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REVIEW

A critical review of methodology and interpretation of mirror self-recognition research in nonhuman primates

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In this paper we critically review conceptual and methodological issues of mirror self-exploration research. We conclude that: (1) mirror self-exploration provides evidence for mirror self-recognition; (2) inter- and intraspecies differences in terms of presence or absence of mirror self-recognition are not yet sufficiently clear, that is, whether its absence in species and individuals is methodological (false negative with respect to trait) or ontological (true negative with respect to trait) in nature; and (3) proposals of hypotheses to account phylogenetically for the existence of inter- and intraspecies differences in mirror self-recognition are premature. Before hypotheses such as these are advanced, the impact of rearing conditions on mirror self-recognition should be examined further.

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MIRROR SELF-EXPLORATION

Basic Design

Gallup (1970) demonstrated that chimpanzees, *Pan troglodytes*, show the kind of nonverbal mirror-guided behaviour that children show at the age of 18–24 months. On initial exposure to a mirror, chimpanzees behave as if the mirror image is another animal of the same species and gender, that is, they show social behaviour. After this social behaviour comes a phase in which chimpanzees experiment with contingencies between their physical body and the mirror image thereof. After a period ranging from a few minutes (10–20 min: Povinelli et al. 1993) to a few days (Gallup 1970) they use the mirror to explore otherwise nonvisible parts of their bodies.

In addition, Gallup (1970) designed a mark test to validate the impressions that emerged from seeing the animals engage in mirror self-exploration (MSE). The chimpanzees were sedated and marked on their right eyebrow ridge and upper left ear. After recovery, a 30-min mirror-absent (control) session and a 30-min mirror-present (test) session were conducted and the number of mark-directed touches in both sessions assessed. Normally reared chimpanzees made more mark-directed touches in the test condition (Gallup 1970; Gallup et al. 1971).

A recent analysis of the temporal patterning of mark-directed and nonmark-directed touches showed this increase to be selective for mark-directed touches and short lasting (Povinelli et al. 1997). This analysis went against the suggestion of Heyes (1994, 1995) that the increase in mark-directed touches is an artefact of anaesthetic recovery instead of an objective measure of MSE (Gallup et al. 1995; see van den Bos 1999 for a review of this debate).

Interspecies Differences in MSE

Not all nonhuman primates show evidence of MSE. Thus far the only nonhuman primates that have unequivocally proved capable of MSE are chimpanzees, bonobos, *Pan paniscus*, and orang-utans, *Pongo pygmaeus* (Gallup 1970; Gallup et al. 1971; Lethmate & Dücker 1973; Suarez & Gallup 1981; Calhoun & Thompson 1988; Swartz & Evans 1991; Lin et al. 1992; Povinelli et al. 1993, 1997; Custance & Bard 1994; Hyatt & Hopkins 1994; White Miles 1994; Kitchen et al. 1996). With respect to gorillas, *Gorilla gorilla*, MSE has been unequivocally demonstrated only in two home-reared individuals (Patterson & Linden 1981; Suarez & Gallup 1981; Ledbetter & Basen

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1982; Law & Lock 1994; Parker 1994; Patterson & Cohn 1994; Swartz & Evans 1994). MSE tests have been negative for gibbons (Lethmate & Dücker 1973 for white-handed, *Hylobates lar*, and dark-handed, *H. agilis*, gibbons) and several Old and New World monkey species (Anderson & Roeder 1989 for capuchin monkeys, *Cebus apella*; Gallup 1970 for stumptailed macaques, *Macaca arctoides*, rhesus macaques, *M. mulatta*, longtailed macaques, *M. fascicularis*; Lethmate & Dücker 1973 for capuchin monkeys, spider monkeys, *Ateles* spp., baboons, *Papio hamadryas*, mandrills, *Mandrillus sphinx*, and liontailed macaques, *Macaca silenus*; Mitchell & Anderson 1993 for longtailed macaques; Suarez & Gallup 1986 for rhesus macaques). However some notable exceptions to the rule that monkeys do not show MSE are the five out of six cottontop tamarins, *Saguinus oedipus*, that passed the revised mark test designed by Hauser et al. (1995). We give possible explanations below for these latter data.

