

We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,900

Open access books available

185,000

International authors and editors

200M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com



Pictorial Competence in Primates: A Cognitive Correlate of Mirror Self-Recognition?

Parron Carole

Additional information is available at the end of the chapter

<http://dx.doi.org/10.5772/intechopen.75568>

Abstract

Alternative interpretation to the long-standing assertion that mirror self-recognition entails self-awareness suggests that mirror self-recognition rather refers to the ability to differentiate its own body from other objects of the environment. From this standpoint, individuals should be able to interpret the mirror reflection as a symbolic representation of the self and to map this image to an internal representation of self. The framework of this chapter is based on the assumption that the cognitive processing underlying self-recognition might be related to the capacity of processing mirror image as a symbolic representation of the real object. To support that purpose, the critical developmental and comparative literature on pictorial competence and self-recognition ability in human infants and primates are contrasted. Furthermore, relationship between mirror self-recognition and pictorial abilities are discussed based upon two experiments. We first observed the behavior of pictorially naïve primates, with a realistic picture. We second assessed whether non-naïve chimpanzees, demonstrating or not self-recognition, would behave with a realistic picture. Finally, I propose a refined postulate that illustrates how the pictorial competence and self-recognition ability may co-develop. The intent of this model is to open up new perspectives for further explorations of self-recognition ability in primates.

Keywords: mirror self-recognition, picture processing, referential stimuli, developmental abilities, monkeys, great apes

1. Introduction

Once upon a time, in a castle, a queen was talking to her image in the mirror: “Mirror, mirror on the wall, who is the fairest one of all?” (based on “Snow White”; the Grimm’s fairy tales, 1812). Rather curiously, Snow White’s step-mother, needed the opinion of her magic mirror to

get an idea about her own reflection, although she could see it by herself. This suggests that the true nature of someone's image in the mirror does not always lay in the eyes of the perceiver. The queen, at least, knew that the reflection in the mirror was hers. Is it the case for non-human primates (hereafter referred to as primates) when they face a mirror? If they are able to recognize themselves, is this have anything to do with self-awareness? Self-recognition implies "... that one can become the object of one's own attention..." and thus possesses the ability "...to infer correctly the identity of the reflection in the mirror as being one-self" [1]. In spite of extensive empirical investigations for the last five decades, this issue is still hotly debated in the field of comparative psychology. The first experimental account of mirror self-recognition (from now MSR) in primates was made by Gallup in the 1970s [2]. The development of an original methodology, that is, the "mark test", was based on prior observation that initial exposure of chimpanzees to a mirror first elicit social responses toward their reflection (e.g. threat or play), but after a while, this behavior eventually vanishes and switches to self-directed behaviors (i.e. inspection of some areas of the body that are only visible with a mirror) [3]. Although the author assumed that self-directed behaviors necessarily imply self-recognition, he attempted to get more objective measures of self-recognition by marking the face of the chimpanzees during anesthesia, in such a way that this mark could only be seen when the chimps looked at their reflection in the mirror. After recovery from anesthesia, some of the chimpanzees used the mirror as a tool to investigate the mark on their face, which was the first evidence that primates can recognize themselves in a mirror. From these results, Gallup concluded that MSR implies not only awareness, but "self-awareness" as these individuals "...are objects of their own attention and are aware of their own existence..." [4, 5]. According to the same author, if chimpanzees do possess the cognitive ability of self-awareness, they should also possess the ability to monitor one's own mental state and to impute knowledge or emotional states to other individuals. These cognitive abilities go far beyond self-recognition since they imply some skills that follow from theory of mind [6]. It must be acknowledged that this theoretical assumption is exciting as it supposes that primates master high-level social skills that were historically confined to humans such as the attribution of intent, deception, reciprocal altruism, empathy, reconciliation? However, it is still debated whether MSR involves these "high-level social and cognitive abilities" related to the theory of mind [7–9] or "lower level cognitive abilities", such as the capacity to differentiate the body self from other objects of the environment, and to attend to stimuli that come from that body self [10]. For disentangling between these two theories, one needs first to precisely define the cognitive capacities that underlie primates' understanding of the true nature of their image in the mirror.

The present chapter attempts to demonstrate that MSR requires at a *minimum* that mirror reflections are processed as external representations of the self, and not as the real self. Therefore, being able of self-recognition might be related to the capacity of processing picture as a symbolic representation of the real object [11], and not to demanding cognitive abilities such as "self-awareness". I will first review the main results provided by the literature on MSR and on picture processing abilities in primates. I will then describe two experiments, carried out with my collaborators, which were aimed at testing the hypothesis that MSR might be based upon the cognitive ability to comprehend symbols. In conclusion, I will discuss our findings in regard to the literature and subsequently propose a novel postulate on the co-developmental course of pictorial comprehension and MSR in primates.

2. Mirror self-recognition in primates: experimental considerations

The pioneering study by Gallup [2] has been at the origin of a now very large literature on MSR in primates. To sum up, that literature confirms that some primates species can use their reflection in a mirror for self-exploration (for a review, see [12]), but claims that MSR abilities strongly depends on the species under consideration. On the one hand, MSR has been demonstrated in the four species of anthropoid primates: chimpanzees, for example [13], bonobos, for example [14], orangutans, for example [15]. MSR in gorillas is much more debated. Some studies indeed showed that gorillas exhibit no mark directed touching [16] nor spontaneous mirror-guided self-exploration [17], while others suggest that gorillas are capable of self-recognition [18–21]. Still, results are controversial even with mirror procedure adapted to the behavioral gorillas' specificity, and aimed at enhancing the gorillas' exploration of the mirror reflection, for example [22–24]. Overall, even if results on gorillas' MSR ability are mixed, according to the studies reporting positive findings, the capacity for self-recognition is at least present in some individuals.

On the other hand, failures to convincingly demonstrate MSR in non-ape primate species appear recurrent in the literature (for a review, see [25]). When facing a mirror, most monkeys' species usually display social responses toward their reflection, treating the image as a conspecific (familiar or not) [26, 27]. Monkeys' social responses generally do not evolve toward self-directed responses [28, 29]. In order to enhance monkeys' self-directed behavior in front of the mirror, researchers attempted to diversify the experimental procedures. Spontaneous responses to a mirror versus photographs and real-time videos performed by Cotton Top-Tamarins were recorded [30]. Subjects showed more attentional responses and frequent non-aggressive looks when facing the mirror compared to the other conditions. However, they did not consistently generate self-oriented behaviors in front of the mirror. Capuchin monkeys' spontaneous behaviors were also recorded when they were facing live video images of themselves [31], but again monkeys did not show any sign of explicit self-recognition. An alternative experimental strategy consists in modifying the nature or the location of the classic dye mark. In an experiment [32] where the classic mark was replaced by an odorant chocolate paste, the marmoset monkeys, while facing a mirror, did not demonstrate any mirror-guided exploration. In another study [33], capuchin monkeys were trained to touch a mark directly visible on various body areas (forearms, calves, and abdomen) to reinforce their experience of the correspondence between their body and its image in the mirror. During the test phase, the mark was confined to the face but monkeys never used their reflection to touch it. Other authors [34, 35] tried to prompt self-recognition in capuchin monkeys by manipulating the mirror's characteristics (e.g. size and number of mirror, angled-mirror, etc.), but also failed to observe any MSR in their subjects.

In macaques, results of MSR ability are more controversial. Macellini and collaborators [36] have attempted to promote own body recognition in pig-tailed macaques, by locating the mark on their chest (only visible via a mirror). When facing the mirror, none of the subjects tried to touch the mark, thus suggesting that they did not relate the mirror reflection to their body. In another study, researchers recorded the spontaneous behavior of rhesus monkeys equipped with a head implant (which is a more salient mark) while the animals were facing a mirror [37]. Macaques performed self-directed behaviors (e.g. active exploration of the

implant and of the genital areas) only in front of the mirror. The same monkeys, however, failed to show any sign of self-recognition in a conventional mark test. Altogether, this experimental procedure appears insufficiently controlled to definitely conclude that these macaques actually demonstrated self-recognition ability (for a comment, see [38]). In a recent challenging study [39], rhesus monkeys were trained to locate a visual-somatosensory stimulus projected on their head. Basically, an irritant laser-pointer light dot was directed at the subject's forehead, and could be both perceived on the skin as a hot spot and as a colored spot in a mirror. This explicit training regimen not only resulted in macaques passing of the classic mark test with dyes of various colors but also showed that macaques subsequently explored spontaneously some unseen body parts. Although this study raised appreciations, for example [40], and excited comments by the scientific community "Clever studies like the one of Chang et al. [39] help expose our preconceptions about ourselves and point the way toward deeper understanding of the way our brains, and the brains of other animals, construct reality and our place within it" [41], it also raised some criticisms. Indeed, according to Anderson and Gallup [42], the trained monkeys might not have really recognized their image in the mirror but might have simply learned to touch the unpleasant location on their face when seeing any monkey image. To tackle this critical issue, Chang and collaborators designed a second experiment [43], replacing the visual-somatosensory stimulus (an irritant spot) by a visual-proprioceptive training. Macaques were trained to locate a spot projected onto a surface in their close personal space, which was visible either directly or through the mirror reflection. In a first phase, macaques were trained to locate the spot when it was both directly visible and through the mirror. During the test phase, subjects failed to pass the mark test as they did not touch the spot when it was projected on themselves. However, in a second training phase, the spot was only visible via the mirror reflection. In the test phase, macaques passed the mark test. This last experiment strongly suggests that under appropriate experimental approach, monkeys are able to pass the mark test. It should encourage researchers to adapt training procedures in order to promote the monkeys' motivation to use the mirror reflection which could also enhance their motivation to explore their own faces.

3. Mirror self-recognition in primates: intra- and inter-species differences

3.1. The mark test: a proper index of self-recognition?

Massive inter-individual differences in MSR abilities have been repeatedly reported in primates [44]. Even in the chimpanzees, the most proficient species in this test, MSR is only accessible to a subset of individuals. Many of them fail the task, for example [45, 46]. One extreme explanation of these inter-individual discrepancies is that non self-recognizer subjects or species actually lack "self-awareness". Only some chimpanzees, orangutans, and gorillas have consequently a visual representation of their self [4, 47]. Yet, other factors may also play a crucial role in the noticeable inter-individual differences. First, among the great ape species, a clear bias exists toward chimpanzees in terms of numbers of animals tested in MSR. About 164 chimpanzees (estimation) have been tested, while the number of orangutans (estimated $N = 5$), bonobos ($N = 10$) and gorillas (estimated $N = 19$) tested is relatively small.

This actual bias may be at the origin of the common idea that chimpanzees are the most proficient species in MSR. Second, rearing conditions of animals are extremely heterogeneous (captive vs. wild-born, different laboratory living conditions) and may probably result either in enhanced social-cognitive functioning (e.g. in the case of some ‘enculturated’ home-reared apes) or in impaired social-cognitive functioning (e.g. in the case of social deprivation, or very small group size). Unfortunately, the precise rearing conditions and previous cognitive experience of many primates tested in MSR are often unknown or at least not sufficiently described. Researchers may have underestimate the cognitive consequences of social factors and previous experimental history in the MSR ability. Third, the standard version of the mark test is good only for positively proving the existence of self-recognition. Indeed, failures only sign an absence of self-directed behaviors but not a lack of self-recognition *per se* (false negatives) (for a review, see [48]). And finally, studies on MSR mostly look for chimpanzees-like behaviors in front of a mirror, as initially described by Gallup [2]. Species’ behavioral repertoires may notably make it more difficult for an animal to detect the contingencies between its body and the mirror image, *a sine qua non* to adopt self-directed behaviors, and eventually achieve MSR. On the one hand, as primates initially mistake their own reflection in the mirror with a conspecific, the exploration of the mirror may substantially vary among species and thus provide different visual and kinaesthetic information, from a qualitative and quantitative point of view. Direct gazing in gorillas, for instance, may result in a response of fear from the subject looked at, or in gaze avoidance to sign appeasement and submission [49]. Macaques display threat gaze during conflicts and avert gaze during friendly approaches [50], while chimpanzees avert gaze in case of potential conflict and make eye contact to reconcile [51]. On the other hand, primates’ spontaneous behaviors in front of a mirror may provide, depending on the innate characteristics of each species, more or less somato-sensitive information, which further promote self-directed behaviors. Monkeys, for instance, are usually less engage in auto-grooming than chimpanzees and thus do not receive direct feedback from their bodies as frequently as the chimpanzees do [52, 53]. Yet, the same mirror tests have been applied to a wide range of species, while it might be inappropriate to test some primates’ species under these conditions given their own social characteristics.

