theoretical implications for comparative cognition, especially referential cognition. This line of research also has potentially strong empirical implications for research being done using pictures as stimuli in different fields, such as cognitive neuroscience. How animals process pictures has been a neglected issue in the past and many questions remain unanswered. So far, evidence for referential cognition are limited in monkeys (Tomasello and Call, 1997) and the question therefore arises of how monkeys process pictures after long exposure to such stimuli, if they have limited abilities for referential thinking. Given the importance of these issues, we encourage researchers to replicate and extend our study with large sample sizes of apes to better understand how picture understanding emerged and evolved in the phylogeny.

Acknowledgements

This research was supported by the European community “Stage in Evolution and Development of Sign Use” (SEDSU) grant. The authors thank the staff and keepers of the CNRS Rousset-sur-ARC, and Wolfgang Köhler Primate Centers, as well as those of the Nuremberg Zoo, who have made this research possible. Alenka Hribar is acknowledged for her help in testing a subset of gorillas and chimpanzees.

References

- Altmann, J., 1980. Baboon Mothers and Infants. Harvard University Press, Cambridge, 242 pp.
- Barley, N., 1986. The Innocent Anthropologist. Penguin Books, London.
- Bovet, D., Vauclair, J., 2000. Picture recognition in animals and in humans: a review. *Behav. Brain Res.* 109, 143–165.
- DeLoache, J.S., 2004. Becoming symbol-minded. *Trends Cogn. Sci.* 8, 66–70.
- DeLoache, J.S., Pierroutsakos, S.L., Uttal, D.H., Rosengren, K.S., Gottlieb, A., 1998. Grasping the nature of pictures. *Psychol. Sci.* 9, 205–210.
- Deregowski, J.B., 2000. Pictorial perception: individual and group differences within the human species. In: Fagot, J. (Ed.), *Picture Perception in Animals*. Psychology Press, London, pp. 397–429.
- Fagot, J., 2000. *Picture Perception in Animals*. Psychology Press, London, 447 pp.
- Fagot, J., Martin-Malivel, J., Dépy, D., 2000. What is the evidence for an equivalence between objects and pictures in birds and nonhuman primates. In: Fagot, J. (Ed.), *Picture Perception in Animals*. Psychology Press, London, pp. 295–320.
- Hayes, C., 1951. *The Ape in Our House*. Harper and Brothers, New York.
- Hermann, E., Melis, A.P., Tomasello, M., 2006. Apes use of iconic cues in the object-choice task. *Anim. Cogn.* 9, 118–130.
- Herrnstein, R.J., Loveland, D.H., 1964. Complex visual concept in the pigeon. *Science* 146, 549–551.
- Itakura, S., 1994. Recognition of line-drawing representations by a chimpanzee (*Pan troglodydes*). *J. Gen. Psychol.* 121, 189–197.
- Looney, T.A., Cohen, P.S., 1974. Pictorial target control of schedule-induced attack in white carneaux pigeons. *J. Exp. Anal. Behav.* 21, 571–584.
- Matsuzawa, T., 1990. Form perception and visual acuity in a chimpanzee. *Folia Primatologica* 55, 24–32.
- Perrett, D.I., Mistlin, A.J., 1990. Perception of facial characteristics by monkeys. In: Stebbins, W.C., Berkley, M.A. (Eds.), *Comparative Perception: Complex Signals*, vol. 2. John Wiley and Sons, New York, pp. 187–215.
- Sackett, G.P., 1966. Monkeys reared in isolation with pictures as visual input: evidence for an innate releasing mechanism. *Science* 3755, 1468–1473.
- Savage-Rumbaugh, E.S., Rumbaugh, D.M., Smith, S.T., Lawson, J., 1980. Reference: the linguistic essential. *Science* 4472, 922–925.
- Tomasello, M., Call, J., 1997. *Primate Cognition*. Oxford University Press, New York, Oxford, 517 pp.
- Tomasello, M., Call, J., Gluckman, A., 1997. Comprehension of novel communicative signs by apes and human children. *Child Development* 68, 1067–1080.
- Vauclair, J., Fagot, J., 1987. Spontaneous hand usage and handedness in a troop of baboons. *Cortex* 23, 265–274.
- Wright, A., 1989. Memory processing by pigeons, monkeys and people. In: Bower, G.H. (Ed.), *The Psychology of Learning and Motivation*, 23. Academic Press, New York, pp. 25–70.