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Siamangs (Hylobates syndactylus) Recognize their Mirror Image

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The ability to recognize oneself in the mirror is assumed to represent an important step towards a higher level of animal intelligence that, ultimately, can lead to human-like self-awareness and empathy. Even though rarely successful in the classical mark test, the siamang's spontaneous behavior in front of the mirror, a visually controlled manipulation of its face, suggests that it interprets the reflection as belonging to itself. As a consequence, the cognitive status of the gibbons may need a serious reevaluation since, in total, at least three species (*Hylobates syndactylus, H. gabriellae, H. leucogenys*) seem to be capable of self-recognition. Their, nonetheless, weak interest in the mirror image is hypothesized to be caused by the comparatively low level of sexual competition in the lesser apes.

Within the order of primates an apparently sharp cognitive divide separates monkeys from apes. This difference concerns practically all categories of mental ability, such as object permanence (Natale et al., 1986; de Blois, Novak, & Bond, 1998), spatial orientation via mental maps (Boesch & Boesch, 1984; Noser & Byrne, 2007), analogical reasoning (Thompson & Oden, 2000), counting (Matsuzawa, 1985; Boysen, 1997), causal understanding (Visalberghi & Limongelli, 1994), imitation (Byrne & Tanner, 2006), symbolic communication (Pika, Liebal, Call, & Tomasello, 2005), and, finally, the existence of true personality traits (Patterson & Gordon, 1993; Uher, Asendorpf, & Call, 2008), all features which monkeys and prosimians seem to lack completely. The vast majority of researchers in the field share this view in one form or another (for the opposite argumentation, see Tomasello & Call, 1997). However, the situation concerning the behavior in front of a mirror, commonly held to be an important criterion for assessing an animal's intelligence, is still an undecided one. Generally, gibbons (*Hylobates sp.*) are considered to be non-self-recognizers when confronted with their mirror image (cf. Rowe, 1996, p. 207). This is explained by the fact that, so far, most investigations except one (Ujhelvi, Merker, Buk, & Geissmann, 2000), emphasize the animals' apparent basic inability in this regard (Lethmate & Dücker, 1973; Hyatt, 1998; Inoue-Nakamura, 1997; Suddendorf & Collier-Baker, 2009). This finding is puzzling given the commonly accepted taxonomic classification of gibbons into the category of apes or hominoids, together with chimpanzees, bonobos, orangutans and gorillas, which meanwhile

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have all been shown to be able to recognize themselves in the mirror. By contrast, monkeys revealed to be true non-self-recognizers, even after an extended (e.g., lifetime) exposure to mirrors (Anderson, 1983; Suarez & Gallup, 1986).

However, gibbons do behave significantly differently from monkeys in one important respect. This difference concerns locomotion. While monkeys usually move quadrupedally through the canopy, gibbons and apes instead maintain an upright body posture (knuckle-walking in the African great apes is a derived trait with the purpose of enhancing speed on the ground). We hypothesize that this is also the main reason why apes differ cognitively from monkeys. The difference may have to do with an enlarged degree of visual self-awareness when upright. While the intelligence of monkeys, despite remarkable achievements in some species (see capuchins), basically remained limited to the use of their hands. apes evolved a new method of consciously controlling the movements of the whole body. Thereby, the first phylogenetic step may have been an initial visual control of the movements of the feet. Gibbons, in contrast to monkeys, show this ability when grasping and manipulating objects with the help of their toes (e.g., for eating a fruit, Fig. 1). In this way, the rest of the body, at least as far as the directly visible, came increasingly under the control of the behaving animal and laid the basis for a more comprehensive level of self-awareness. The underlying proximate mechanism that was necessary to allow this development was already present in the monkeys' visual control of the hand: the ability to perceive contingency, understood as the degree of synchrony between the internally given command to perform a given movement (motor output) and the accompanying visual feedback coming through the eyes (sensory input). Such a process of "kinesthetic-visual matching" between the (felt) movements of the subject's body and the (seen) movements of the reflection appears to be essential for successful mirror selfrecognition (Mitchell, 1997). Hence, only an animal that has the capability to visually guide not only the movements of its hands (as monkeys do), but also those of the whole body (as monkeys can not) will be able to interpret the movements of the perfectly contingent mirror image as stemming from its own actions. The finding that human infants must first learn to walk independently (between 10 and 16 months; Bayley, 1993) before they become able to recognize themselves in the mirror (between 15 and 24 months; Bard, Todd, Bernier, Love, & Leavens, 2006), bears this out. Following our hypothesis, the gibbons, too, by having been the first primates that evolved an obligatorily upright locomotion style (for the close functional proximity to human bipedality, see Vereecke, D'Août, & Aerts, 2006), should show clear signs of a beginning self-awareness. To test this hypothesis, we chose the largest of the known gibbon species, the siamang (Hylobates syndactylus; body weight: 10 - 15 kg, brain: 120 g), for our investigation.