Development of MSE

Because the developmental course of MSE in nonhuman primates has been thoroughly studied only in chimpanzees we discuss its development only for this species. We compare it with the development of MSE in humans to highlight some similarities and differences in development between chimpanzees and humans.

At 4–6 months of age, children treat the mirror image as if it is another child, that is, they show social behaviour. At the end of the first year, children begin to search for the image behind the mirror and to test contingencies of movement. This stage is followed by a period in which they avoid the image. Self-directed behaviours typically emerge at the age of 18–24 months (Mans et al. 1978).

In chimpanzees, the first two phases (social behaviour and contingency testing) appear at the same age as in humans (Robert 1986). However, chimpanzees develop the capacity for MSE later in life than humans. The youngest chimpanzees reported to have shown MSE were 28 and 30 months old (Bard 1998). Povinelli et al. (1993) found the onset of occurrence of MSE in their cross-sectional sample of 105 chimpanzees to be between 4.5 and 8 years with most individuals showing MSE at 6–8 years. Thus, in addition to showing MSE at an older mean age, the variation in the age of onset of MSE seems to be greater in chimpanzees than in humans.

A peculiar finding of Povinelli et al. (1993) was a 'decline in adulthood', that is the percentage of chimpanzees showing MSE aged 16–20 years and older was lower than that of younger chimpanzees. We discuss possible explanations for this result below. In adult humans failure to show MSE is seen only in some senile dementic or profoundly retarded people (see Biringer et al. 1989).

Intraspecies Differences in MSE

As mentioned, children pass the mark test around the age of 2 years. Failure to show MSE is found in children suffering, for example, from autism (Spiker & Ricks 1984; Mitchell 1997). From the age of 2 years on, all healthy humans are capable of MSE. In contrast to humans, there seems to be considerable individual variation in the capacity to show MSE within nonhuman primate species. Of the orang-utans tested only 80% show MSE (Lethmate & Dücker 1973; Suarez & Gallup 1981; White Miles 1994). For chimpanzees, the percentage of individuals passing the mark test ranges from 100% (Gallup 1970, N=4) to less than 10% (Swartz & Evans 1991, N=11). Of the 105 chimpanzees tested by Povinelli et al. (1993) only 20% spontaneously showed MSE (35% when the youngest subjects aged 1–5 years are excluded). Only half of the chimpanzees that spontaneously showed MSE passed the mark test in the latter study.

Questions Regarding MSE

From this overview three questions arise.

(1) What is MSE? For instance, what is the precise relationship between MSE and theory of mind?

(2) Are the inter- and intraspecies differences in MSE among nonhuman primates due to true negative scores (absence of the trait) or to false negative scores (presence of the trait but failure to show MSE because of methodological factors)? An answer to this question requires a precise analysis of the methodology of MSE research.

(3) If the inter- and intraspecies differences in MSE are indeed based on true positive and negative scores (presence or absence of the trait) and not on methodology, how can these differences be interpreted? Can phylogenetic factors account for these findings or should an explanation be sought in ontogenetic influences?

We deal with each of these questions in turn in the following sections.

INTERPRETATION OF MIRROR SELF-EXPLORATION

The finding that chimpanzees show MSE led Gallup and others (Gallup 1983, 1985, 1994, 1997; Gallup & Povinelli 1993) to the interpretation that this behaviour implies or is an expression of self-recognition and self-awareness, and to associate Premack & Woodruff's (1978) theory of mind (ToM) with this ability. Theory of mind can be defined as an organism's insight into its own mental state (self-awareness) and into those of other individuals (e.g. their beliefs, desires, feelings and intentions) and to act accordingly (cf. Premack & Woodruff 1978; Heyes 1998). Social-cognitive capacities that follow from ToM are, for instance, intentional deception and cognitive empathy (Byrne 1995; de Waal 1996). The foregoing is the strong interpretation of MSE.

Others are more moderate in their interpretation: they do believe that MSE is evidence for self-recognition but are not inclined to associate this ability with self-awareness and ToM. Swartz (1997), for example, stated that self-recognition, as shown by MSE, merely means that the animal differentiates itself from other environmental objects; the animal understands the nature of the mirror image as a reflection of its own body and can thus use the mirror as a tool for autogrooming or related behaviour.

It seems, however, that an animal realizes it is in control of its own body (i.e. beyond stimulus-driven behaviour) when it shows MSE. When an animal touches a mark on its face while looking at the mirror image it shows that it has a, perhaps simple, representation of its body. Thus it could be argued that MSE is evidence for self-awareness although perhaps in a simple form.