3.2. Symbolic pictorial competence: an index of mirror self-recognition ability?

In the following, I will propose an alternative explanation to inter-species discrepancies in MSR. Before using the concept of “self-awareness”, I would recommend first to analyze the perceptual information conveyed by the mirror image in order to infer the cognitive processes at work in the MSR task. When the monkeys look at a mirror, they often express social behaviors, for example [27]. This behavior suggests that they perceive a very realistic pictorial representation of a monkey, and probably mistake the mirror reflection of themselves with a real monkey: they process the “picture” as the “real object” itself. This perceptual phenomenon has already been described in the literature and named “confusion mode” of picture processing [54]. Apes express self-directed behaviors when facing a mirror, for example [13] thus suggesting that they do not perceive the mirror reflection as another individual but rather as a representation of themselves. According to Bard and collaborators [11], self-recognition implies “an understanding that the self can exist and can be represented: the mirror image is a representation of the self as an iconic symbol”. This ability to understand the image

as a symbolic representation infers an “equivalence mode” of picture processing [54]. This “equivalence mode” refers to a situation in which the subject associates the real object with its picture while being perfectly aware that the picture is different from the real object. In that sense, the picture, as well as the mirror image, is a referential stimulus: it is an object which represents another object. Animals must interpret the relation between the picture and its referent to use this medium as symbols and sources of information about the world. Self-recognition ability may thus appeal to the capacity of inferring the dual nature of the mirror reflection. An overview of the comparative literature on picture perception hereafter will highlight the conditions under which the pictures are processed, or not, as an iconic symbol by primates.

4. Picture perception by primates

Three levels of picture processing in monkeys can be outlined [54]: *Confusion, Independence and Equivalence*. The *confusion mode* refers to a situation in which the perceiver simply mistakes the real object and its depiction. The picture is processed as if it was the real object. The *independence mode* defines a situation in which the animal does not map the picture and the depicted object. The picture is processed based on its physical characteristics, regardless the meaning of the depicted object. The *equivalence mode* refers to a situation in which the animal processes the picture as a symbolic representation of the real object. The perceiver associates the real object with its picture while being perfectly aware that the picture is different from the real object. This equivalence mode is precisely the one, which might be required to interpret the reflection in the mirror as a representation of self.

4.1. The confusion mode of picture processing

Monkeys often react to pictures the way they would normally do in front of conspecifics: they express emotions. Macaques exhibit emotional responses (e.g. lip-smacking), when they observe pictures of faces [55], and express fear gestures in front of pictures of highly emotional objects [56]. Young macaques present signs of disturbance and vocalizations when seeing threat pictures [57]. In addition to pictorial stimuli conveying some emotions, pictures of highly motivating stimuli, that is, realistic food, has also been used to observe monkeys' reactions. The few studies existing showed that monkeys confused picture of food with real food and tended to process it, as they would normally do with real food. Bovet and colleagues were the first to illustrate this confusion behavior in [58]. Baboons were first trained to categorize food objects and non-food objects and showed positive transfer to novel objects. They were then trained with cut-out pictures of both food and non-food objects, and with the same pictures on a paper background. Categorical transfer occurred for cut-out photographs but not consistently for the whole ones, suggesting that the more pictures appear realistic, the more monkeys are deceived. Parron and collaborators [59] designed a simpler procedure in which pictorially naïve baboons had just to select one food picture (banana's picture) over a non-food one (pebble's picture). Results showed that subjects massively selected the realistic picture of banana and even, in some cases, ate this picture. Altogether, because these behaviors are perfectly appropriate in response to the presentation of real objects (i.e. a conspecific or food) but inappropriate in front of pictures, this suggests that monkeys recognized the depicted objects but did not process the pictures as some representations. To sum up, studies in monkeys suggest that naïve subjects processed realistic pictures in a confusion mode.

4.2. The independence mode of picture processing

A close analysis of the results reported in the literature leads to the conclusion that in many cases primates apply perceptual alternative strategies to perform picture recognition tasks. Under some specific experimental conditions, the animals process pictures based on a combination of perceptual features and patterns regardless of their representational content. For categorizing human versus non-human pictures, for example, capuchin monkeys used the colored features of the pictures, as humans' photos incidentally contained more red pixels than the non-human set of photos [60]. Two studies on face perception by baboons also provide an illustration of the perceptual strategies used by these animals to recognize pictures. Baboons were able to discriminate pictures of human faces on the sole basis of variations in the facial contour [61], and used the pixel similarities between training and probe pictures to categorize human versus baboon faces [62]. Apes, like monkeys, do not always process pictures as referential stimuli. For example, when tested in a matching to sample task using pictures, chimpanzees fail to show any transfer between real objects learnt by tactile inspection and pictures of the same objects [63]. The authors concluded that the "chimpanzees did not realize that a photograph is a visual stimulus that must be read". In another study, [64], where apes were tested to see whether they would be able to use pictures to infer the location of a hidden reward, results showed that iconic cue might help them to search for the reward but their poor performances eventually suggested that they did not fully grasp the informative content of the cue.

4.3. The equivalence mode of picture processing

Given the amount of studies on picture perception, we could expect to find more clear-cut evidence of a referential use of pictures by primates. For example, findings from a study on capuchin monkeys suggested allegedly positive evidence of an equivalence mode of picture processing [65]. After training, the subjects were able to discriminate images of in-group and out-group conspecifics' faces, and probably based their responses on the experience they have established with the depicted individuals in their real life. Nevertheless, as it will be detailed in Section 5, the experience animals had previously developed with tasks involving picture processing may have change drastically the way they interpreted the pictorial stimulus in this experiment. These capuchin monkeys received actually prior exposure to pictures of faces in other experiments, for example [66], which may have facilitated the positive transfer to grayscale images, and may also explained the absence of monkeys' social responses to pictures of faces. Comparable results were reported in crested macaques [67]. The subjects were able to discriminate members of their own social group from unfamiliar individuals, and were even better at recognizing higher ranking familiar individuals. As in [65], authors concluded that macaques applied their knowledge of their dominance hierarchies to the pictorial representation of their real group mates. Although this result rules out the independence mode of processing, the small sample size (three individuals who do not always perform similarly) along the absence of information on the past experience of these animals with pictures preclude unambiguous conclusions on picture perception in these monkeys. In [68], capuchin monkeys were able to match objects with their color photographs (and vice-versa), and even associate real objects with the corresponding black and white photographs, silhouettes and line drawings. However, the objects used in this experiment had no explicit representational content for the monkeys (e.g. a small wooden puppet or a cigarette lighter), and were never encountered in capuchins' real life before.

The most convincing evidence of an equivalence mode of picture processing comes from the so-called ape-language studies. Rumbaugh and collaborators [69] were the instigators of a pioneering project, “the Lana Project”, at the Yerkes Regional Primate Research Center in Atlanta. This project was aimed at studying the language-like skills of apes, by using a new device designed to enhance teaching an ape to communicate with humans. So far, behavioral experiments studying language skills in apes suffered from a lack of experimental controlled conditions, slowing down the comprehension of apes’ system of communication. Therefore, they developed an automated computer-controlled system: the chimpanzee was facing a keyboard displaying distinctive lexigrams and was trained to associate a real object or a picture to a specific symbol. This system actually improved both efficiency (e.g. increased number of trials per day) and objectivity (e.g. no interaction with a human experimenter and automated responses’ recording).

This pioneering system was also used to study the ape-language skills by Savage-Rumbaugh and collaborators [70], at the Language Research Center in Atlanta. This project conducted to the historical first non-humans communication with humans by using symbolic language. Basically, some chimpanzees received, since a young age, extensive language training and first learned to use some lexigrams to name objects, and then to combine these lexigrams to produce a complex form of communication. With regard to our topic on pictorial competence in primates, we will consider the case of Sherman and Austin, two trained male chimpanzees, who were able to associate real food and tool objects to two lexigrams that served to “label” these categories [71]. Their performance in this “naming task” with real objects effectively transferred to pictorial depictions of tool and food items. They were able to make categorical judgments about objects when presented with only symbolic information, in the absence of the referent. They obviously did not confuse pictorial depictions with real objects. These two trained-language chimpanzees more likely processed the pictures considering their representational content, and not their pictorial expression.

Along the same line of research, Matsuzawa ([72] for an historic review), directly inspired by preceding ape-language studies conducted in Atlanta, developed a new project: “the Ai project” in 1978 at the Primate Research Institute in Kyoto University. Ai, a female chimpanzee, was intensively trained in various perceptual and cognitive tasks since her first year of age, with a computer-controlled apparatus. Over the years, she acquired a multitude of remarkable cognitive skills, including the use of visual symbols. Similarly to Sherman and Austin, she was trained to “name” some individuals by using lexigrams. When the same individuals were then represented on pictures [73], and line drawings [74], she could properly name them. Again, this result strongly suggests that chimpanzees may process the pictures considering their representational content, that is, in an equivalence mode. In another experiment, Tanaka [75] tested the ability of Ai, three other adult naive chimpanzees and three naive juveniles in a picture recognition task. The subjects were first trained to select some pictures of flowers among pictures of other natural objects. They were then tested with new pictures of flowers and some increasingly degraded stimuli: colored sketches, color clip art (cartoon-like pictures) and black and white line drawings of flowers. Ai was the unique adult chimpanzee to transfer from the flower picture to the non-photographic images of the flower. Noticeably, Ai is not only a language-trained chimpanzee, but she has also been previously

exposed to line drawings [74]. The three juveniles, unlike the naïve adults, showed positive transfer of their previous category learning to the degraded stimuli. Their good performance may be due to their better learning ability, as it is established that young animals show greater cognitive flexibility, for example [76, 77]. Close and Call [78] used a similar procedure with sub-adult and adult naïve chimpanzees. The subjects were presented with colored, black and white sketches, and line drawings of the training pictures (tree vs. flower). Adolescent chimpanzees generally outperformed the adults, particularly in the recognition of the black and white sketches stimuli. None of the chimpanzees initially showed a positive transfer to the line drawings stimuli. However, the adolescent chimpanzees finally learned to categorize line drawings after a moderate period of training. These findings are broadly consistent with those of Tanaka [75], as after training, juvenile chimpanzees, unlike naïve adults, similarly showed in [75] and in [78] positive transfer of their previous category learning (colored pictures) to the degraded stimuli (black and white pictures or line drawings). Overall, it suggests that learning abilities may be enhanced by training during a critical period of chimpanzees' development that further enables adults to achieve various cognitive tasks.

5. The dynamic hypothesis of picture processing

The heterogeneity of the findings reported above suggests that some complex factors concurrently shape the perceptual and cognitive processes, and all together, this calls for a revision of the theoretical assumptions underlying picture perception in primates. Ontogeny, phylogeny, as well as the animal's level of experience with pictures seem to account for the observed performance variability in primate picture understanding. Actually, *training regimen* with pictorial display seems to influence drastically primates' behavioral responses. Untrained chimpanzees either failed to match real objects with their pictures when the objects were previously explored haptically [63] or to match real objects with line drawings of objects [75, 78]. It is only after training with degraded pictures that an equivalence mode of picture processing gradually emerged, at least in juveniles in these studies [75, 78]. A similar experiment with macaques trained to match objects and their pictures, and only when they were visible *at the same time*, also resulted in successful objects/pictures matching [79, 80].

The attractiveness of meaningful pictures (i.e. representing some objects of interest for monkeys) can be explained by the lack of experience of monkeys with this kind of new display, but may also vanish as a consequence of *repeated exposures*, which eventually result in habituation (i.e. decrease of response). When macaques are repeatedly presented with a "meaningless" picture (representing an abstract stimulus) and a "meaningful" picture (representing a real object), their response rate rapidly dropped for the "meaningful" picture, but remained constant for the "meaningless" picture [81]. In a two-alternative forced choice task, pictorially naïve baboons got rapidly habituated to pictures of -initially very attractive- realistic picture of bananas [59]. During the first test trial, 100% of the individuals participated but only half of the group responded three test trials later. In a recognition task using familiar versus unfamiliar faces, macaques showed a significant decrease in accuracy after 44 repetitions of the same stimuli, which suggests that they habituated to the stimuli and lacked interest in the task [67].