Figure 1. Male siamang (Hylobates syndactylus) eating an apple with his right foot.

Method

Subjects and Facility

It was approximately one year before the present investigation that both animals (Nelson, 5 year old male, from a zoo in the Netherlands; Yala, 5 year old female, from Switzerland) came to the zoological garden of Herberstein in Austria where they met for the first time and slowly began to form a pair. For the duration of the study a permanent mirror $(50 \times 70 \text{ cm})$ was mounted on the wall of the animals' home cage $(35 \text{ m}^2, \text{height: } 3 \text{ m})$. From there a transparent swinging door led to a spacious outer area with natural vegetation (wooded area of approx. 1500 m²) that was accessible 24 hours a day, allowing the animals to move freely between both sections. The proposal for this study was reviewed by the management of the zoo of Herberstein whose guidelines concerning research with caged animals follow the recommendations of the OZO (Österreichische Zoo Organisation, www.ozo.at).

Mark Test

For reasons of animal welfare we refrained from anesthetizing the animals. After habituation to the mirror (2 days) we marked the completely black animals by surreptitiously applying white chocolate cream to their forehead while feeding them with some titbit (peanut) through the cage's wire mesh. We consciously chose chocolate as a marking substance to a) avoid false negative results caused by a lack of motivation (like humans, the animals love chocolate) and, b) provoke true negative results (i.e. attempts to get to the chocolate on the reflection) if there was a real lack of understanding (for details, see Heschl & Burkart, 2006). To prevent any cue from the odor, four hidden containers with chocolate cream were placed in such a way as to produce a spatial distribution of the smell as homogenous as possible. No disturbing influence of olfaction was observed (e.g., searching for one of the hidden containers). The test was conducted on day 3, after the disappearance of social reactions towards the mirror and the transition to investigative behavior in the course of days 1 and 2 (tactile exploration of mirror, contingency testing with regard to reflection). Each animal was tested separately.

We compared the behavior of the animals with and without the presence of the mirror, and got the same negative result, i.e. no mark-directed reactions, as did another recent study (Suddendorf & Collier-Baker, 2009). Since it is not inconceivable that the manifestation of a complex psychological capacity such as mirror self-recognition would be a feature depending on several hardly controllable factors (unknown environmental influences, social stress, motivation, etc.), we changed our strategy. We left the mirror in the cage of the animals and observed their behavior for a prolonged period of time. By doing so we concentrated on the ultimately decisive behavior exclusively and ignored the many other parameters one could additionally assess (e.g., frequency and duration of looking into mirror). Only when the subject showed a behavior that could be clearly identified as being simultaneously self-directed and mirror-mediated was it counted as self-recognizing.