As an argument against the suggestion that MSE implies ToM, in children some important manifestations of ToM, such as the understanding of false belief, which is (one of) the crucial test(s) for ToM (e.g. Heyes 1998), develop at a later age than MSE, that is, at 36–48 versus 18–24 months (Gergely 1994; Gopnik & Meltzoff 1994). However, an extensive analysis of children's linguistic use of belief and desire terms between 18 and 60 months shows that understanding the difference between one's own beliefs and those of others (of which false belief is the prime example) is preceded by understanding the difference between one's own desires and those of others, which in itself is preceded by understanding the difference between one's own emotions and those of others (Bartsch & Wellman 1995). In other words, the transition between 'not having ToM' and 'having ToM' is gradual and stretches over different domains. This is consistent with the notion that imitation and pretence, which are also based on representational thinking, develop at the same age as, or shortly after, MSE (Custance & Bard 1994; Gopnik & Meltzoff 1994). Thus it could be argued that the development of ToM in humans starts at the age of 18–24 months, with mirror self-recognition being one of its first manifestations (cf. Baron-Cohen 1995; Byrne 1995; Whiten 1996).

Finally, one group of researchers is even more conservative in their interpretation of MSE and states that these behavioural patterns may not even imply self-recognition. Heyes (1994, 1996) for example, stated that it is not necessary for an animal to recognize that the mirror image represents its own body in order to use the information provided by the mirror for self-inspection. The animal may see the mirror image as another animal and upon seeing a mark on its face touch its own face thinking 'He has got a mark on his head; I wonder whether I have too' (Heyes 1994, page 917). Mitchell (1993a,b, 1997) also warned against the gratuitous assumption that mirror-mediated mark touching equals self-recognition, as some children wipe a nonexistent mark off their own nose after seeing a mark on someone else's.

Chimpanzees, however, have never been observed to respond to facial marks on other animals by touching comparable areas on their own faces (Gallup 1994). Rather, they groom the mark on the other animal's face, although few systematic studies have actually been conducted regarding the behaviour of chimpanzees towards conspecifics with facial marks (K. Bard, personal communication). Furthermore, chimpanzees have never been observed to attempt to groom the mirror image which would, in view of the aforegoing, be the most likely species-typical response were this mirror image viewed as a marked conspecific (cf. K. Bard, personal communication). Therefore it seems plausible to regard mirror self-exploration (whether or not during a mark test) as an expression of visual self-recognition. In the remainder of this paper we therefore refer to MSE as mirror self-recognition (MSR).

METHODOLOGICAL ANALYSIS OF MSR RESEARCH

General

Research on self-recognition, self-awareness and ToM in nonhuman primates is crucial to extend our knowledge on, and insight into, the evolution of these (related) traits. It is therefore not only important to operationalize concepts in a concrete and complete way, but also crucial that (1) tests are straightforward and have a single interpretation, (2) (positive and negative) results are representative for the species under study and (3) negative results are the result of an absence of the trait (true negative) rather than an inability to perform (false negatives). When tests that involve (a certain degree of) 'subjective assessment' and that are applied across different but related species are used, questions about their reliability and validity therefore need to be considered thoroughly (cf. Heyes 1993, 1994, 1998).

Delineating Mirror Responses and Interpretation

The first problematic methodological point in studying MSR is its subjective character.

First, it is necessary to define explicitly what 'mirror-mediated self-exploration' is (cf. Heyes 1994). Does this include mere touching of the body or is only autogrooming considered as MSR? Does MSR consist of exploring only otherwise nonvisible parts of the body, such as the face, or also barely visible parts, such as genitals and the back?

Second, judging whether an animal is engaged in self-exploratory behaviour while looking in the mirror remains (somewhat) subjective (Heyes 1996). Although this problem can partly be solved by using several observers and accounting for the interobserver reliability beforehand or by blind coding (see Eddy et al. 1996; cf. Povinelli et al. 1997), a behaviour pattern as subtle as gazing at the mirror image while touching the face can easily be either missed or overstated. Self-exploratory behaviours in monkeys, for example, may be more difficult to detect than in apes because monkeys move more rapidly than apes (Thompson 1997).

