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Further reflections on self-recognition in primates

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Abstract. A review of the literature, together with a reanalysis of existing data and some additional data, was used to show that Heyes' (1994, *Anim. Behav.*, **47**, 909–919) recent critique of self-recognition research in primates is without merit. Heyes' contention, that self-recognition is an artefact of incomplete recovery from anaesthetization and species differences in ambient face touching, is contrary to (1) the temporal parameters of the mark test, (2) responses that chimpanzees, *Pan troglodytes*, make to control body marks (i.e. those that can be seen without a mirror), (3) results from studies that have not used anaesthesia, (4) responses that chimpanzees make to unmarked portions of the face, (5) the absence of a correlation between developmental changes in face touching and self-recognition, (6) differences among chimpanzees in patterns of mirror self-directed behaviour and normal self-grooming and (7) the absence of substantial species differences in face-touching behaviour.

According to Heyes (1994), there is no compelling evidence that non-human primates are capable of recognizing themselves in mirrors, and even if they were, she contended that such a capacity has no bearing on their ability to conceive of themselves. Heyes argued that research in this area has been fundamentally flawed by the existence of species differences in ambient face-touching behaviour and the use of testing procedures that fail to give subjects an adequate opportunity to recover from the effects of anaesthetization. The purpose of this paper is to demonstrate that the arguments advanced by Heyes about the absence of evidence for self-recognition are untenable.

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Heyes made two distinct claims, (1) that chimpanzees, *Pan troglodytes*, are not capable of using mirrors to explore parts of themselves never seen before or to locate novel marks applied to parts of their bodies that can only be seen in a mirror, and (2) even if they could, it would not be evidence for self-awareness. For purposes of clarity, we assess Heyes' claim that chimpanzees are not capable 'of using a mirror as a source of information about their own bodies' (page 913). We defer the issue of whether this capacity has important cognitive implications to future research.

Self-recognition Methodology

Because Heyes' critique of the self-recognition literature derives principally from an analysis of an experiment on chimpanzees reported by Gallup (1970), it is important to review the basic paradigm that he used. Gallup reported that patterns of social behaviour directed by chimpanzees towards mirrors, although pronounced at first, were replaced by the emergence of self-directed behaviour. That is, rather than continuing to respond to the mirror as such, the chimpanzees

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began to use the mirror to respond to themselves and to gain access to parts of their bodies that they could not otherwise see. Thus it appeared that the chimpanzees had learned to correctly decipher mirrored information about themselves, and had come to realize that the source of the behaviour depicted in the mirror was their own. In an effort to validate these impressions, Gallup devised an unobtrusive and more rigorous test. After 10 days of mirror exposure, the chimpanzees were anaesthetized and marked on the uppermost portion of an eyebrow ridge and the top half of the opposite ear with a bright red, odourless, non-irritating, alcohol-soluble dye. The animals were then returned to their cages and allowed to recover from anaesthesia in the absence of the mirror. There are three special properties to this procedure (see Gallup 1994 for an extended discussion of methodological issues in self-recognition research). First, because the dye was applied while the animals were unconscious, they would have no information about the application of these marks. Second, the dye was carefully chosen so that, once dry, it would be free from any tactile or olfactory cues. Finally, the marks were strategically placed at predetermined points on the chimpanzees' faces so that the animals could not see them without a mirror.

Once the animals had completely recovered from the effects of anaesthesia they received food and water and then were observed for 30 min to determine the number of times that they happened to touch any marked portion of the face. At the conclusion of this baseline/pre-test phase, the mirror was brought back into the room and positioned in front of the chimpanzee's cage as an explicit test of self-recognition. Upon seeing the red marks on their faces in the mirror, the animals reached up and attempted to touch the marks while carefully monitoring the results in the mirror.

Of the four chimpanzees that Gallup tested, there was only one instance in which a facial mark was touched prior to the reintroduction of the mirror. In stark contrast to their behaviour during this pre-test phase, however, when the mirror was brought back into the room there was a total of 27 mirror-mediated mark-directed responses.