Data Collection during Long-Term Observation

Mirror self-recognition (MSR): the relevant criterion for discerning mere self-reference (e.g., scratching in the presence of the mirror) from true self-recognition was defined by the orientation of the animal's gaze. Such an understanding can be deduced from the fact that in order to manipulate a part of the face not visible without the mirror in a directed, i.e. visually guided, way, it is necessary for the animal to concentrate on the face in the mirror and, at the same time, interpret it as that of one's own. This becomes particularly evident when one compares such a behavior with cases of normal self-manipulation of the face, where gaze, since having no target, is usually permanently rambling around (see documentary by Anderson, 1997). Hence only those cases where the animal continually monitored its activity in the mirror during the manipulation of a particular part of its head or face with its hand were accepted as positive. In addition, to avoid possible chance effects, the searched for behavior had to last for at least 3 seconds (for a detailed discussion of methodology, see Bard et al., 2006). Three areas were defined as the targets of manipulation: lower face (chin, mouth, nose), middle face (cheeks, eyes, ears), and upper face (eyebrows, forehead, hair). Contingency testing that merely consists of doing something (e.g., moving head or hand back and forth) and simultaneously observing the effect it produces in the mirror, without at the same time touching one's own body, was not counted as a proof of self-recognition because it lacks a clear reference to the self and thus can easily be confounded with socially motivated behavior. To improve the estimation of gaze direction a one-way mirror (50 x 70 cm) was used that allowed one of the two observers to directly check the orientation of the subject's eyes. An observation period of 2 h each day was randomly selected between 9 a.m. and 4 p.m. (random number algorithm: HP-15C). Independent observations of the relevant behavior were taken by a) one observer looking through the one-way mirror and b) a second observer standing outside the cage (position with lateral view on test animal when in front of mirror). The positions of the two observers (behind mirror, outside cage) were exchanged daily. The duration of the behavior was determined with a stopwatch (minimal length: 3 s). Only those observations that were interpreted by both observers as positive (interobserver agreement: 100%; Cohen's kappa = 1.00) were accepted as valid. The total investigation covered 90 days.

Results

As already indicated in the method section the animals failed in the mark test (day 3). During 30 minutes, not a single attempt to remove the conspicuous mark was observed even though the animals were kept in a small enclosure (approx. 6 m², height: 2.5 m) around the mirror, confronting them repeatedly with their altered appearance. However, contrary to monkeys (Heschl & Burkart, 2006), no true negative reaction, i.e. any attempt to lick the marking substance (white chocolate cream) from the mirror image, occurred either (in a separate control test, the animals instantaneously licked chocolate from the surface of the mirror, thereby demonstrating that they are very well able to understand the difference between a real object and its reflection). The data from the subsequent long-term observation (Fig. 2) show that the animals nevertheless do exhibit truly self-referring behaviors in front of the mirror (Table 1), even though at a rather low frequency (sum total for male: N = 7, female: N = 5). During this time, the temporal distribution of the reactions shown by both sexes appears to be quite even, without any significant tendency towards an increase of interest in their

reflection over the course of the observation period. However, after the birth of a young by the female on day 61, no more reactions occurred in either sex (X^2 (1) male: p < 0.01, female: p < 0.05, together: p < 0.001).

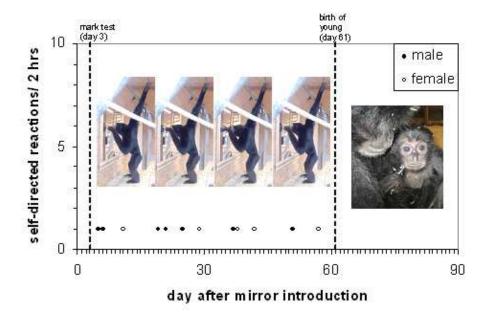


Figure 2. Frequency of spontaneous self-directed behavior of a pair of siamangs mediated by the reflection in the mirror. Only one self-directed reaction occurred for each animal during a particular session (male: 7 reactions, female: 5 reactions). After the birth of a young (day 61) no more reactions occurred. The inserted sequence of video pictures (from video 2) shows that the animal's gaze remains fixed on the mirror image during the whole behavior pattern (duration: > 3 s), the decisive criterion for assuming self-recognition.

A comparison of the targets of the observed self-directed reactions, which in general all belonged to the category of self-grooming behavior, revealed a pattern that suggests a slightly greater interest of the male for the lower parts of the face (6 lower face : 2 middle face : 1 upper face), as compared to the female, who seemed to be more interested in the upper parts of the face (2 lower face : 2 middle face : 4 upper face). The number of targets was greater for both sexes (male: 9, female: 8) than the number of mere reactions (male: 7, female: 5) since in 5 cases the reaction included two targets (e.g., lower + middle face). The mean total duration of the exhibited behavior was 4.4 ± 0.7 s for the male and 5.1 ± 2.1 s for the female. A detailed description of the observed behavior patterns is given in Table 1.