The mirror mark test may overcome these problems as this test allows one to discriminate more objectively whether the animals use the mirror to explore themselves, that is, touch the marks (Gallup 1970). Those animals that are classified by their spontaneous self-directed behaviour as showing evidence of MSR are more likely to pass the mark test than those that are not (Suarez & Gallup 1981; Swartz & Evans 1991; Povinelli et al. 1993) indicating that both conditions measure the same phenomenon.

Species-specific Responses

The second problematic methodological point of MSR research is that mirror tests have been applied to a wide range of species. One could question their validity as a tool to study self-recognition across species, that is, whether it is justifiable to use a test designed for humans (and chimpanzees) on other species. As Zazzo (in de Lannoy 1993, page 338) put it: 'the study of an animal's behaviour in front of a mirror is ''not a study in phylogeny but an elucidation of a human behavior'' '. In general, negative MSR results (neither spontaneous nor mark-directed exploratory behaviour) raise the question of whether these are true negatives (absence of the relevant trait) or false negatives (absence of the ability to show the relevant trait through the mirror). The underlying assumption is, of course, that the trait is present regardless of the mirror or, in other words 'the mirror is a means of bringing the trait to the surface but is not producing it'.

The interspecies differences in the outcome of mirror tests may reflect factors other than a differential ability to recognize oneself. Certain species' characteristics may make it more difficult for an animal to detect the contingencies between its body and the mirror image. If the animal does not go through this phase of contingency testing it may not learn the reflecting properties of the mirror and may never enter the stage in which MSR is shown; instead it may continue to see the mirror image as a social stimulus, eventually habituating to and ignoring it. According to Byrne (1995), for example, gorillas may fail to show MSR because they are very gentle in their investigation and tend to 'look but not touch', making it more difficult to learn the properties of mirrors. Gibbons may fail to show MSR because they are more auditory than visually focused in communication than chimpanzees. Monkeys may have little chance to detect contingencies between body and mirror image because they engage in autogrooming less than chimpanzees and thus do not receive direct feedback from their bodies (Heyes 1994, 1995).

Similarly, some primates may experience the stare of their image on their first encounter with the mirror as such a threat that they avoid the reflection altogether thereafter. Direct eye contact has different functions and elicits different reactions in different species (van Hooff 1962). According to de Waal (in Baron-Cohen 1995, page 101) chimpanzees avoid eye contact during conflicts and reconcile only when eye contact has been made, whereas rhesus monkeys do the opposite: 'threat stare' during conflicts and 'avert gaze' during friendly approaches. Thus for chimpanzees, it may be easier to judge the stare of their image as nonthreatening on their first encounter with the mirror than for monkeys and hence they may pass this phase more easily than monkeys. This 'threat stare' problem in MSR research can be resolved by using multiple mirrors placed in angles as introduced by Anderson & Roeder (1989). This revised mirror test, however, still led to negative results in longtailed macaques (Anderson & Roeder 1989). Yet it is possible that absence of direct eye contact was the reason why cottontop tamarins passed a revised mark test, in which the white hair on their heads was colour dyed, but failed a classic mark test (Hauser et al. 1995). Whereas Hauser et al. (1995) hypothesized that a lack of saliency (face versus hair) was the major factor contributing to the differential results on the classic versus the revised mark test in this species, it is possible that diverting the attention to the top of the head instead of to the eyebrow ridge and ear meant that the monkeys did not experience a 'threat stare' by the mirror image. The results of Hauser et al. (1995) underline the possibility that failures to find MSR in some species have a methodological rather than a phylogenetic basis.

Motivational Factors

A third problematic methodological point of MSR research is that in order to pass a mirror test an animal needs to be motivated to behave accordingly (i.e. show MSE). The motivation to show self-exploration is easily influenced by circumstances and can vary between species and individuals. Thus some animals may fail to pass a mirror test because they are more easily distracted by the experimental setting or the observer or are more easily distressed than others.

Motivational factors such as these could explain why some animals fail the mark test after having shown spontaneous MSR. In Povinelli et al.'s (1993) experiments only half of the chimpanzees that showed spontaneous self-exploratory behaviours while looking at their mirror image passed the mark test. Similarly, only one out of four chimpanzees that showed spontaneous MSR in Swartz & Evans's (1991) experiments passed the mark test. These results suggest that the mark test is a more conservative measure for MSR than the normal mirror test and may produce false negatives. Although Povinelli et al. (1993) explained their finding by suggesting that some chimpanzees forgot their self-image in the interval between tests it has been shown that chimpanzees can pass a second mark test after a delay of 1 year (Calhoun & Thompson 1988).