These basic results have been replicated in both chimpanzees and orangutans, *Pongo pygmaeus*, by a number of different investigators (e.g. Gallup et al. 1971; Lethmate & Dücker 1973; Suarez & Gallup 1981; Calhoun & Thompson 1988; Povinelli et al. 1993).

Is Self-recognition an Artefact of Anaesthetization?

Heyes (1994) contended that studies such as these, which purport to show evidence of self-recognition based on the subject's ability to locate facial marks that it can only see in a mirror, are suspect, because they invariably test animals before they have completely recovered from the effects of anaesthesia. Thus on the pre-test (prior to the reintroduction of the mirror), she argued that the animals may still be sedated and therefore simply show a lower or depressed level of ambient face-touching behaviour than occurs later when the mirror is presented as an explicit test of self-recognition. According to her argument, animals that pass the mark test never really use the mirror to locate the facial marks, but simply contact these marks more often coincident with higher ambient levels of overall face touching.

How plausible is this argument? In the first place, it would be counter-productive for anyone to knowingly conduct a test of self-recognition on animals that were still sedated and/or otherwise encumbered by the effects of anaesthetization. In the studies that have employed anaesthesia, the investigators waited until the animals appeared to have fully recovered from the effects of anaesthetization. As a control for the effects of anaesthetization in the original study, Gallup tested several comparable chimpanzees that were also anaesthetized and marked but that lacked the benefit of prior mirror exposure. Unlike their mirror-experienced counterparts, none of the control subjects showed any evidence of self-directed behaviour, nor were they able to locate the source of the marks that could only be seen in the mirror. Control animals all acted as though they were seeing another chimpanzee and engaged in a variety of species-typical social responses directed towards the mirror.

Temporal Parameters of the Mark Test

In evaluating Heyes' arguments, it is important to consider the temporal parameters of the testing sequence employed in most studies of self-recognition. Heyes' anaesthetization hypothesis requires the existence of an extraordinarily steep

recovery gradient in nevertheless normally appearing subjects to obtain the rather dramatic differences in mark touching that are typically reported between the pre-test and test. Because the 30-min test phase in which the mirror is reintroduced immediately follows the pre-test, the window of time during which differential recovery would have been sufficient to produce such a time-bound effect would have to be very brief. Contrary to what Heyes' analysis suggests, rather than increase monotonically as the test session proceeds, most mark-directed responses appear conditional upon the reintroduction of the mirror and occur shortly after the mirror is brought back into the room. Moreover, once the animals discover that these marks are inconsequential, their interest rapidly wanes. Is it merely a question of waiting another few hours to be absolutely sure there are no lingering (but otherwise undetectable) effects of anaesthesia? In fact, investigators have used injection-test intervals involving several different anaesthetic agents ranging from 2 to 7 h (e.g. Calhoun & Thompson 1988; Povinelli et al. 1993). We find it difficult to believe that there is a sufficient recovery gradient in subjects that appear completely alert and unencumbered by any residual effects of anaesthesia to bridge post-recovery periods of this magnitude.

Responses to Control Body Marks

Heyes also failed to consider data from studies that have applied control marks to body parts that the subjects can see directly (e.g. Suarez & Gallup 1981). In such studies, in addition to marking facial features, which can only be seen in a mirror, marks are also applied to the stomach or wrist to provide an independent assessment of the animal's interest in and motivation to touch superimposed marks. Rather than increase as a function of time, as Heyes' recovery from anaesthetization account predicts, responses to control body marks are most prevalent during the pre-test phase (before the mirror is presented) and wane thereafter. On the other hand, responses to comparable facial marks that can only be seen in the mirror become pronounced contingent upon the reintroduction of the mirror. Moreover, instead of being greater than what is obtained for control marks prior to the reintroduction of the mirror (as Heyes' analysis based on progressive recovery from anaesthetization implies), the incidence of responding to marks that subjects can only see in the mirror is comparable to what is found for control marks on the pre-test (Suarez & Gallup 1981).