Noticeably, over the last decade, the development of experimental settings using touch screens to display pictures has significantly increased. Unlike procedure using real pictures, which not always allows animals to manipulate pictures, the use of touch screens may promote animal's understanding to the physical nature of pictures (e.g. flatness and unreachability of the depicted objects). This repeated experience probably leads animals to rapidly switch from a confusion mode of processing to an independence or an equivalence mode of processing, depending on the task demand and on the animals' cognitive abilities.

The past experience of primates with tasks involving picture understanding lead the same animals to a certain *degree of expertise*. It should be reminded that the most proficient individuals in processing pictures as symbolic representations are the language-trained individuals, for example [71–74]. Indeed, Savage-Rumbaugh [70] evidenced that the learning process of symbols in apes is achieved by association. Indeed, they first needed an explicit training before they could use symbols referentially.

Based upon the above results of the literature, the animals' mode of picture processing seems not to be predetermined by the species but more likely by the subjects' own experimental history. Picture processing by primates is likely not limited to only one of the three different modes: confusion, independence, and equivalence. These modes evolved and should be regarded as components of a dynamic system, in which the trajectories between the three modes are under the influence of the animal's experience with pictures [82]. On the ground that pictorially naïve monkeys, just like young human infants [83], confuse realistic pictures with their referent objects [59], one can hypothesize that this confusion mode takes place at an early stage in the system of picture processing, likely the starting point in the dynamic scheme. From here, the experience with two-dimensional representation could direct the animals from the “confusion” starting point toward one of the two possible trajectories of the picture processing dynamic system. In the low-level road, experience (for instance, in the case of repeated

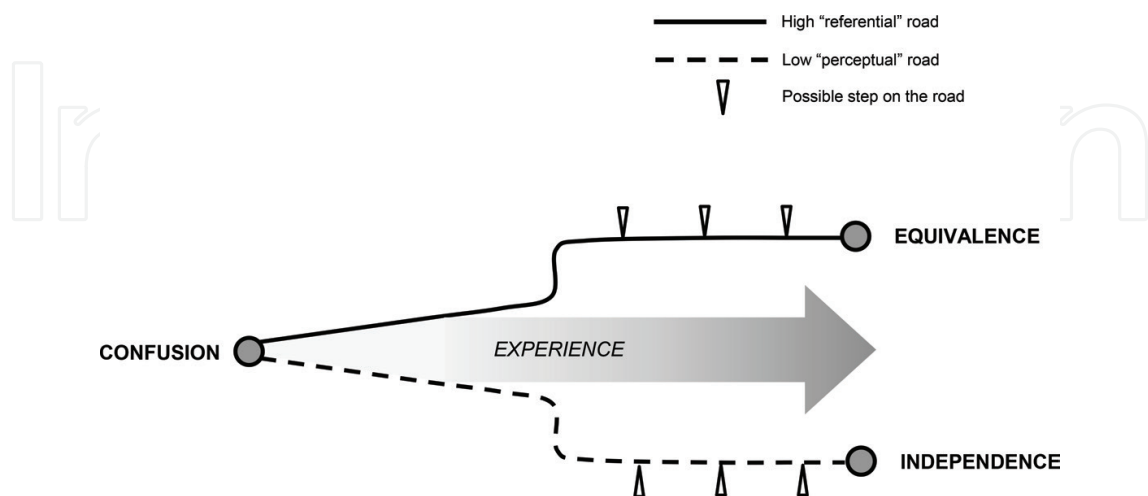


Figure 1. The three different levels of picture processing: confusion, independence, and equivalence and the two possible trajectories following experience with pictorial representations: the high “referential” road and the low “perceptual” road.

exposure and habituation) may push the animals toward the independence mode where the picture is defined by its physical characteristics and becomes meaningless. Another option is that experience, as in young human infants [84], drives the animals toward a high-level road or the road of equivalence mode, that is, the animals would ultimately be able to process pictures as iconic symbols (see **Figure 1**) [82]. According to the different cognitive processing underlying these two roads, from now, they will be referred as the low “perceptual” road and the high “referential” road. The capacity to take or not the high “referential” road correlates with other referential skills such as MSR will be assessed in the two studies detailed hereafter.

6. Empirical approach

In our first study, we showed that when pictorially naive baboons and gorillas looked at an attractive-realistic picture of banana for the first time, they often mistake the picture and the real object depicted. After smelling, or attempting to smell the depicted banana, they may even eat the picture. This striking behavior was only observed in baboons and gorillas, but never in chimpanzees. We thus hypothesized that the pictorial understanding of chimpanzees relying on an equivalence mode of processing might be at the origin of their MSR ability. They may process the mirror reflection as an iconic symbol and interpret it as a representation of their self. By contrast, the confusion mode of processing displayed by gorillas and baboons is consistent with their inability to pass the mark test. In order to assess this hypothesis, a second study comparing the chimpanzees’ ability for MSR and picture understanding was running. We were expecting that the positive MSR chimpanzees would never mistake the banana picture with a real banana as they were also able to process their image in the mirror as a representation. By contrast, since they do not possess a referential ability, the non-self-recognizer chimpanzees would potentially process the banana picture like baboons and gorillas in our previous experiment.

6.1. Picture processing in monkeys and great apes

The first study reported here assessed the behavioral responses to photographs by pictorially naive baboons, gorillas and chimpanzees and was published in [59]. It involved 55 baboons (*Papio anubis*): 26 males and 29 females (mean age 6.9 years, S.D. = 4.6 years) from the CNRS Rousset-sur-Arc Primate Center (France), 7 chimpanzees (*Pan troglodytes*): 3 males and 4 females (mean age 9.75 years, S.D. = 7.3 years) from the Wolfgang Kohler Primate Research Center of the Leipzig Zoo, and 4 gorillas (*Gorilla gorilla*): 1 male and 3 females (age 24.5 years, S.D. = 11.15 years) from the zoos of Leipzig or Nuremberg (Germany). Monkeys and apes, habitually housed in social group, were either tested in groups or isolated, depending on the specificity of their living quarters. Their participation was always voluntary. All animals were selected at purpose because they have no known exposure to videos, still pictures, or drawings, and were thus pictorially naive. We hypothesized that testing monkeys and apes at an equivalent level of expertise with two-dimensional stimuli would provide cues on the evolution of picture comprehension within the primate phylum. This research adhered to the legal requirements of the current French laws and the European directive 2010/63/EU (see **Figure 2**).

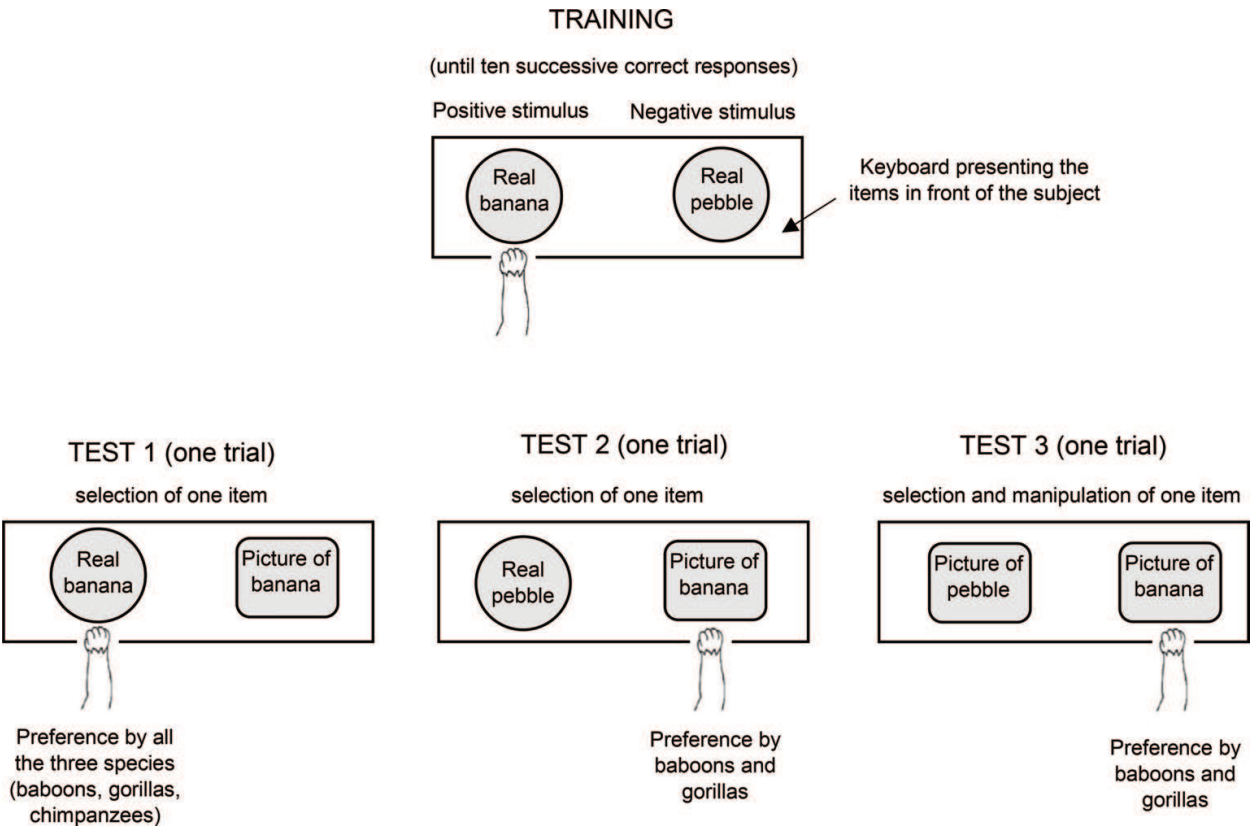


Figure 2. Illustration of the experimental protocol and summary of the results obtained for the three consecutive test trials. These results show that baboons, gorillas, and chimpanzees demonstrated a massive preference for the real banana compared to the picture of banana in test trial 1. When the subjects had to choose between the picture of banana and any other items in test trial 2 (the real pebble) and in test trial 3 (picture of pebble), baboons and gorillas clearly exhibited a preference for the picture of banana (*two-tailed binomial tests, $p < 0.05$ in all the three test conditions). Because of the small sample of chimpanzees, results preclude from any conclusion about the picture's preference in this naïve chimpanzees' group.

6.1.1. Procedure

A two-alternative forced choice task was used to train the subjects to select a real slice of banana (positive stimulus) over a real pebble (negative stimulus) when these items were presented simultaneously on two display panels. Subjects received a food reward when they selected the positive stimulus. These trials were repeated until a clear preference for the real banana slice emerged.

The test procedure consisted in three successive test trials per participant, using different pictures for each test that always subtended the same size as the real objects. Test trial 1 assessed the discrimination of a real slice of banana from a picture of a banana slice. Test trial 2 assessed the attractiveness of the three-dimensional real object in comparison to two-dimensional picture, by presenting a picture of a banana slice and a real pebble. Test trial 3 assessed whether preference for the real banana slice learned during training would transfer to the picture of the banana slice when the two real training objects (banana and pebble) were now presented as pictures. The participants could freely reach and manipulated the selected stimulus only in that last test trial.

6.1.1.1. Coding scheme

We coded the subjects' spontaneous behavior expressed with the picture during test trial 3; it was the very first manipulation of a picture, revealing the initial reaction of the naïve subjects with such an object. We used a hierarchical coding scheme to characterize the different behaviors observed during test 3 and grouped them in four categories. "touch or grasp"; "smell"; "bring to mouth"; "eat": in that last case, the animal ate the stimulus either partially or entirely. Chewing is observed and the animal ingests at least some parts of the stimulus (see images **Figure 3**).

6.1.2. Results

In test 1, all the species showed a clear preference for the real banana (vs. the picture of banana). In test 2, only baboons and gorillas showed a preference for the picture of banana (vs. the real pebble). In test 3, baboons and gorillas still showed a significant preference for the picture of banana (vs. the picture of pebble). In contrast, chimpanzees showed no clear preference for either picture. **Figure 4** shows the frequencies of each action obtained in baboons, gorillas and chimpanzees during the first bout of picture manipulation. Strikingly, 17 baboons and the 4 gorillas ate the picture of banana as if it was a real piece of banana. Some individuals even attempted to spell the depicted banana. These animals clearly did not process the picture of the banana as a representation. Interestingly, not only the chimpanzees expressed no reliable preference for the banana picture in these tests, but also never ate that stimulus, leaving open the possibility that the pictorial banana was a referential stimulus.