To obviate the possibility that motivational factors (motivation to touch the marks) affect the outcome of a mark test it is important to use control procedures (Suarez & Gallup 1981; Povinelli et al. 1993; Gallup et al. 1995). The most commonly used control procedure is one in which, in addition to face marks, a wrist mark is applied before testing. If the animal repeatedly touches and grooms the wrist mark (which is accessible without a mirror) but pays no attention to the face marks in the mirror-present condition, the animal is said to be motivated to touch marks but to have no insight into the properties of the mirror. However, the problem with applying control wrist marks is that the animal may habituate to the mark (the mark is neither harmful nor rewarding) and thus shows no interest in the face marks during the mark test. This problem can be minimized (although not resolved) by varying the colour of the wrist and face marks (Gallup 1994).

If an individual does not touch the face marks or the wrist mark nothing can be said about its understanding of

the properties of the mirror. In an attempt to obviate the impact of motivational differences in children, Asendorpf et al. (1996) revised the classic mark test. They showed children a doll with a mark before the test and asked them to clean its face. If the children did not try to wipe their own faces during the mark test they were offered a tissue and asked to 'clean the face' to stimulate mark-directed behaviour. Compared with the results of the classic mark test (Asendorpf & Baudonnière 1993), the percentage of 'recognizers' increased while the percentage of ambiguous cases decreased in this revised mark test. In using mark tests on animals one could avoid motivational influences by pretraining sessions in which mark wiping (for example on the wrist or on a doll) is reinforced. Some have argued that reinforcing mark-directed touches could lead to passing the mark test as the result of rule training (rule: wipe off mark) rather than based on an expression of actual self-recognition (Spiker & Ricks 1984). However, animals that do not recognize themselves would touch the mark on the mirror image but not on themselves. Accordingly, these pretraining sessions would not lead to false positive results (absence of trait but positive results because of methodological flaws).

Concluding Remarks

Given that certain species' characteristics and individual motivational factors may influence the results of the classic mirror tests, it would be interesting to try to find alternative ways of measuring self-recognition and compare the outcomes of these new tests with those of the classic mirror tests.

In attempting to measure self-recognition accurately, the question arises as to what constitutes its essence. One problem with research on self-recognition is that the majority of experiments have followed an 'inductive' approach. That some primates show self-exploration in front of a mirror has been taken as indicative of self-recognition, self-awareness and ToM (see above). Such interpretations have been made post hoc and are mainly based on the outcome of a single experimental paradigm: the behaviour in front of a mirror. The interpretational difficulties and criticisms have mainly been counteracted by more sophisticated methodological analyses (e.g. Povinelli et al. 1997) rather than by more sophisticated conceptual analyses. In our view, what is needed is a 'deductive' approach rather than the current 'inductive' one, in which (1) the essence of the concept of self-recognition/self-awareness is clearly stipulated and (2) a range of tests based on this conceptual essence is designed to measure self-recognition/self-awareness such that (3) animals can nonverbally indicate in an experimental paradigm that they understand this concept. In our view, the essence of self-recognition/self-awareness is that it is cue independent, that is, self-recognition expresses itself in relation to different cue complexes. The mirror tests used thus far constitute only one such cue complex in which visual–kinaesthetic matching (Mitchell 1993a, b, 1995, 1997; Mitchell et al. 1994) is one crucial factor for self-recognition to occur.

Two major ways exist to create and measure cue independency. One way is to apply tests in more modalities. One could, for example, in addition to testing for visual self-recognition, test for auditory self-recognition (in e.g. gibbons) by assessing the animal's reaction to playback tapes of the voices of a stranger, its partner and itself. Although Parker et al. (1994, page 16) stated that 'self-awareness as indicated by MSR . . . is a multimodal achievement that differs markedly from such simpler phenomena as auditory self-recognition (which in some birds is mediated by a single neuron)', it is conceivable that auditory self-recognition in nonhuman primates constitutes a more complex phenomenon. In addition, although an animal can hear its own voice as it utters sounds, it sounds different to other individuals. In this context it would be interesting to study at what age children recognize their own voice on tape.