Studies Without Anaesthesia

Heyes admitted that 'if the mark-touching effect is really an anaesthetic artefact, then one would expect it to have been replicated only in studies using an anaesthetic' (page 911). In an attempt to show that evidence of self-recognition is restricted to those studies that use anaesthesia, Heyes reviewed four studies that were conducted without anaesthetization. Two of these (Anderson 1983; Povinelli 1989), however have no bearing on her hypothesis because they involved species (elephants, *Elephas maximus*, and macaques, *Macaca artoides*), that fail to show any evidence of mirror-mediated patterns of self-directed behaviour in the first place. Of the two remaining studies she cited, one (Robert 1986) involved an infant chimpanzee and orangutan that were far too young to show self-recognition (see Povinelli et al. 1993; Miles 1994). In the fourth study (Lin et al. 1992), Heyes argued that the incidence of mark-directed responding is equivocal and the results are not comparable to other studies, because the frequency of mark touching was not measured in the absence of a mirror. There are other problems with Lin et al.'s study (see Povinelli et al. 1993), including that much of their data were also derived from subjects that were too young to show self-recognition.

A number of other studies, however, have obtained evidence of mirror-mediated mark-directed behaviour without the use of anaesthesia (e.g. Lethmate & Dücker 1973; Patterson 1984; Calhoun & Thompson 1988; Miles 1994). Lethmate & Dücker, for example, found that both chimpanzees and orangutans that had been surreptitiously marked by a familiar caretaker while they were awake evidenced hardly any mark touches until later when the mirror was presented; they then showed a dramatic increase in both mark-directed and self-directed responding (for one chimpanzee, the incidence of such responding went from one on the pre-test to 21 on the test).

Specificity of Mark-directed Responses

In his original study, Gallup (1970) was careful to mark the chimpanzee's right upper eyebrow

ridge and the top half of the opposite ear. This strategy allows for a retrospective test of the anaesthetic recovery hypothesis. If responses to the marks have nothing to do with mirrored information about the self, then contacts to these areas should be no more frequent than to comparable unmarked locations on the subject's face. That is, if the contacts to the marks are independent of mirrored information, and instead are due to ambient face/head-touching behaviour, then the number of contacts to the right eyebrow ridge with a red mark should be no higher than comparable touches to the left, unmarked eyebrow ridge. The same obviously holds true for marked and unmarked ears.

To test this hypothesis, Povinelli (this study) instructed seven undergraduate and graduate student volunteers to observe a videotape of a 30-min mark-test session of a 3.5-year-old chimpanzee (Megan). Before this test, Megan had shown standard evidence of self-recognition based on repeated compelling episodes of self-exploratory behaviour which were systematically recorded during her spontaneous interactions with a mirror (Povinelli et al. 1993). The tape that the seven observers viewed depicted the subject in a single cage in front of a large, covered mirror. The subject had been anaesthetized and marked on her right eyebrow ridge and left ear using a red dye (with no discernible tactile or olfactory cues) approximately 6 h earlier. The tape revealed an experimenter uncovering the mirror and the subject's subsequent behaviour during a 30-min period. The observers had been instructed to view the tape separately, rewinding and reviewing portions if necessary, and to record the number of times any part of the subject's hands contacted four areas on her head: her marked right eyebrow, her unmarked left eyebrow, her marked left ear and her unmarked right ear.

The mean number of contacts to each of the four facial areas recorded by the seven observers is shown in Fig. 1. The distribution of contacts to the four regions of the face are consistent with Gallup's (1970) argument that (some) chimpanzees are able to use mirrored information about themselves to orchestrate selective, self-exploratory behaviour. In contrast, these results provide no support for Heyes' view that contacts to the marked regions result from a generalized increase in ambient face-touching behaviour because of post-anaesthetic recovery. Were that