Table 1Mirror-mediated self-directed behavior shown by a pair of siamangs during a 3 month observationperiod.

Day 5	Male, after moving away from a position parallel to mirror, suddenly turns back and, from a standing position, scratches area of nose and right cheek; 4.8 s (see video 2)
Day 6	Male takes a suspensory position (rope) in front of mirror for some seconds, then approaches mirror and, from a standing position, scratches area of eyebrows; 3.3 s
Day 11	Female sits down in front of mirror on bale of straw and looks directly into mirror; after a while she touches area of eyebrows and repeatedly (3x) skims with fingers over hair; 6.7 s
Day 19	Male approaches mirror directly from rapidly brachiating through cage, stops abruptly in front of mirror and, from a standing position, intensively scratches mouth and nose area; 4.2 s
Day 21	Male, from a suspensory position (rope) in front of mirror, scratches mouth area from distance; 5.8 s
Day 25	Male and female sit in front of mirror (on bale of straw), both looking directly into mirror; after a while male approaches mirror and starts scratching mouth; 3.6 s
Day 29	Female, after having spent some time in a lying position on bale of straw, slowly sits up, looks into mirror and scratches mouth and left cheek; 3.5 s
Day 37	Male looks into mirror from a suspensory position (rope), seems to check his appearance by visually scanning reflection; after a while he approaches mirror and scratches left ear; 4.7 s
Day 38	Female, after having rested for a while on bale of straw, sits up in front of mirror and starts grooming nose and area of eyebrows; 6.4 s
Day 42	Female sits in front of mirror (on bale of straw), observes male moving around in cage through mirror, then touches hair and eyebrow area repeatedly; 3.9 s
Day 51	Male takes a suspensory position (rope) in front of mirror, swallows piece of banana and then removes a small particle (food leftover) from nose; 4.2 s
Day 57	Female sits on bale of straw in front of mirror and looks into mirror; after a while she scratches left cheek and then slowly skims over hair with help of fingers (2x); 4.9 s

Discussion

Given that, by relying on basically the same proximal mechanism (use of reflection in mirror for guiding self-directed behavior), any kind of mirrormediated, self-directed behavior is as valid a sign of self-recognition as is a successful reaction in the mark test, it appears justifiable to treat siamangs as potentially self-conscious animals, along with great apes (Gallup, 1970), dolphins (Reiss & Marino, 2001), elephants (Plotnik et al., 2006) and, possibly, magpies (Prior, Schwarz, & Güntürkün, 2008). Such a conclusion is corroborated by the fact that only those primate species that show mirror-mediated, self-directed behaviors (chimpanzee: 45% of tested animals, N = 163; bonobo: 50%, N = 16; orang-utan: 85%, N = 6; gorilla: 29%, N = 21) also have the potential to be successful in the mark test (chimpanzee: 43%, N = 97; bonobo; not tested; orangutan: 50%, N = 6; gorilla: 31%, N = 13; data from Swartz, Sarauw, & Evans, 1999). By contrast, monkeys have so far shown neither any self-directed behaviors that would have been demonstrably mediated by the mirror, nor have they successfully passed a single mark test, even when being trained with special approaching techniques (Anderson & Roeder, 1989; Roma et al., 2007). However, the siamangs' behavior in front of the mirror is not as surprising as one would think since there already exists at least one report of a successful mark test with a 1.5 year old, hand-reared individual dated from 1980¹. A few months after the completion of the present study, we conducted an additional mark test with the same animals plus their meanwhile 1.5 year old offspring. As in the first test (day 3) the adult animals seemed not to take any notice of their altered appearance (red mark on nose) during 60 minutes of observation, but now the young animal showed one clearly positive reaction: it first noticed the change in the appearance of its mother, then noticed the same change of its own appearance in the mirror and finally began removing the disturbing mark with the help of the reflection (video 4: mother in the front, young behind, male in the background; mirror leftmost). Hence, in total (present study; report about Fadoro; Suddendorf, & Collier-Baker, 2009), the siamangs' performance in front of the mirror amounts to 45% selfdirected reactions and 18% successful mark tests of all individuals tested (N = 11) which comes close to some values for the great apes (see above).