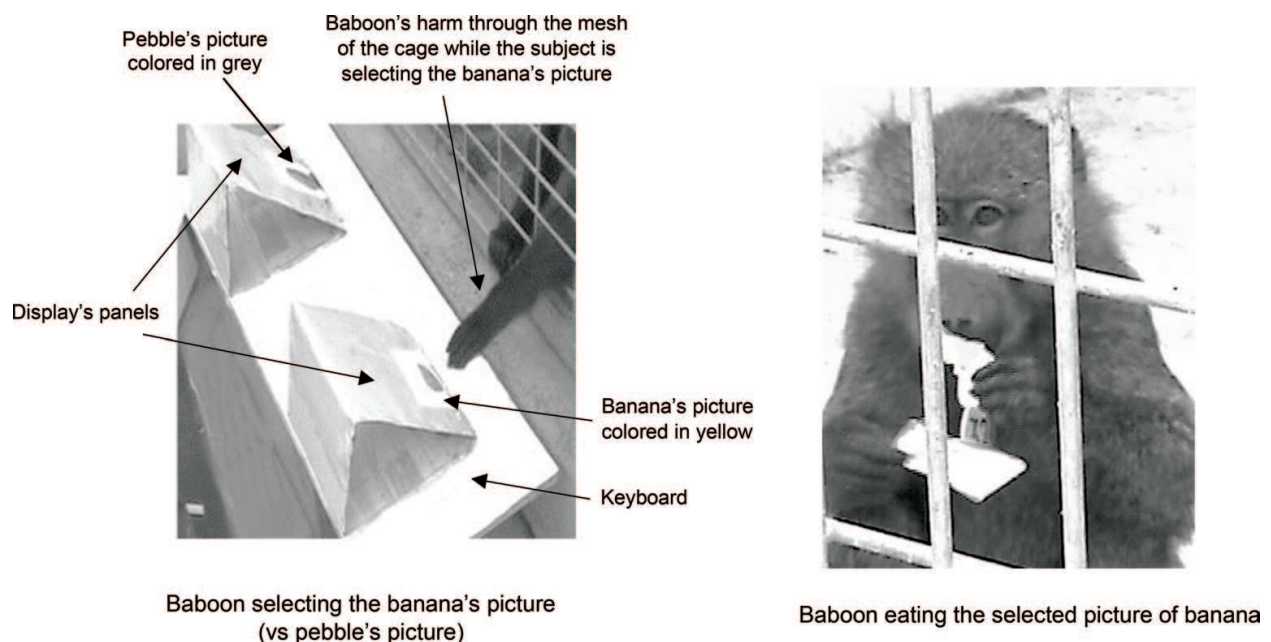


Figure 3. Illustration of the behavioral sequence during test trial 3.



Figure 4. Frequencies of each action observed in baboons, chimpanzees, and gorillas during the first bout of banana picture manipulation, in test trial 3 where subjects had to choose between a banana picture and a pebble picture (illustration from [59]). These results show that baboons massively selected the picture of banana in that test (43 out of the 46 participants). Among them, 16 baboons selected and grasped the picture of banana, 5 smelt it, 5 brought it to mouth, and 17 ate the picture of banana. Similarly, the four gorillas who selected the banana picture ate it. Finally, the five chimpanzees who selected the picture of banana grasped, smelt or brought it to mouth but never ate it.

The demonstration that naive baboons confused real food objects and their picture is in agreement with previous observations from picture processing’ experiments in monkeys, for example [57, 58]. The fact that baboons, a species known to fail in self-recognition task [85] and that gorillas, a species less efficient than chimpanzees in MSR, for example [23], both confuse the real object with its picture is consistent with the hypothesis that pictorial ability may correlate MSR skill. In addition, chimpanzees, subjects who frequently succeed in the MSR task, for example [13], showed no confusion in picture processing. Our data might support the hypothesis that the cognitive foundation supporting the use of pictures as referents is more developed in chimpanzees than it is in gorillas and monkeys. Unfortunately, because that research provided no information on MSR of these subjects, it remains unclear whether a relationship actually exists between MSR abilities and iconic symbol use. The second study (unpublished), conducted in collaboration with Joël Fagot and William Hopkins, was thus aimed at alleviating that limitation.

6.2. Picture processing and self-recognition in chimpanzees

Under our hypothesis that self-recognition ability might be based upon the cognitive ability to symbolize, we were expecting that the positive MSR animals would both be able to process their image in the mirror as a representation, and to map that referential stimulus to their internal visual representation of their self. By contrast, the negatively tested animals would be unable to succeed in that mapping process, because the mirror image is processed as a real object, rather than as a representation.

The participants were 32 chimpanzees (*Pan troglodytes*): 9 males and 23 females, from 8 to 22-year-old, all housed in social group of 2–3 individuals in indoor/outdoor enclosures at the Yerkes Regional Primate Research Center. The Yerkes Center is fully accredited by the American

Association for Accreditation of Laboratory Animal Care. American Psychological Association guidelines for the ethical treatment of animals were adhered to during all aspects of this study.

The chimpanzees were proposed two tasks. The first one is a test of MSR inspired from Gallup [2]. The second test is a replica of Parron and collaborators [59] procedure. Conjoint analyses of the findings obtained in these two tests were expected to highlight possible relations between MSR and picture understanding.

6.2.1. The self-recognition task

A camera (with a 2.7 inches LCD screen) taped subjects' behavior when they were facing or not the screen. Each subject received two videotaped sessions, each lasted 3 minutes. The first session was a control condition with the screen turned away from the subject (mirror away condition). That session served for baseline measurement for general self-directed actions. Test session 2 replicated the procedure of session 1, but now with the screen turned toward the subject displaying an image observed by the subject, and therefore used as a "mirror" (mirror condition) (see **Figure 5**).

The coding considered five behavioral categories: "Face-directed actions" defined as manual actions oriented toward the face, such as touching the cheek or the inside of the mouth; "Facial expressions" such as opening the mouth to exhibit the teeth; "Contingent body motions", such as alternate right/left or forward/backward body movements; "others": any behavior different from the previous ones.

When the screen was toward the subjects, a total of 384 actions were recorded for the group, they were distributed as follows: face directed (22.9%); facial expressions (28.6%); contingent body motions (25.5%) and others (45.8%) (see **Figure 6**). Results showed that chimpanzees displayed more actions when the screen was toward them than when it was turned away

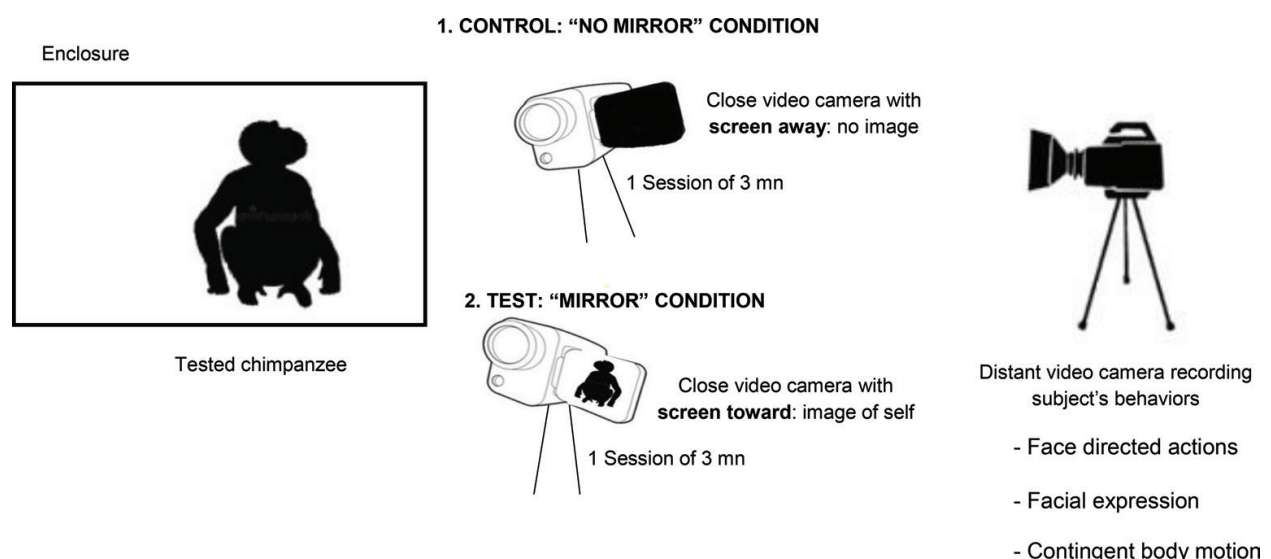


Figure 5. Schematic illustration of the experimental protocol of the self-recognition task in chimpanzees.

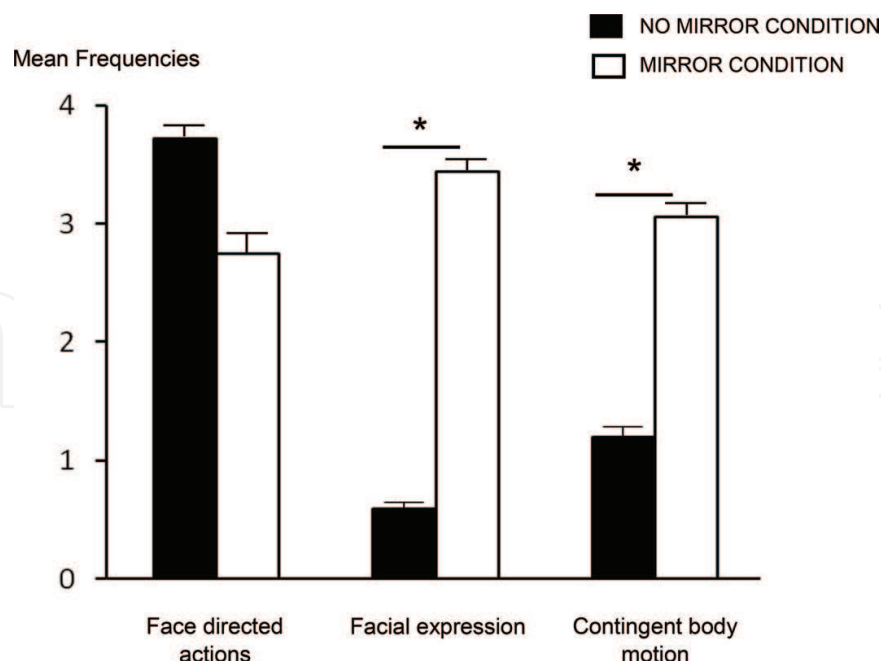


Figure 6. Mean frequencies of each behavioral category observed in chimpanzees depending on the orientation of the screen: away from the subject (no mirror condition), toward the subject (mirror condition). (*Tukey tests, $p < 0.05$). These results globally show that some of the tested chimpanzees displayed some specific behaviors only in front of the mirror, suggesting that these subjects expressed self-recognition. Indeed, even if they did not exhibit more face-directed actions in front of the screen, they nevertheless exhibited more facial expression and contingent body motion in the condition where they could observe themselves: the mirror condition.