The other way to measure cue independency is to stay in one modality and apply tests with several independent cue complexes. Kitchen et al. (1996) showed that chimpanzees are capable of MSR with both normal mirrors and mirrors that produce distorted and multiplied images. Although it could be argued that this is a case of cue independency, MSR in this case is still based on contingency testing rather than feature recognition. Nevertheless, these results do show the chimpanzee's ability for abstraction.

When trying to find alternative ways of measuring MSR, one should be wary of readily accepting a skill requiring the use of a mirror as indicative of self-recognition, as this easily leads to false positive findings. For example, Menzel et al. (1985) interpreted their finding that chimpanzees (but not rhesus monkeys) could locate and reach for objects with the use of a mirror as evidence of self-recognition. However, the Japanese monkeys, *Macaca fuscata*, in Itakura's experiments (cited in Swartz & Evans 1991, page 494) failed to pass the mark test despite their ability to learn to obtain food rewards with the use of mirrors. Furthermore, in Robinson et al.'s (1990) experiment infants could locate objects otherwise out of view with the use of mirrors regardless of whether their image was available to them. These results suggest that spatial problem-solving tests involving the use of mirrors do not provide a direct measure of self-recognition.

When attempting to measure cue independency within the visual modality one could assess self-recognition with the use of synchronous videos, asynchronous videos, photographs and mirrors. This creates four different cue complexes varying along different dimensions such as movement patterning (dynamic versus static) and timing (immediate versus nonimmediate). Only if the animal passes the tests with all cue complexes can it be said to show evidence of fully developed visual self-recognition.

Bigelow's (1981) study of children suggests that, although as a measure of self-recognition she used object location rather than a mark test, self-recognition from prerecorded videotapes and photographs (where there is no contingency in movement) requires a higher level of development than self-recognition from mirror images and synchronous videotapes: children recognized

themselves from mirror images and simultaneous videotapes at a younger age (mean age of 20 and 22 months) than from prerecorded videotapes and photographs (mean age of 24 and 25 months).

INTERPRETATION OF DIFFERENCES IN MSR

If the inter- and intraspecies differences in MSR are not methodological in nature but are indeed based on differential capabilities of some species and individuals for self-recognition, the question arises as to what can explain these differences. The data on interspecies differences in MSR seem to suggest that humans, chimpanzees and orang-utans do, and gorillas, gibbons and Old World monkeys do not, possess this capability. Povinelli & Cant (1995) have presented a hypothesis (the 'clambering hypothesis') to explain why self-awareness as shown by MSR evolved in some species but not in others. They suggested that self-awareness evolved in the large orang-utan-like ancestors of the hominoids so that they could move about the forest canopy (arboreal clambering) in safety. Unlike the locomotor patterns of other primates this clambering consisted of nonstereotyped, flexible responses. Gallup (1997) elaborated on this hypothesis by suggesting that whereas orang-utans nowadays still use their self-awareness for their clambering, the other hominoids have come down from the trees where self-awareness, which is an energetically costly trait, is no longer adaptive for locomotion. Humans learned to use self-awareness for other (social) purposes instead of manoeuvring through branches, but in gorillas this trait has been lost through genetic drift (although the capacity can apparently be regained in a stimulating environment, as shown by the two home-reared gorillas showing MSR; see Povinelli & Cant 1995) and chimpanzees are in the process of losing it. Thus according to Gallup, self-awareness as shown by MSR is a polymorphic trait in chimpanzees (i.e. some have it and some do not), explaining the intraspecies differences in MSR.

Although the inter- and intraspecies differences in MSR make it tempting to hypothesize about the evolution of this trait, there are some problems with the reasoning of the evolutionary significance of self-awareness. First, although the frequency of occurrence of a trait under active selection pressure will change across generations, it is not true that a capacity has to be 'used or lost' nor that a trait must confer a selective advantage in order to remain in the gene pool (Hoffmann 1994). Second, if a genetic trait 'has been lost' in a species then no amount of enriched environment can bring it about (Hoffmann 1994). Third, it is not clear why humans came to use self-awareness for social purposes whereas chimpanzees, which also live in highly complex social organizations (de Waal 1992, 1996), did not.