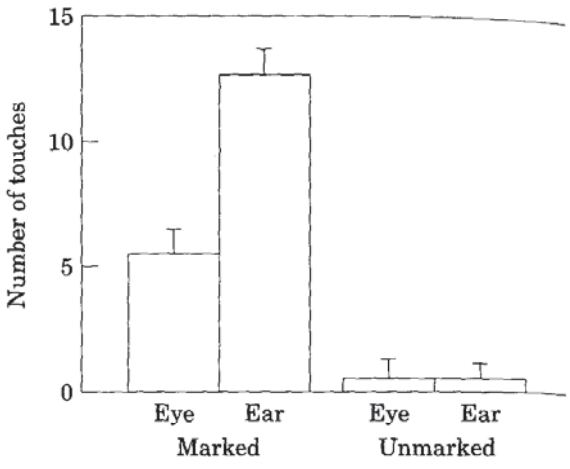

Figure 1. Mean (+SD) number of contacts (scored by seven observers) to each of four (marked and unmarked) facial areas by a chimpanzee during a test of self-recognition.

the case, the distribution of contacts should have been roughly equivalent across all four facial areas, not selective to those areas that were marked. The strength of the observers' agreement on this point is striking. A repeated-measures ANOVA using the individual observers' scores as the data set revealed an extremely robust overall effect ($F_{3,18}=526.81$, $P<0.0001$). Tukey–Kramer post-hoc tests indicated significant differences ($P<0.001$ or smaller in all cases) in all pair-wise comparisons, except between the two unmarked regions. These results confirm that although observers watched the tapes separately, they all witnessed and recorded the same phenomenon: a substantial and selective pattern of touches to marked, but not unmarked facial regions. To be absolutely certain that the observers were not selectively focusing on mark-directed touches because they were more obvious or interesting, six additional undergraduate and graduate students were recruited to observe the tape separately and record only the number of contacts that the subject made to the unmarked eyebrow and ear. Indeed, these observers were told that there might be some and perhaps many contacts to these areas. None the less, these observers reported no higher levels of contact to the unmarked areas than did the seven original observers.

Megan's responses are typical of other chimpanzees who have been tested in a controlled and rigorous fashion (e.g. Povinelli et al. 1993). This is not to say that all increases in mark-directed

responding following the uncovering of the mirror should be taken as evidence of self-recognition. Both Gallup (1994) and Povinelli et al. (1993) outlined several problems with mark tests and suggested a number of ways to handle such methodological issues. The technique described above, however, is a powerful means of distinguishing between contacts that are the direct result of processing mirrored information about the self, and those that are the result of increased arousal following mirror exposure (see experiment 5 in Povinelli et al. 1993). Suffice it to say that data such as these invalidate Heyes' post-anaesthetic recovery hypothesis.

Ambient Face Touching

Heyes is correct that chimpanzees do engage in ambient levels of touching and picking at parts of their bodies, including parts that they cannot directly see. Povinelli et al. (1993) noted that previous studies may have confused ambiguous instances of face touching with mirror-guided self-directed behaviour (e.g. Lin et al. 1992).

The existence of ambient face touching among chimpanzees permits still another test of Heyes' anaesthetization hypothesis. Povinelli et al. (1993) reported a rather striking developmental transition among chimpanzees, with animals younger than 6 years of age rarely showing self-recognition. Most adolescents show compelling signs of self-recognition; however, among adults aged 16 years or older there is a decline in the proportion of chimpanzees that appear to recognize themselves in mirrors. Applying Heyes' hypothesis to these data, one would expect younger chimpanzees to show lower ambient levels of face touching than adolescents, and adults ought to fall somewhere in between. To test this implication, Povinelli (this study) instructed a trained observer to record the number of times that chimpanzees touched their faces with their hands (excluding contacts that occurred in the context of feeding) during two 5-min samples. The observer was not informed as to the purpose of the study, and subsequent debriefings revealed that the observer did not guess its true purpose. Forty-one chimpanzees were observed from five different social groups and all had previously participated in a study of self-recognition roughly 2 years earlier. The demographics of these groups are indicated in Table I.