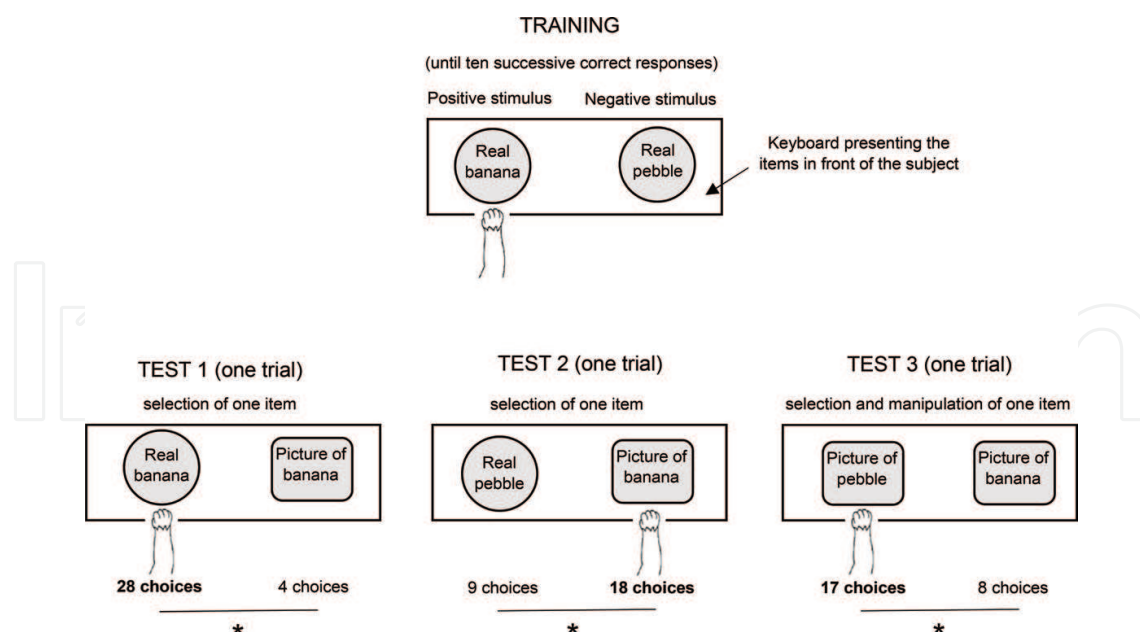


Figure 7. Illustration of the experimental protocol and the frequencies of banana picture choices compared to the other item for the three tests trials in chimpanzees. (*Two-tailed binomial tests, $p < 0.05$). These results show a massive preference for the real banana compared to the picture of banana in test trial 1. When the subjects had to choose between the picture of banana and the real pebble in test trial 2, they clearly exhibited a preference for the picture of banana while they preferred the picture of pebble in test trial 3. Altogether, these mixed results preclude from any conclusion about the picture's preference in this group of chimpanzees. We can notice that all the 32 chimpanzees participated to the first test trial while their number decreased for the two following test trials. It suggests that some subjects may have lost interest in the task when no real food was proposed.

from them ($F(1,31) = 4.90$; $p < 0.05$) and realized an increasing number of facial expressions and contingent body motions (Tukey Honestly Significant Differences test, $p < 0.05$), but not face-directed actions, when the screen was toward them. Although there were no reliable effects for face-directed actions at the group level, four chimpanzees demonstrated an increased frequency of face-directed actions (one-tailed binomial tests, $p < 0.05$) when they saw the screen and thus will be considered as self-recognizers hereafter.

6.2.2. The picture-understanding task

The 32 chimpanzees were submitted to the picture task following the same procedure as [59], previously described above.

In test 1, the group had a significant preference for the real banana compared to the banana picture; (two-tailed binomial test, $p < 0.05$). In test 2, 5 chimpanzees expressed no choice, but the rest of the group had a significant preference for the banana picture over the real pebble; (two-tailed binomial test, $p < 0.05$). There was by contrast no preference for the picture of banana at the group level in test 3, and 7 chimpanzees did not choose any item (two-tailed binomial test $p > 0.05$) (see **Figure 7**).

The behavior of the four self-recognizers chimpanzees as determined above was contrasted with that of the 28 non self-recognizers, and showed no reliable difference between the two groups of subjects (Chi-square tests all $ps < 0.05$). As we found no relation between self-recognition

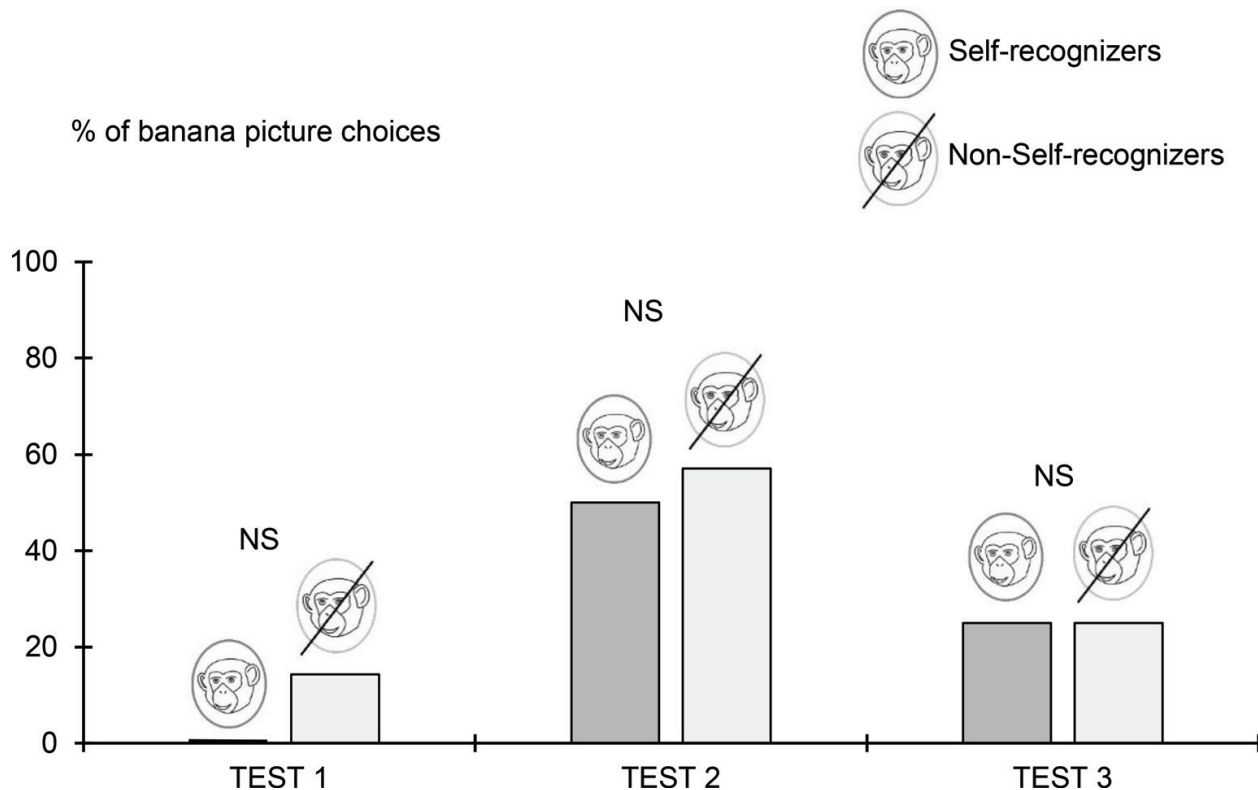


Figure 8. Percentages of banana picture choices in test trials 1–3 of the picture task, according to the self-recognition abilities of the chimpanzees. These results show no difference between self-recognizer and non-self-recognizer subjects as they both selected the banana picture by the same proportion in the three test conditions, independently from their self-recognition abilities. (Chi-square tests all $ps < 0.05$).

	Take	Smell	Bring to mouth	Eat
Self-recognizer	1/4	1/4	0	1/4
Non-self-recognizer	5/28	2/28	4/28	3/28

Table 1. Frequencies of actions observed for the self-recognizer and non-self-recognizer chimpanzees who selected the banana picture in test 3.

and picture processing, it suggests that self-recognizer and non-self-recognizer chimpanzees behaved indistinctively in the picture task, and that the proportion of banana picture selected did not differ as a function of MSR ability (see **Figure 8**).

We also examined the actions performed on the banana picture, once reached in test 3 (see **Table 1**), due to our expectation that only the non-self-recognizer chimpanzees would process the picture as if it was a real object. The number of “take”, “smell” and “bring to mouth” actions were minimal, precluding firm conclusion at the group level. Altogether, four instances of eating behaviors were observed, and one of them was expressed by a self-recognizer chimpanzee. That sole observation invalidates our hypothesis that only non-self-recognizer chimpanzees would confuse the actual object and its picture.

7. Discussion

The main originality of our research was to test the hypothesis of a correlation between self-recognition and picture understanding in chimpanzees. Unfortunately, our results did not provide any evidence in support of our assumption that self-recognizer chimpanzees would behave differently with pictures than non-self-recognizer ones. However, these findings should not be taken into account to reject our assumption, as some procedural issues were probably the source of our negative results. On the first hand, our procedure might have been inappropriate to reveal MSR ability, as one chimpanzee who failed to demonstrate self-directed behaviors in our task previously passed the mark test in [13]. It is very likely that the small surface of our camera screen (2.7 inches) might have limited the exploration of the subjects as it did not display the entire subject’s reflection. Noticeably, the other studies, assessing self-recognition in primates, used a larger screen (around 15 inches) to display video images, for example [31, 86, 87]. Consequently, the proportion of self-recognizer chimpanzees, particularly small in our study (4/32), might not reflect the reality, regarding the ratios usually reported in the literature, for example, 8/12 in [13]. On the other hand, our picture task might have been irrelevant to test pictorial competence of non-naïve chimpanzees. Overall, chimpanzees, independently of their MSR ability, showed a minimal interest in pictures, which might be explained by the familiarity of these chimpanzees with iconic stimuli, for example [88]. As a result, the low frequencies of manipulations precluded any interpretation of the chimpanzees’ behaviors with the banana picture.

Overall, besides our two studies, empirical findings on MSR and pictorial competence in primates are so disparate across species and procedures, that inferring a correlation between

both competences from that sole approach appears insufficient. Nevertheless, paralleling the abundant developmental studies in human infants and comparative findings in primates will help in scaffolding a new postulate.

7.1. Developmental course of picture understanding

In their first 2 years of life, children probably miss the symbolic nature of pictures. It is only very gradually that pictorial competence develops, for example [89]. Nine-month-old infants manually explore the pictures as if they were trying to pick-up the depicted objects [83]. They do so even more for realistic pictures compared to non-realistic ones [90]. It is not until 18–24 months of age that children prefer upright to inverted pictures [91] and point at depicted objects rather than manually explore them [83]. In addition, from 24 to 30 months, children can follow a request to put a toy at a place specified to them on a picture and can use information provided with a picture to find the object in the depicted room [92]. Nevertheless, even at age 4, children can show confusion about the properties of pictures and depicted objects [93], and the consequences of actions on pictures and objects [94]. Interestingly, the development of pictorial competence in children fits with the dynamic hypothesis of picture processing in primates described in Section 5. Primates, like infants, begin to process the picture as if it was the real object (confusion mode) and evolves on the high “referential” road of picture processing. They may then achieve the ultimate level, where pictures are processed as referential stimuli (the equivalence mode). Altogether, studies in children and primates suggest that being able to interpret and understand pictures as symbols is a very complex and protracted process.

7.2. Developmental course of mirror self-recognition

7.2.1. *The two levels preceding mirror self-recognition*

Rochat [95] proposed to divide infants’ self-awareness ability into six different levels (from 0 to 6). As disentangling the cognitive abilities of levels 1 and 2 described in [95] is problematic in primates, these two levels will be grouped in only one: the level 1 of “contingency learning”. The first two levels of MSR development emerge at the same age in humans and chimpanzees [96]. At level 0, “LEVEL OF CONFUSION”, the mirror image is confounded with the reality of the environment it reflects. Indeed, by 4–6 months of age, children treat the mirror image as if it is another child, and primates (monkeys and great apes) display social behavior in front of the mirror. At level 1, “LEVEL OF CONTINGENCY LEARNING”, children by 12 months of age begins to search for the image behind the mirror and test contingencies of their movements. Chimpanzees also explore the physical properties of the mirror and begin to detect the contingency between their own bodies and the mirror reflection. Macaques, under certain experimental procedure, are also capable to take their own body as a referential to establish a correspondence between kinesthetic information and external visual effects. They use the mirror to direct their manual searches for otherwise invisible targets [97, 98], to locate and grab an object attached behind their heads [99], or use televised images of their hands to learn to pick-up food [100]. This kinesthetic-visual matching ability warrants the individuals to grasp the correspondence between what the visual image of the body in the mirror looks like and what the body movements feel like [101] and may actually play the role of precursor for self-directed behaviors.

7.2.2. *The level of mirror self-recognition*

The “LEVEL OF IDENTIFICATION” signifies the emergence of self-directed behaviors. Children by around 15 months of age start passing the mark test; and almost all succeed by 24 months of age [26, 102]. In spite of massive inter-individual differences in MSR ability, it is well documented that chimpanzees develop this ability later in life than humans do, around 6–8 years [46]. Although monkeys systematically fail to pass the mark test, it may be unrelated to their self-recognition ability. It is very likely that, while being able to match kinesthetic and visual information under certain conditions, both species specificity (sensory-motor specializations) and inherent motivation of individuals for interacting with the environment influence monkeys’ behaviors displayed in front of a mirror [48]. Indeed, the role of the motivation may be underestimated when comparing the responses of infants, apes and monkeys. Intensive maternal interventions maximize the infants’ motivation to explore the mirror and also help to focus their interest in their own face, for example [102]. Somehow, infants are trained to appreciate the connection between themselves and their mirror image [103]. Apes are also naturally motivated to look at the mirror reflection since they are usually more engaged in mutual gaze during social interactions than other primates’ species. In contrast, monkeys primarily use the tactile mode to display reciprocal engagement and are more socially inclined to avert direct gaze [104].