In addition, one could wonder whether the data on the inter- and intraspecies differences indeed call for phylogenetic explanations such as those of Povinelli & Cant (1995) and Gallup (1997). To advance hypotheses on the evolution and origin of traits, such as MSR, based exclusively on laboratory data, such as mirror tests on animals living in captivity, requires that: (1) the data are representative for the species as a whole, that is, a sufficient number of animals are tested; (2) these data are unambiguous, that is, the trait is expressed in all test situations thought to measure it; and (3) the positive or negative test outcome, implying the presence or absence of the trait, is not the result of living under laboratory conditions.

Let us consider whether this is the case in the trait under study.

Sample Size

Among the great and lesser ape species a clear bias exists towards chimpanzees in terms of numbers of animals tested for MSR. About 164 (conservative estimate) chimpanzees have been tested (Gallup 1970; Gallup et al. 1971; Lethmate & Dücker 1973; Suarez & Gallup 1981; Calhoun & Thompson 1988; Swartz & Evans 1991; Lin et al. 1992; Povinelli et al. 1993; Custance & Bard 1994; Hyatt & Hopkins 1994; Kitchen et al. 1996). In contrast only four gibbons (Lethmate & Dücker 1973) have been tested for MSR and the number of orang-utans (estimated N=5; Lethmate & Dücker 1973; Suarez & Gallup 1981; White Miles 1994), bonobos (N=10; Hyatt & Hopkins 1994) and gorillas (estimated N=19; Patterson & Linden 1981; Suarez & Gallup 1981; Ledbetter & Basen 1982; Law & Lock 1994; Parker 1994; Patterson & Cohn 1994; Swartz & Evans 1994) tested is (relatively) small as well. Accordingly it may be questioned whether sufficient data exist to decide whether a watershed exists at the level of orang-utans or gibbons.

ToM and MSR: Conflicting Results

If self-recognition indeed codevelops and is associated with the first stages of ToM as suggested above, the prediction would follow that chimpanzees and orang-utans but not gorillas show evidence (indicating the roots) of ToM. Contrary to this prediction, all great ape species including gorillas show behaviour indicative of the early developmental stages (i.e. comparable to children of 2–3.5 years old) of ToM (Patterson & Linden 1981; Povinelli et al. 1992b, 1994; Byrne 1993, 1995, 1996; Patterson & Cohn 1994; White Miles 1994; Povinelli & Preuss 1995; Hart & Karmel 1996; Whiten 1996; Gómez 1998).

Two explanations are possible for these seemingly conflicting data. First, as mentioned above, gorillas may not be easily prone to mirror-directed behaviour unless stimulated under home-reared conditions. Second, the data on ToM may be overstated: most (of these ToM) data, especially so for gorillas and orang-utans, stem from anecdotes, of which many were observed in home-reared individuals. So unless more data are obtained in gorillas under controlled conditions little can be said at present on these seemingly conflicting data.

In contrast to the great ape species, monkey species have not been observed to show behaviour indicative of the early developmental stages of ToM (Cheney & Seyfarth 1990; Povinelli et al. 1992a; Mitchell &

Anderson 1993). Hauser & Santos (1998), however, found indications of the understanding of false belief in cottontop tamarins, the only monkey species thus far showing MSR (Hauser et al. 1995). The clambering hypothesis fails to give an explanation for these findings.

If MSR and ToM are related, a second prediction is that comparable distributions of MSR and ToM occur within species. Contrary to this prediction, de Waal et al. (de Waal & Van Roosmalen 1979; de Waal 1992, 1996; de Waal & Aureli 1996) showed that group-living chimpanzees (as opposed to macaques) uniformly show behaviour suggestive of consolation after conflicts. Consolation is considered to be an expression of empathy, a capacity that in children codevelops with MSR and seems to be at least a precursor of ToM. Accordingly one would expect self-recognition among chimpanzees to be as uniformly distributed as is empathy.

Two explanations are possible for these seemingly conflicting data. First, consolation may not be a good indicator of ToM. Indeed, de Waal & Aureli (1996, page 99) stated that infant rhesus macaques also show affiliative responses to distressed conspecifics, but that these responses almost entirely disappear at a later age. If this is consolatory behaviour, consolation is not a good indicator of ToM. Second, rearing conditions may affect the distribution: consolation has been studied in animals living (and reared) under optimal group-living laboratory and zoo conditions, whereas MSR in most cases has been studied in animals living (and reared) under suboptimal group-living laboratory conditions. In the next section we argue that the latter conditions may have affected the development of MSR.