Table I. Mean (± SE) number of hand-to-face contacts by chimpanzees per 5 min

Group	Number of touches	*N*
Nursery peer-reared groups		
3-year-olds	9.1 (4.1)	15
6–7-year-olds	9.3 (6.4)	9
Family groups		
Adults	15.1 (7.0)	11
Dependent offspring (age range 9–48 months)	14.8 (7.4)	6

If Heyes' account were valid, one would expect a linear ordering of the groups in terms of mean number of face touches from highest to lowest as follows: 6–7-year-olds>adults>3-year-olds>dependent offspring of adults. The results offer no support for Heyes' contention that apparent instances of mirror self-exploratory behaviour are simply a by-product of ambient levels of face touching (Table I). Although an ANOVA revealed an overall effect of group ($F_{3,47}=3.113$, $P<0.05$), Tukey–Kramer multiple comparison post-hoc tests revealed no significant difference between any two groups. There were no differences between 3-year-olds and 6–7-year-olds in the mean number of touches per 5 min (Table I), despite the fact that 6–7 years of age was the point at which Povinelli et al. discovered a developmental transition in mirror-mediated self-exploratory behaviour in this same population of animals. Also contrary to Heyes' account, there was no difference between the adults and their offspring who were housed in the same group.

Other Mark Test Considerations

The anaesthetization hypothesis is rendered all the more implausible when one considers other details of the reports of self-recognition. In the original study, Gallup (1970) noted a number of instances in which chimpanzees carefully inspected (looked at and/or smelled) the fingers that came in contact with the facial marks that could only be seen in the mirror. Inspecting the fingers is not a high-probability ambient response, and in the instances observed by Gallup it was always conditional upon having just touched one of the marks that the animal could only see in the mirror. Povinelli et al. (1993) reported similar

observations. The anaesthetization hypothesis is also contrary to the fact that subjects that pass the mark test typically show compelling patterns of mirror-mediated self-directed responding prior to anaesthetization (e.g. Gallup et al. 1971; Povinelli et al. 1993).

We would not typically score random face/mark touching as evidence of either self-directed or mark-directed responding in the first place. To qualify as an instance of mark-directed (or self-directed) behaviour, most investigators require that the response appears to be mirror-mediated, so responses to facial marks that occur when the animal is not oriented towards or looking at the mirror are not scored as mark-directed (see Povinelli et al. 1993).

Is Self-directed Behaviour an Artefact of Normal Self-grooming?

A related feature of Heyes' argument is that the appearance of self-directed behaviour by chimpanzees looking at themselves in mirrors has nothing to do with mirror-guided body inspection. Heyes contended that the chimpanzee's initial social reactions to mirrors displace normal baseline levels of self-grooming, but as the social behaviour wanes, self-grooming returns and is mistaken by observers for mirror-guided self-exploratory behaviour.

T. J. Eddy, D. J. Povinelli & G. G. Gallup (unpublished data) recently developed a technique to distinguish between self-grooming and mirror-guided self-exploratory behaviour. Chimpanzees with extensive experience with mirrors were videotaped while they were observing one of two stimuli, either a mirror or a comparably sized video monitor depicting other familiar young chimpanzees. These recordings displayed the chimpanzees' reactions to the stimuli, but did not reveal what they were seeing. T. J. Eddy et al. found that observers who do not know what the chimpanzees were seeing reported much higher levels of self-directed behaviour when 7–10-year-old chimpanzees were looking at a mirror than when they were watching a videotape of other chimpanzees. On the other hand, and consistent with the developmental data reported by Povinelli et al. (1993), observers failed to assign differential ratings to the two stimulus conditions when the chimpanzees were 3 years old. Thus, contrary to Heyes' thesis, mirror-mediated patterns of self-directed behaviour in chimpanzees old enough to show self-recognition can be reliably distinguished from instances of normal self-grooming, general scratching or body touching (see also Eddy et al., in press).

Species Differences in Face Touching

Heyes also contended that a principal reason that monkeys and (some) apes differ in their apparent ability to recognize themselves in mirrors is that monkeys engage in much lower ambient or baseline levels of face-touching behaviour than do apes. In support of this assertion, she cited a report by Dimond & Harries (1984), which ostensibly showed that monkeys rarely touch their own faces. Suarez & Gallup 1986, however, failed to replicate Dimond & Harries' findings. Suarez & Gallup found internal discrepancies in Dimond & Harries' data, along with a number of computational errors, the use of inappropriate statistical tests, and conclusions that either did not follow from or were actually contrary to their own data. In an attempt to replicate Dimond & Harries' findings with monkeys using more rigorous procedures under better controlled conditions, Suarez & Gallup discovered a level of face-touching behaviour in an independent sample of rhesus macaques *Macaca mulatta*, and pigtailed macaques, *M. nemestrina*, that was more comparable to what Dimond & Harries found for apes, and over 10 times higher than what they reported for monkeys. Thus, little evidence supports Heyes' account of species differences in self-recognition as a mere by-product of differences in ambient face touching.