From an evolutionary point of view, is there any meaning for individuals of monkeys’ society to develop an interest in their *own* facial features? Chang and collaborators [39, 43] designed two studies using some pioneering training procedures to promote the monkeys’ motivation to explore their own face. In the first study [39], a visual-somatosensory training helped macaques to interpret the mirror image as their own reflection. While macaques were facing a mirror, an irritating red laser spot was projected onto their face, producing a somatosensory feeling, which encourages them to touch the spot. In order to reinforce the learning process, they also received food reward after successful trials. Following 12–38 days of training, a non-irritating laser was used to project a spot on the macaques’ face and food reward was no longer delivered during the test session and subjects yet passed the mark test. They even further spontaneously used the mirror to inspect some hidden parts of their bodies. In their second study [43], Chang and collaborators improved their procedure to exclude criticisms arguing that the extensive training received by monkeys may have promotes some behaviors that merely look-like self-recognition. They used a visual-proprioceptive training to motivate monkeys to locate a spot, visible either directly or through the mirror reflection, projected onto a surface in their close personal space. Macaques further failed to pass the mark test. However, in a second phase, the spot was only visible via the mirror reflection, monkeys, after training, eventually passed the mark test. These pioneering results not only demonstrate that under certain training conditions promoting the contingency learning, monkeys pass the mark test but they also highlight the crucial role of motivation as, unless being compelled to do it, monkeys did not spontaneously use the mirror reflection to touch the projected spot.

7.2.3. *Toward a self-concept: the “level of permanence” and the “level of meta-awareness”*

Around 3 years of age, infants recognize picture (even taken in the past) and delayed videos of themselves [105, 106], and reach the “LEVEL OF PERMANENCE” [95]. This level signifies

that the self is identified beyond the here and now of mirror experience. A permanent self is expressed as invariant over time and appearance changes.

As well as human infants, primates have also been tested with pictures to evaluate their self-recognition ability. Monkeys do not recognize pictorial representations of themselves, for example [27]. By contrast, some studies on chimpanzees or gorillas provide some evidence of self-recognition from pictures. Viki, a home-raised chimpanzee, recognized pictures depicted in books and other materials and imitate actions illustrated in films, photographs, and line drawings. When tested in a categorization task, she was able to sort photographs of chimpanzees and humans into two piles, and not that surprisingly, places her own photography on the human pile [107]. Koko, a sign-language trained gorilla, recognized herself on photograph and even labeled her name on it [108]. Ai, the language-trained chimpanzee, used symbolic labels for individuals, transferred the symbols to label pictures of the individuals, including herself [109]. Remarkably, the sole individuals reported to recognize themselves on pictures, were all intensively trained to associate pictures and objects (from an abundant exposure or a language training) and to process them as some representations. That pictorial competence has probably promoted their ability to recognize themselves on pictures.

Self-recognition can be subdivided into two successive levels: First, the “LEVEL OF IDENTIFICATION”, already described above, implies the emergence of self-directed behaviors meaning that individuals manifest recognition and identify that what is in the mirror is “Me”. Second, the “LEVEL OF PERMANENCE” refers to a “self-concept”, where the self is identified beyond the temporal and spatial animal’s experience with a mirror. In that level, self-recognition can occur in absence of a mirror, from delayed videotapes and photographs. This process requires higher cognitive ability that emerges later in the development. This statement is consistent with findings on object permanence in primates. Infant chimpanzees [110] and gorillas [111] are reported to attain the stage 6 in object permanence: that is, these animals are able to take into account the invisible displacements of objects to find objects hidden in successive locations [112]. Monkey species seem to be limited to stage 5 in object permanence [112]: that is, they can only find hidden objects when the displacements are visible [110, 111, 113]. “Level of permanence” and “stage 6 in object permanence” imply a mental representation capacity where the object of interest, the self, is conceived as something permanent in time and space. By contrast, the “level of identification” and “stage 5 in object permanence” might imply a cognitive capacity less demanding, as the object of interest and its representation are simultaneously present in time and space.

Based on the classification of Rochat [95], the ultimate level, to achieve “self-consciousness”, is named the “LEVEL OF META SELF-AWARENESS”. This level implies that the self is recognized not only from a first person perspective, like in the previous level, but also from a third person’s perspective. In other words, individuals are not only aware of what they are (self-concept) but also of how they are in the mind of others (self-consciousness).

Developmental literature in humans and primates shows that cognitive abilities arising from theory of mind actually emerge independently of MSR. In normal children, who pass the mark test between 15 and 24 months [26], complex cognitive abilities such as intentional deception, perspective-taking and empathy develops considerably later in life, for example [114]. In spite

of confusing results, it is now acknowledged that apes can show MSR even without being able to attribute intent and emotions in others, as these capacities seem to emerge, if they do, in later phases of their development [115].

Altogether, these results suggest that, through the developmental course of complex cognitive abilities, self-concept may extend far beyond the MSR. Self-recognition demonstrated by self-directed behavior in front of a mirror corresponds to the level of identification while self-awareness, not only requires to achieve first the “level of permanence”, but also the subsequent level of “self-consciousness”. Moreover, it appears that pictorial competence as implied by an equivalence mode of picture processing may progressively emerge after the development of self-directed behaviors in front of a mirror. Since, MSR may not require self-awareness, then monkeys, who reach stage 5 in object permanence, should be able to achieve the “level of differentiation”, that of MSR.

7.3. Pictorial competence and self-recognition correlation: a refined postulate

Empirical findings and theoretical proposals of the literature have contributed to support and refine my initial assumption that a dynamic pictorial competence correlates self-recognition ability. This model of correlation (see **Figure 9**) is based on the ontogenetic sequence of cognitive abilities observed in infants, and comparative findings in primates. I acknowledge that establishing a such correlation across species is somehow problematic as it would require comparability in procedures and in assessment. Nevertheless, I believe that, even if the time scale and the quantitative nature of cognitive processes may differ from humans to great apes and from great apes to monkeys, this model may open up new perspectives as it is the first attempt to correlate symbolic cognitive ability to embodied cognition and to self-recognition competence.

The starting point of this model is the level of “CONFUSION”: the animals mistake the two-dimensional stimulus (pictures or mirror image) with the real object represented (an object or their self). Then, following a growing experience in “ASSOCIATIVE LEARNING”, animals learn both visual-visual matching and kinesthetic-visual matching. The former ability allows the animals to establish an association between the picture and the real object depicted, and the latter to use the mirror to locate objects that are outside their direct visual field. After repeated exposure to the stimulus (picture or mirror), if animals habituate to the stimulus, they may follow the low “perceptual” road of cognitive processing which corresponds to the level of “INDEPENDENCE”. Pictures are then processed as a combination of physical features, regardless of their referential content, and the mirror is perceived as a common object, with no reflective properties. More likely, the extensive phase of associative learning allows animals to reach the level of “IDENTIFICATION” which corresponds to the cognitive ability to identify object from representation. Although animals progress on the high “referential” road of cognitive processing, they do not yet fully grasp the referential nature of picture. This level also corresponds to MSR ability, which certainly required contingency learning but not a complex representational capacity related to self-awareness. With the development of more complex cognitive abilities, which remain to be determined, animals reach the “LEVEL OF REPRESENTATION”. By forming a mental representation of the real object, animals are now capable to compare this mentally held information to the external visual stimulus. Therefore, they are able to interpret the picture as a representation of a real object (equivalence mode

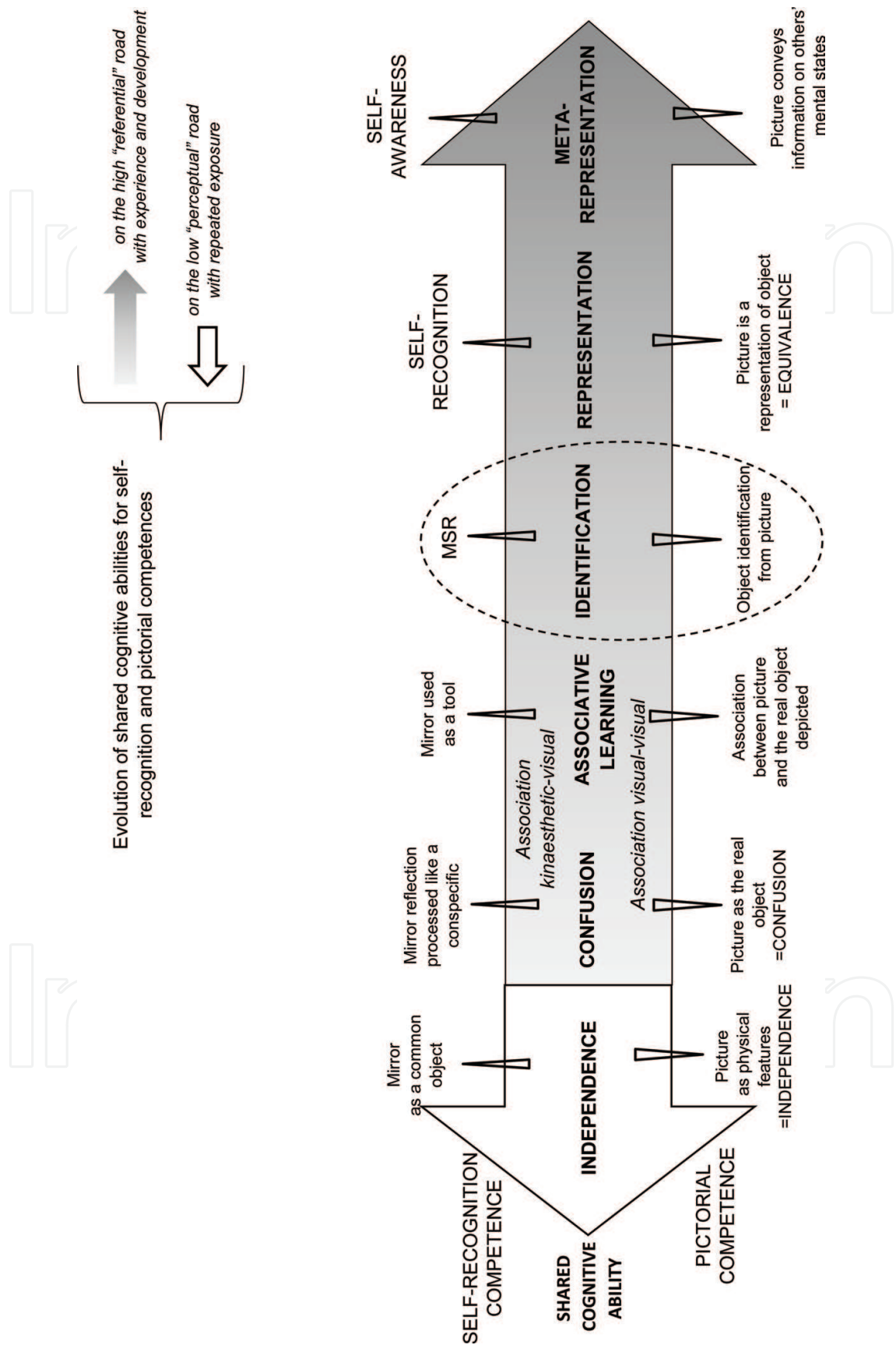


Figure 9. A conceptual model of the developmental course of shared cognitive abilities underlying self-recognition and picture processing in primates.

of picture processing), and to recognize themselves from more ambiguous medium such as pictures. Finally, the ultimate “LEVEL OF META-REPRESENTATION” corresponds to the development of cognitive abilities, which seems to follow from theory of mind. At this stage, a self-awareness concept is expected to emerge. Regarding the pictorial competence, one can hypothesize that animals might be able to interpret symbolic medium to understand other’s minds and to transfer this knowledge to the real world.