That the siamangs seem to be particularly intelligent is corroborated by the fact that they have recently been shown to be capable of intentional communication via body gestures and this at the level of the great apes (Pika et al., 2005). Another study just demonstrated that their understanding of object permanence achieves Piaget's stage 6 (highest), which includes the solution of

¹ "Fadoro, during two consecutive 15-min observation periods before mark application, the first without and the second with a 50×70 cm mirror present, never touched his head at any point but behaved as usual. Nor did he touch his head during a 10-min observation period in the absence of the mirror after having been surreptitiously marked on his forehead. After reintroduction of the mirror, Fadoro approached it, glanced into the mirror, arrested his movements for a few seconds, then wiped his hand over his marked forehead removing the greater part of the mark, looked at his hand and then into the mirror, and resumed habitual behavior" (Ujhelyi et al., 2000).

invisible displacements (experimental paradigm: locating a hidden object that, without being visible for the subject, changes position; Fedor et al., 2008). In human infants, stage 6 regularly co-occurs with the ability to recognize oneself in the mirror (Bertenthal & Fischer, 1978). Some of our own observations fit into this picture. One of the keepers told us that the male (Nelson) occasionally poked its tongue towards her when disturbed by an event (e.g., cleaning of cage by keeper). By chance we succeeded to record this behavior (Fig. 3) that is otherwise shown only by great apes and humans. It is a nice demonstration of the fact that already these animals possess a beginning voluntary control over their facial expressions, which represents an additional option for recognizing the (perfect) contingency between one's own movements and that of the reflection (for the close relationship between facial play and mirror self-recognition, see Parker, 1991). However, we do not think that the siamangs are in any way special among the gibbons. There exist observations that other lesser ape species have a comparable degree of selfawareness. Ujhelyi, Merker, Buk, & Geissmann (2000) were the first to describe several unequivocal instances of clearly mirror-mediated self-directed behavior in both Hylobates leucogenys and Hylobates gabriellae. In addition, Suddendorf and Collier-Baker (2009) observed a similar behavior in 7 specimens of gibbons (species name not given), but did not classify it as a reliable sign of selfrecognition. This contrasts with the so far most comprehensive study done with chimpanzees (N = 105) in which 9 subjects that showed self-referring reactions in front of the mirror without passing the final mark test (only 11 animals were successful) were nevertheless categorized as positive with regard to selfrecognition (Povinelli et al., 1993).



Figure 3. Intentional tongue poking by the male (against experimenter) after having been disturbed during a grooming session with its partner; see video 3 for gestural character of behavior (criteria: 1. deliberate orientation by turning head to addressee; 2. typical, i.e. ontogenetically ritualized performance, cf. Tomasello, 1996).