The Mark Test Revisited

By focusing primarily on the mark test, Heyes made what has become a common mistake among critics of research on self-recognition (e.g. Epstein et al. 1981; Thompson & Boatright-Horowitz 1994). The mark test was never meant to be taken as synonymous with self-recognition. Rather, it was originally devised as a means of validating impressions that arose out of seeing animals ostensibly use mirrors to respond to themselves. The existence of compelling instances of mirror-mediated patterns of self-directed behaviour are not only what prompted the development of the mark test, but such behaviour patterns, when

carefully documented using rigorous criteria, remain among the most fundamental data for distinguishing between organisms that are and are not capable of processing mirrored information about themselves (e.g. Povinelli et al. 1993). Although these behaviour patterns have been commonly noted in chimpanzees, no one has ever reported compelling evidence of mirror-mediated, self-directed responses in monkeys, which even after prolonged exposure spanning periods of years often continue to react to themselves in a mirror as though confronted by another monkey (e.g. Gallup & Suarez 1991; Anderson 1994).

Lack of Convergent Evidence?

We have attempted to show that Heyes' claims about how chimpanzees do not display mirror-mediated patterns of self-exploration are unfounded. What about Heyes' additional claim that the data from the study by Menzel et al. (1985) using live video 'are not compelling' (page 913)? After reviewing Menzel et al.'s study, Heyes concluded that 'To find out if the chimpanzees were really using the mirror [sic: video] to guide their hand movements it would have been necessary to include a control condition in which subjects had access only to a (pre-recorded) video showing the spot's location, but not their hand' (page 914). Yet a careful reading of Menzel et al.'s paper reveals that precisely such a control condition was included: 'Control tests showed that the chimpanzees discriminated which of two simultaneously presented monitors showed the live monitor image and which showed a tape . . . [including] . . . a tape that showed only the backside of the door, with target objects on it . . . without a reaching hand in the picture' (page 214).

Conclusions

Heyes' criticisms of self-recognition as an artefact of anaesthetization and species differences among primates in face touching are groundless. In attempting to discredit self-recognition research, Heyes not only failed to adequately represent the existing literature, but she also failed to present new evidence to support her position and neglected to provide any constructive suggestions for future research.

Two questions can be posed about self-recognition. Does it exist? And if it exists, is it important? We have deliberately restricted our critique of Heyes' paper to the first question. Whether organisms that can recognize themselves in mirrors are fundamentally different from those that lack this capacity will only be resolved through additional research. In the meantime, however, it is important to note that theorizing about self-recognition, its implications for self-conception and a corresponding capacity for mental state attribution has been a rich source of testable hypotheses about both the evolution and ontogeny of social intelligence (e.g. Gallup 1982; Bischof-Kohler 1988; Asendorpf & Baudonniere 1993; Gallup & Povinelli 1993; Povinelli 1993).

REFERENCES

Anderson, J. R. 1983. Responses to mirror-image stimulation, and assessment of self-recognition in mirror- and peer-reared stumptailed macaques. *Q. Jl exp. Psychol.*, **35B,** 201–212.

Anderson, J. R. 1994. The monkey in the mirror: a strange conspecific. In: *Self-awareness in Animals and Humans* (Ed. by S. T. Parker, R. W. Mitchell & M. L. Boccia), pp. 315–329. New York: Cambridge University Press.

Asendorpf, J. B. & Beaudonniere, P.-M. 1993. Self-awareness and other-awareness: mirror self-recognition and synchronic imitation among unfamiliar peers. *Devl Psychol.*, **29,** 88–95.

Bischof-Kohler, D. 1988. Uber der zusammenhang von empathie und de fahigkeit, sich im spiegel zu erkennen. *Schweiz. Z. Psychol.*, **47,** 147–159.