7.4. Conclusion

My original hypothesis, that being able of self-recognition might be related to the capacity of processing picture as a symbolic representation of the real object, is consistent with this model of cognitive correlation. The following main outcomes may be drawn up. First, the pictorial competence correlating MSR cognitive stage may be less complex than that corresponding to the equivalence mode of processing. MSR seems rather co-develops with an extensive experience in associating picture and object until the grasping of their correspondence. As monkeys are reported to possess this associative cognitive ability, they should be able to display MSR. It therefore suggests that monkeys’ repetitive failures to pass the mark test may be unrelated to self-recognition ability *per se*, and more likely due to the procedural constraints of this test. Second, due to over interpretations of MSR responses, the strong statement that skills related to self-recognition have evolved until a cognitive gap in the phylogeny has been spread. This assumption may be partially left unsupported as, according to this model of cognitive correlation (**Figure 9**), both great apes and monkeys achieve the same level of cognitive capacities at the MSR stage. This observation should encourage investigations on the origin of such MSR responses discrepancies in the literature. Third, the traditional interpretation of MSR as an index of self-awareness [4, 5] raises serious doubts based on the ontogenetic emergence of MSR. Indeed, the development of complex cognitive abilities related to self-awareness occurs much later than MSR ability. Finally, MSR is a quite good illustration of how inappropriate experimental procedure, may lead to erroneous interpretations on the animals’ cognitive abilities. The fact mirror self-recognition is so automatic and effortless for most of us that has probably encouraged an anthropocentric bias in the design of experimental procedure. Swartz in [116] already underlined how “a single method of measurement may contain sources of measurement error that are unique to that method”. Yet, multiplying the methods of measurement would be unfruitful if the construction of the tests is still anthropocentrically based and keeps on favoring the human-like species. To conclude, future reflection on the experimental approach in comparative cognition, which is still heavily anthropocentric, may help to move away from our preconceptions and would certainly shed new light on animal cognitive mechanisms that were, until then, confined to humans. Would this perspective help researchers working on comparative cognition to live happily ever after? To be continued....

Acknowledgements

I would like to thank the animal care and the facilities teams of the Yerkes National Primate Research Center in Atlanta, the Wolfgang Kohler Primate Center at the Leipzig Zoo, the

Nuremberg Zoo, and the station of primatology of Rousset, for their support. I would like to thank Joel Fagot, Josep Call and William Hopkins for their hospitality and complete cooperation in the experiments. I am very grateful to Marie Montant for providing her smart comments, and to Ethan Conia, of the Saint-Claude facility team, for his help in the finalization of the chapter.

Author details

Parron Carole

Address all correspondence to: carole.parron@univ-amu.fr

Laboratory of Cognitive Psychology, National Center of Scientific Research (CNRS)-
Université d'Aix-Marseille, France

References

- [1] Morin A, DeBlois S. Gallup's mirrors: More than an operationalization of self-awareness in primates? *Psychological Reports*. 1989;**65**(1):287-291
- [2] Gallup GG. Chimpanzees: Self-recognition. *Science*. 1970;**167**(3914):86-87
- [3] Gallup GG. Mirror-image stimulation. *Psychological Bulletin*. 1968;**70**:782-793
- [4] Gallup GG. Self-awareness and the emergence of mind in primates. *American Journal of Primatology*. 1982;**2**(3):237-248
- [5] Gallup GG. Self-awareness and the evolution of social intelligence. *Behavioural Processes*. 1998;**42**(2):239-247
- [6] Premack D, Woodruff G. Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*. 1978;**1**(4):515-526
- [7] Savage-Rumbaugh ES, Rumbaugh DM, Boysen S. Symbolic communication between two chimpanzees (*Pan troglodytes*). *Science*. 1978;**201**(4356):641-644
- [8] Povinelli DJ, Eddy TJ. Chimpanzees: Joint visual attention. *Psychological Science*. 1996;**7**(3):129-135
- [9] Swartz KB. Self-recognition in nonhuman primates. In: Greenberg G, Haraway M, editors. *Comparative Psychology: A Handbook*. New York: Garland; 1998. pp. 849-855
- [10] Hart D, Karmel MP. Self-awareness and self-knowledge in humans, apes, and monkeys. In: Russon AE, Bard KA, Parker ST, editors. *Reaching into Thought: The Minds of the Great Apes*. New York: Cambridge University Press; 1996. pp. 325-347
- [11] Bard KA, Todd BK, Bernier C, Love J, Leavens DA. Self-awareness in human and chimpanzee infants: What is measured and what is meant by the mark and mirror test? *Infancy*. 2006;**9**(2):191-219

- [12] Anderson JR, Gallup GG. Self-recognition in nonhuman primates: Past and future challenges. In: Haug M, Whalen RF, editors. *Animal Models of Human Emotion and Cognition*. Washington, DC: American Psychological Association; 1999. pp. 175-194
- [13] Lin AC, Bard KA, Anderson JR. Development of self-recognition in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*. 1992;**106**(2):120-127
- [14] Hyatt CW, Hopkins W. Self-awareness in bonobos and chimpanzees: A comparative perspective. In: Parker ST, Mitchell R, Boccia ML, editors. *Self-Awareness in Animals and Humans: Developmental Perspectives*. Cambridge University Press New-York. 1994. pp. 248-253
- [15] Suárez SD, Gallup GG. Self-recognition in chimpanzees and orangutans, but not gorillas. *Journal of human evolution*. 1981;**10**(2):175-188
- [16] Swartz KB, Evans S. Social and cognitive factors in chimpanzee and gorilla mirror behavior and self-recognition. In: Parker ST, Mitchell R, Boccia ML, editors. *Self-Awareness in Animals and Humans: Developmental Perspectives*. New-York: Cambridge University Press; 1994. pp. 189-206
- [17] Ledbetter DH, Basen JA. Failure to demonstrate self-recognition in gorillas. *American Journal of Primatology*. 1982;**2**(3):307-310
- [18] Parker ST. Incipient mirror self-recognition in zoo gorillas and chimpanzees. In: Parker ST, Mitchell R, Boccia ML, editors. *Self-Awareness in Animals and Humans: Developmental Perspectives*. New-York: Cambridge University Press; 1994. pp. 301-307
- [19] Patterson FGP, Cohn RH. Self-recognition and self-awareness in Lowland Gorillas. In: Parker ST, Mitchell R, Boccia ML, editors. *Self-Awareness in Animals and Humans: Developmental Perspectives*. New-York: Cambridge University Press; 1994. pp. 273-290
- [20] Posada S, Colell M. Another gorilla (*Gorilla gorilla gorilla*) recognizes himself in a mirror. *American Journal of Primatology*. 2007;**69**(5):576-583
- [21] Allen M, Schwartz BL. Mirror self-recognition in a gorilla (*Gorilla gorilla gorilla*). *Journal of Integrative Biosciences*. 2008;**5**:19-24
- [22] Nicholson IS, Gould JE. Mirror mediated object discrimination and self-directed behavior in a female gorilla. *Primates*. 1995;**36**(4):515-521
- [23] Shillito DJ, Gallup GG, Beck BB. Factors affecting mirror behaviour in western lowland gorillas, *Gorilla gorilla*. *Animal Behaviour*. 1999;**57**(5):999-1004
- [24] Shumaker RW, Swartz KB. When traditional methodologies fail: Cognitive studies of great apes. In: Bekoff M, Allen C, Burghardt GM, editors. *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition*. Cambridge, MA: MIT Press; 2002. pp. 335-343
- [25] Anderson JR, Gallup GG. Which primates recognize themselves in mirrors? *PLoS Biology*. 2011;**9**(3):e1001024

- [26] Anderson JR. The development of self-recognition: A review. *Developmental Psychobiology*. 1984;**17**(1):35-49
- [27] Anderson JR. The monkey in the mirror: A strange conspecific. In: Parker ST, Mitchell R, Boccia ML, editors. *Self-Awareness in Animals and Humans: Developmental Perspectives*. New-York: Cambridge University Press; 1994. pp. 315-329
- [28] Suarez SD, Gallup GG. Social responding to mirrors in rhesus macaques (*Macaca mulatta*): Effects of changing mirror location. *American Journal of Primatology*. 1986;**11**(3):239-244
- [29] Gallup GG, Suarez SD. Social responding to mirrors in rhesus monkeys (*Macaca mulatta*): Effects of temporary mirror removal. *Journal of Comparative Psychology*. 1991;**105**(4):376-379
- [30] Neiworth JJ, Anders SL, Parsons RR. Tracking responses related to self-recognition: A frequency comparison of responses to mirrors, photographs, and videotapes by cotton top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*. 2001;**15**(4):432-438
- [31] Anderson JR, Kuroshima H, Paukner A, Fujita K. Capuchin monkeys (*Cebus apella*) respond to video images of themselves. *Animal Cognition*. 2009;**12**(1):55-62
- [32] Heschl A, Burkart J. A new mark test for mirror self-recognition in non-human primates. *Primates*. 2006;**47**(3):187-198
- [33] Roma PG, Silberberg A, Huntsberry ME, Christensen CJ, Ruggiero AM, Suomi SJ. Mark tests for mirror self-recognition in capuchin monkeys (*Cebus apella*) trained to touch marks. *American Journal of Primatology*. 2007;**69**(9):989-1000
- [34] Anderson JR, Roeder JJ. Responses of capuchin monkeys (*Cebus apella*) to different conditions of mirror-image stimulation. *Primates*. 1989;**30**(4):581-587
- [35] Paukner A, Anderson JR, Fujita K. Reactions of capuchin monkeys (*Cebus apella*) to multiple mirrors. *Behavioural Processes*. 2004;**66**(1):1-6
- [36] Macellini S, Ferrari PF, Bonini L, Fogassi L, Paukner A. A modified mark test for own-body recognition in pig-tailed macaques (*Macaca nemestrina*). *Animal Cognition*. 2010;**13**(4):631-639
- [37] Rajala AZ, Reininger KR, Lancaster KM, Populin LC. Rhesus monkeys (*Macaca mulatta*) do recognize themselves in the mirror: Implications for the evolution of self-recognition. *PLoS One*. 2010;**5**(9):e12865
- [38] Anderson JR, Gallup GG. Do rhesus monkeys recognize themselves in mirrors? *American Journal of Primatology*. 2011;**73**(7):603-606
- [39] Chang LJ, Gianaros PJ, Manuck SB, Krishnan A, Wager TD. A sensitive and specific neural signature for picture-induced negative affect. *PLoS Biology*. 2015;**13**(6):e1002180
- [40] Toda K, Platt ML. Animal cognition: Monkeys pass the mirror test. *Current Biology*. 2015;**25**(2):R64-R66
- [41] Huttunen AW, Adams GK, Platt ML. Can self-awareness be taught? Monkeys pass the mirror test-again. *Proceedings of the National Academy of Sciences*. 2017;**114**(13):3281-3283

- [42] Anderson JR, Gallup GG. Mirror self-recognition: A review and critique of attempts to promote and engineer self-recognition in primates. *Primates*. 2015;**56**(4):317-326
- [43] Chang L, Zhang S, Poo MM, Gong N. Spontaneous expression of mirror self-recognition in monkeys after learning precise visual-proprioceptive association for mirror images. *Proceedings of the National Academy of Sciences*. 2017;**114**(12):3258-3263
- [44] Swartz KB. What is mirror self-recognition in nonhuman primates, and what is it not? *Annals of the New York Academy of Sciences*. 1997;**818**(1):65-71
- [45] Swartz KB, Evans S. Not all chimpanzees (*Pan troglodytes*) show self-recognition. *Primates*. 1991;**32**(4):483-496
- [46] Povinelli DJ, Rulf AB, Landau KR, Bierschwale DT. Self-recognition in chimpanzees (*Pan troglodytes*): Distribution, ontogeny, and patterns of emergence. *Journal of Comparative Psychology*. 1993;**107**(4):347-372
- [47] Gallup GG. Self-recognition: Research strategies and experimental design. In: Parker ST., Mitchell R, Boccia L., editors. *Self-Awareness in Animals and Humans: Developmental Perspectives*. New-York: Cambridge University Press; 1994. pp. 35-50
- [48] De Veer MW, van den Bos R. A critical review of methodology and interpretation of mirror self-recognition research in nonhuman primates. *Animal Behaviour*. 1999;**58**:459-468
- [49] Yamagiwa J. Functional analysis of social staring behavior in an all-male group of mountain gorillas. *Primates*. 1992;**33**(4):523-544
- [50] De Waal FBM, Luttrell LM. Toward a comparative socioecology of the genus *Macaca*: Different dominance styles in rhesus and stumptail monkeys. *American Journal of Primatology*. 1989;**19**:83-109
- [51] De Waal FBM. *Chimpanzee Politics: Power and Sex among Apes*. New York: Harper & Row; 1982. 223 p
- [52] Heyes CM. Social learning in animals: Categories and mechanisms. *Biological Reviews*. 1994;**69**(2):207-231
- [53] Heyes CM. Self-recognition in primates: Further reflections create a hall of mirrors. *Animal Behaviour*. 1995;**50**(6):1533-1542
- [54] Fagot J, Martin-Malivel J, Dépy D. What is the evidence for an equivalence between objects and pictures in birds and nonhuman primates? In: Fagot J, editor. *Picture Perception in Animals*. Psychology Press Ltd, East Sussex; 2000. pp. 295-320
- [55] Perrett DJ, Mistlin AJ. Perception of facial characteristics by monkeys. In: Stebbins WC, Berkley MA, editors. *Comparative Perception. Vol. II. Complex Signals*. New York: John Wiley & Sons; 1990. pp. 187-213
- [56] Wright PC. The nocturnal primate niche in the new world. *Journal of Human Evolution*. 1989;**18**(7):635-658