The sudden disappearance of the animals' interest in their mirror image after the birth of their first common infant (day 61) allows two interpretations. First, it could be a simple shift of the time budget available for the different categories of behavior patterns. This seems to have been the case in the young mother who, from the very first day on, intensively cared for her young. The male, however, could very well have continued to check its visual appearance from time to time, even if only of mere boredom. But that was not the case. To the contrary, it also stopped with all courtship activities (e.g. display behavior) frequently shown before the arrival of the offspring, and even refrained from mating with its partner for the rest of the observation period (the first matings reappeared only months later when the young began to move independently). This finding suggests that the subjects' motivation to deal with their reflections could somehow be linked to sexual advertising and competition. If this is true, the existing data about mirror self-recognition in the great apes would make even better sense, because species with high competition should show an equally high and active interest in the mirror and vice versa. A comparison of the known behavior in front of mirrors with paternity rates that, at least for males, reflect the amount of sexual competition. supports such a relationship: Chimpanzees, bonobos (multiple matings, paternity rate: 40 - 50%; Boesch et al., 2006; Gerloff et al., 1999) and orangutans (limited control over females, paternity rate: 30 - 50%; Utami, Goossens, Bruford, de Ruiter, & van Hooff, 2002; Utami, Atmoko, & van Hooff, 2004) sometimes spend even extended periods of time with both inspecting and manipulating their visual appearance (see documentary by Anderson 1997), whereas gorillas (stable longtime relationships between males and females, paternity rate: 85-100%; Bradley, Doran-Sheehy, Lukas, Boesch, & Vigilant, 2004; Bradley et al., 2005), if not handreared (Patterson & Cohn, 1994), seem rather to completely ignore their mirror image (Suarez & Gallup, 1981; for an exception, see Posada & Colell, 2007). This does of course not imply that the tendentially more "vain" species like orangutan, chimpanzee, and bonobo would consciously consult the mirror, as modern humans usually do, to verify and possibly enhance their physical attractiveness through appropriate measures. Instead it may merely be the result of an increased responsiveness to the external appearance of conspecifics that simultaneously makes their own reflection more interesting for them.

As a consequence, the low interest of both the siamangs (occurrence of self-referring reactions in present study: once every 8 days for male, once every 12 days for female) and the gorillas (only 29% of 21 individuals showed self-referring reactions; Swartz, Sarauw, & Evans, 1999) in their reflection could be a plausible explanation for the animals' usual failure in the mark test since, to pass the test, it is necessary to possess a sufficiently detailed and regularly updated knowledge of the appearance of one's face. This appears to require a much more intensive occupation with the mirror image as it has been observed so far mainly in orangutans, chimpanzees and bonobos (see documentary by Anderson, 1997). The strong influences of motivation and associated experience also become apparent if one takes a closer look at the ontogeny of mirror self-recognition. Studies with chimpanzees have shown that even though the first evidence of self-recognition already emerges around the age of 2.5 (Lin. Bard, & Anderson, 1992), the peak of successful mark tests (75% of tested animals) is not reached until the age class of 8-15 years (Povinelli et al., 1993). Thereafter (age: 16-39 years) the level of success again decreases towards the low value of the juveniles (6-7 years: approx.

25%). Since it is unlikely that older animals simply have lost the ability for selfrecognition, the reason for this change may rather be a social one. Whereas young adults, with the advent of sexual maturity (around 10-12 years), begin to compete for access to sexual partners and thus show a particular interest in their own appearance (enhanced through the effect of a mirror), older individuals normally have already stabilized their position within the group. In this way the respective social system of a given species may very well have a significant influence on the animals' behavior in front of the mirror.

Last but not least, the inclusion of the gibbons as a group into the category of self-recognizing animals would also have consequences for the interpretation of the apes' cognitive phylogeny. Most importantly, it would corroborate the idea that, in the first place, it was their novel style of locomotion and only secondarily their social system (Dunbar & Shultz, 2007; the first apes probably were solitary or monogamous), their increasing body weight (Povinelli & Cant, 1995; gibbons are lightweights) and their protein-rich food (Milton, 1999; only chimpanzees consume meat in relevant quantities) that paved the way for the acquisition of a whole series of new cognitive capacities. In this perspective, brachiation was not only an accidental, but rather the decisive step that finally turned monkeys into the first fully self-aware primates. Indirect evidence for such a scenario comes from the tropical rainforests of the New World. There, the extant larger monkey species (howler monkey, woolly monkey, spider monkey) never could evolve into real ape-like creatures because their highly active grasping tail, by tendentiously lifting the caudal part of the body, appears to have hindered them from developing the same fully upright climbing style as is typical for the apes. If one confronts one of those species with a mirror, they behave like any other monkey in such a situation, i.e. they show that they are unable to recognize themselves (Lethmate & Dücker, 1973).

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Supplemental Material

Video 1 – Visual control of prehensile foot

Video 2 – Self-grooming via mirror

Video 3 – Intentional tongue poking

Video 4 – Positive mark test

To see the videos please go to:

http://www.kfunigraz.ac.at/zoowww/personal/heschl/ev/research.htm