Rearing Conditions and MSR

Before advancing an evolutionary theory to explain inter- and intraspecies differences in MSR, the confounding effects of differences in rearing conditions should be excluded. It appears that social-cognitive capacities such as self-recognition, self-awareness and ToM, which appear to rely on the development of a specific neural network (orbito-frontal cortex, amygdala and parts of the temporal cortex, Baron-Cohen 1995; medial frontal cortex, Frith 1998), require adequate social input to develop properly (see van den Bos 1997, in press). In the same way as early social stimulation, while these (higher) brain structures are still developing, can result in enhanced social-cognitive functioning (as seems to be the case in some 'enculturated' home-reared apes, see Call & Tomasello 1996), social deprivation can result in impaired social-cognitive functioning. For many of the primates tested for MSR, the exact rearing conditions are unknown or at least not adequately described. That it is important to control for rearing conditions follows from Gallup et al.'s (1971) experiment which showed that chimpanzees reared in social isolation do not show self-recognition. In similar vein, Davenport & Rogers (1970) showed that social-cognitive functioning is impaired in isolation-reared chimpanzees. Whereas the effects of total social isolation on social cognition are clearly drastic, minor social deprivation (such as short-term social deprivation or inadequate social contact) during ontogeny may still have an impact on the development of capacities such as self-recognition and ToM. Therefore differences in rearing conditions in terms of social contact could, at least in principle, explain the findings of intraspecies differences in MSR.

In discussing their results on MSR in chimpanzees, Povinelli et al. (1993) mentioned that some results might have been due to differential rearing conditions. They stated (page 356) that statistical comparisons between captive mother-reared and nursery-peer-reared animals were meaningless because: 'our samples of captive mother-reared versus nursery-peer-reared subjects were limited by the fact that all of the captive mother-reared chimpanzees were under 3 years old'. Thus, although the extent to which these animals had experienced social deprivation is unknown, the majority of the subjects were nursery-peer-reared. If some of these nursery-peer-reared chimpanzees experienced a lack of or inadequate social contact during some part of their development, this might explain the 'polymorphy' in MSR found in these subjects. Furthermore, differential rearing conditions could explain why the percentage of 'recognizers' among the older subjects was relatively low. Although Povinelli et al. (1993) discarded this explanation in discussing the 'decline' in adulthood by stating that all chimpanzees lived in stable breeding units, they did mention that some chimpanzees showed stereotypies. It is well established that social deprivation leads to stereotypic behaviour (Davenport & Rogers 1970; Fittinghoff et al. 1974; Dienske & Griffin 1978; Walsh et al. 1982; Goosen et al. 1983; Fritz et al. 1992; Pazol & Bloomsmith 1993; Marriner & Drickamer 1994). If it were mainly the older subjects that showed stereotypic behaviours, this could very well explain the 'decline' in adulthood found by Povinelli et al. (1993).

Currently we are exploring the possibilities of investigating the impact of early social deprivation on MSR and self- and other awareness.

CONCLUSIONS

From this review two conclusions may be drawn.

First, it is not yet clear which nonhuman primate species show evidence of MSR. Although the data seem to indicate that orang-utans and chimpanzees are, and gorillas, gibbons and all but one monkey species are not, capable of MSR, more research is needed to exclude methodological factors in these findings. The finding of MSR and the understanding of false belief in cottontop tamarins (Hauser et al. 1995; Hauser & Santos 1998) may either highlight the impact of methodology on MSR or indicate a case of convergent evolution in great apes such as chimpanzees and orang-utans and New World monkeys such as cottontop tamarins (and perhaps some other closely related New World monkey species).

Second, as to intraspecies differences it is not yet clear whether these differences are due to rearing conditions or indeed reflect polymorphy.

Both conclusions preclude any hypothesis on the evolutionary origin of MSR. Accordingly this challenges the hypothesis put forward by Povinelli & Cant (1995), and Gallup's (1997) extension thereof, which, given the data at present, is premature and also does not explain the tamarin findings. More experiments are needed to understand the distribution and development of MSR and its relation to ToM.

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