- [57] Sackett GP. Monkeys reared in isolation with pictures as visual input: Evidence for an innate releasing mechanism. *Science*. 1966;**154**(3755):1468-1473
- [58] Bovet D, Vauclair J. Functional categorization of objects and of their pictures in baboons (*Papio anubis*). *Learning and Motivation*. 1998;**29**(3):309-322
- [59] Parron C, Call J, Fagot J. Behavioural responses to photographs by pictorially naive baboons (*Papio anubis*), gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *Behavioural Processes*. 2008;**78**(3):351-357
- [60] D'amato MR, Van Sant P. The person concept in monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes*. 1988;**14**(1):43-56
- [61] Martin-Malivel J, Fagot J. Perception of pictorial human faces by baboons: Effects of stimulus orientation on discrimination performance. *Learning & Behavior*. 2001;**29**(1):10-20
- [62] Martin-Malivel J, Mangini MC, Fagot J, Biederman I. Do humans and baboons use the same information when categorizing human and baboon faces? *Psychological Science*. 2006;**17**(7):599-607
- [63] Winner E, Ettliger G. Do chimpanzees recognize photographs as representations of objects? *Neuropsychologia*. 1979;**17**(3):413-420
- [64] Herrmann E, Melis AP, Tomasello M. Apes' use of iconic cues in the object-choice task. *Animal Cognition*. 2006;**9**(2):118
- [65] Pokorny JJ, de Waal FB. Monkeys recognize the faces of group mates in photographs. *Proceedings of the National Academy of Sciences*. 2009;**106**(51):21539-21543
- [66] Pokorny JJ, de Waal F. Face recognition in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*. 2009;**123**(2):151-160
- [67] Micheletta J, Whitehouse J, Parr LA, Waller BM. Facial expression recognition in crested macaques (*Macaca nigra*). *Animal Cognition*. 2015;**18**(4):985-990
- [68] Truppa V, Spinozzi G, Stegagno T, Fagot J. Picture processing in tufted capuchin monkeys (*Cebus apella*). *Behavioural Processes*. 2009;**82**(2):140-152
- [69] Rumbaugh DM, Warner H, Glasersfeld E. The Lana project: Origin and tactics. In: Rumbaugh DM, editor. *Language Learning by a Chimpanzee*. New York: Academic Press; 1977. pp. 87-90
- [70] Savage-Rumbaugh ES, Rumbaugh DM, Smith ST, Lawson J. Reference: The linguistic essential. *Science*. 1980;**210**(4472):922-925
- [71] Savage-Rumbaugh ES. *Ape Language: From Conditioned Response to Symbol*. New York: Columbia University Press; 1986. 433 p
- [72] Matsuzawa T. The Ai project: Historical and ecological contexts. *Animal Cognition*. 2003;**6**(4):199-211
- [73] Matsuzawa T. Form perception and visual acuity in a chimpanzee. *Folia Primatologica*. 1990;**55**(1):24-32

- [74] Itakura S. Recognition of line-drawing representations by a chimpanzee (*Pan troglodytes*). The Journal of general psychology. 1994;**121**(3):189-197
- [75] Tanaka M. Development of the visual preference of chimpanzees (*Pan troglodytes*) for photographs of primates: Effect of social experience. Primates. 2007;**48**(4):303-309
- [76] Bartus RT, Dean III RL, Fleming DL. Aging in the rhesus monkey: Effects on visual discrimination learning and reversal learning. Journal of Gerontology. 1979;**34**(2):209-219
- [77] Mell T, Heekeren HR, Marschner A, Wartenburger I, Villringer A, Reischies FM. Effect of aging on stimulus-reward association learning. Neuropsychologia. 2005;**43**(4):554-563
- [78] Close J, Call J. From colour photographs to black-and-white line drawings: An assessment of chimpanzees' (*Pan troglodytes*) transfer behaviour. Animal Cognition. 2015;**18**(2):437-449
- [79] Malone DR, Tolan JC, Rogers CM. Cross-modal matching of objects and photographs in the monkey. Neuropsychologia. 1980;**18**(6):693-697
- [80] Tolan JC, Rogers CM, Malone DR. Cross-modal matching in monkeys: Altered visual cues and delay. Neuropsychologia. 1981;**19**(2):289-300
- [81] Humphrey NK. Vision in a monkey without striate cortex: A case study. Perception. 1974;**3**(3):241-255
- [82] Fagot J, Thompson RK, Parron C. How to read a picture: Lessons from nonhuman primates. Proceedings of the National Academy of Sciences. 2010;**107**(2):519-520
- [83] DeLoache JS, Pierroutsakos SL, Uttal DH, Rosengren KS, Gottlieb A. Grasping the nature of pictures. Psychological Science. 1998;**9**(3):205-210
- [84] DeLoache JS. Becoming symbol-minded. Trends in Cognitive Sciences. 2004;**8**(2):66-70
- [85] Benhar EE, Carlton PL, Samuel D. A search for mirror-image reinforcement and self-recognition in the baboon. In: Kondo S, Kawai M, Ehara S, editors. Contemporary Primatology: Proceedings of the 5th International Congress of Primatology; New York: Karger; 1975. pp. 202-298
- [86] Menzel EW, Savage-Rumbaugh ES, Lawson J. Chimpanzee (*Pan troglodytes*) spatial problem solving with the use of mirrors and televised equivalents of mirrors. Journal of Comparative Psychology. 1985;**99**(2):211-217
- [87] Law LE, Lock AJ. Do gorillas recognize themselves on television. In: Parker ST, Mitchell R, Boccia ML, editors. Self-Awareness in Animals and Humans: Developmental Perspectives. New-York: Cambridge University Press; 1994. pp. 308-312
- [88] Parr LA, Winslow JT, Hopkins WD, de Waal F. Recognizing facial cues: Individual discrimination by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). Journal of Comparative Psychology. 2000;**114**(1):47-60
- [89] Troseth GL, Pierroutsakos SL, DeLoache JS. From the innocent to the intelligent eye: The early development of pictorial competence. Advances in Child Development and Behavior. 2004;**32**:1-35

- [90] Pierroutsakos SL, DeLoache JS. Infants' manual exploration of pictorial objects varying in realism. *Infancy*. 2003;**4**(1):141-156
- [91] DeLoache JS, Uttal DH, Pierroutsakos SL. What's up? The development of an orientation preference for picture books. *Journal of Cognition and Development*. 2000;**1**(1):81-95
- [92] DeLoache JS, Burns NM. Early understanding of the representational function of pictures. *Cognition*. 1994;**52**(2):83-110
- [93] Robinson EJ, Nye R, Thomas GV. Children's conceptions of the relationship between pictures and their referents. *Cognitive Development*. 1994;**9**(2):165-191
- [94] Flavell JH, Flavell ER, Green FL, Korfmacher JE. Do young children think of television images as pictures or real objects? *Journal of Broadcasting & Electronic Media*. 1990;**34**(4):399-419
- [95] Rochat P. Five levels of self-awareness as they unfold early in life. *Consciousness and Cognition*. 2003;**12**(4):717-731
- [96] Robert S. Ontogeny of mirror behavior in two species of great apes. *American Journal of Primatology*. 1986;**10**(2):109-117
- [97] Anderson JR. Mirror-mediated finding of hidden food by monkeys (*Macaca tonkeana* and *M. fascicularis*). *Journal of Comparative Psychology*. 1986;**100**(3):237-242
- [98] Itakura S. Mirror guided behavior in Japanese monkeys (*Macaca fuscata fuscata*). *Primates*. 1987;**28**(2):149-161
- [99] Itakura S. Use of a mirror to direct their responses in Japanese monkeys (*Macaca fuscata fuscata*). *Primates*. 1987;**28**(3):343-352
- [100] Iriki A, Tanaka M, Obayashi S, Iwamura Y. vSelf-images in the video monitor coded by monkey intraparietal neurons. *Neuroscience Research*. 2001;**40**(2):163-173
- [101] Mitchell RW. Kinesthetic-visual matching, imitation, and self-recognition. In: Bekoff M, Allen C, Burghardt G, editors. *The Cognitive Animal*. Cambridge, MA: MIT Press; 2002. pp. 345-351
- [102] Amsterdam B. Mirror self-image reactions before age two. *Developmental Psychobiology*. 1972;**5**(4):297-305
- [103] Nielsen M, Dissanayake C, Kashima Y. A longitudinal investigation of self-other discrimination and the emergence of mirror self-recognition. *Infant Behavior and Development*. 2003;**26**(2):213-226
- [104] Bard KA, Myowa-Yamakoshi M, Tomonaga M, Tanaka M, Costall A, Matsuzawa T. Group differences in the mutual gaze of chimpanzees (*Pan troglodytes*). *Developmental Psychology*. 2005;**41**(4):616-624
- [105] Povinelli DJ. The unduplicated self. In the self. In: Rochat P, editor. *Early Infancy*. Amsterdam, The Netherlands: North-Holland-Elsevier; 1995. pp. 162-192
- [106] Povinelli DJ. The self: Elevated in consciousness and extended in time. In: Moore C, Lemmon K, editors. *The Self in Time: Developmental Perspectives*. Mahwah, New Jersey: Lawrence Erlbaum Associates, Inc.; 2001. pp. 79-96

- [107] Hayes KJ, Nissen CH. Higher mental functions of a home-raised chimpanzee. *Behavior of Nonhuman Primates: Modern Research Trends*. 1971;**4**:59-115
- [108] Patterson FG. Conversations with a gorilla. *National Geographic*. 1978;**154**:438-465
- [109] Itakura S. A chimpanzee with the ability to learn the use of personal pronouns. *The Psychological Record*. 1992;**42**(2):157-172
- [110] Wood S, Moriarty KM, Gardner BT, Gardner RA. Object permanence in child and chimpanzee. *Learning & Behavior*. 1980;**8**(1):3-9
- [111] Natale F, Antinucci F, Spinozzi G, Potí P. Stage 6 object concept in nonhuman primate cognition: A comparison between gorilla (*Gorilla gorilla gorilla*) and Japanese macaque (*Macaca fuscata*). *Journal of Comparative Psychology*. 1986;**100**(4):335-339
- [112] Piaget J. *The Construction of Reality in the Child*. New York: Basic Books; 1954 p. 386
- [113] Natale F, Antinucci F. Stage 6 object-concept and representation. In: Antinucci F, editor. *Cognitive Structure and Development in Nonhuman Primates*. Hillsdale (NJ): Lawrence Erlbaum; 1989. pp. 97-112
- [114] Gopnik A, Meltzoff AN. Minds, bodies and persons: Young children's understanding of the self and others as reflected in imitation and "theory of mind" research. In: Parker ST, Mitchell R, Boccia ML, editors. *Self-Awareness in Animals and Humans: Developmental Perspectives*. Cambridge University Press New-York. 1994. pp. 166-186
- [115] Povinelli DJ. What chimpanzees (might) know about the mind. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors. *Chimpanzee cultures*, Cambridge, MA: Harvard University Press. 1994. pp. 285-300
- [116] Swartz KB. The concept of mind in comparative psychology. *Annals of the New York Academy of Sciences*. 1990;**602**:105-111