Calhoun, S. & Thompson, R. L. 1988. Long-term retention of self-recognition by chimpanzees. *Am. J. Primatol.*, **15,** 361–365.

Dimond, S. & Harries, R. 1984. Face touching in monkeys, apes and man: evolutionary origins and cerebral asymmetry. *Neuropsychologia*, **22,** 227–233.

Eddy, T. J., Gallup, G. G., Jr & Povinelli, D. J. In press. Age differences in the ability of chimpanzees to distinguish mirror-images of self from video images of others. *J. comp. Psychol.*

Epstein, R., Lanza, R. P. & Skinner, B. F. 1981. 'Self-awareness' in the pigeon. *Science*, **212,** 695–696.

Gallup, G. G., Jr. 1970. Chimpanzees: self-recognition. *Science*, **167,** 86–87.

Gallup, G. G., Jr. 1982. Self-awareness and the emergence of mind in primates. *Am. J. Primatol.*, **2,** 237–248.

Gallup, G. G., Jr. 1994. Self-recognition: research strategies and experimental design. In: *Self-awareness in Animal and Humans* (Ed. by S. T. Parker, R. W. Mitchell & M. L. Boccia), pp. 35–50. New York: Cambridge University Press.

Gallup, G. G., Jr., McClure, M. K., Hill, S. D. & Bundy, R. A. 1971. Capacity for self-recognition in differentially reared chimpanzees. *Psychol. Rec.*, **21,** 69–74.

Gallup, G. G., Jr & Povinelli, D. J. 1993. Mirror, mirror on the wall which is the most heuristic theory of them all? *New Ideas Psychol.*, **11,** 327–335.

Gallup, G. G., Jr & Suarez, S. D. 1991. Social responding to mirrors in rhesus monkeys (*Macaca mulatta*): effects of temporary mirror removal. *J. comp. Psychol.*, **105,** 376–379.

Heyes, C. M. 1994. Reflections on self-recognition in primates. *Anim. Behav.*, **47,** 909–919.

Lethmate, J. & Dücker, G. 1973. Untersuchungen am sebsterkennen im spiegel bei orangutans einigen anderen affenarten. *Z. Tierpsychol.*, **33,** 248–269.

Lin, A. C., Bard, K. A. & Anderson, J. R. 1992. Development of self-recognition in chimpanzees (*Pan troglodytes*). *J. comp. Psychol.*, **106,** 120–127.

Menzel, E. W., Jr, Savage-Rumbaugh, E. S. & Lawson, J. 1985. Chimpanzee (*Pan troglodytes*) spatial problem solving with the use of mirrors and televised equivalents of mirrors. *J. comp. Psychol.*, **99,** 211–217.

Miles, H. L. W. 1994. Me Chantek: the development of self-awareness in a signing orangutan. In: *Self-awareness in Animals and Humans* (Ed. by S. T. Parker, R. W. Mitchell & M. L. Boccia), pp. 254–272. New York: Cambridge University Press.

Patterson, F. G. 1984. Self-recognition by *Gorilla gorilla gorilla*. *Gorilla*, **7,** 2–3.

Povinelli, D. J. 1989. Failure to find self-recognition in Asian elephants (*Elephas maximus*) in contrast to their use of mirror cues to discover hidden food. *J. comp. Psychol.*, **103,** 122–131.

Povinelli, D. J. 1993. Reconstructing the evolution of mind. *Am. Psychol.*, **48,** 493–509.

Povinelli, D. J., Rulf, A. B., Landau, K. R. & Bierschwale, D. T. 1993. Self-recognition in chimpanzees (*Pan troglodytes*): distribution, ontogeny, and patterns of emergence. *J. comp. Psychol.*, **107,** 347–372.

Robert, S. 1986. Ontogeny of mirror behavior in two species of great apes. *Am. J. Primatol.*, **10,** 109–117.

Suarez, S. D. & Gallup, G. G., Jr. 1981. Self-recognition in chimpanzees and orangutans, but not gorillas. *J. hum. Evol.*, **10,** 175–188.

Suarez, S. D. & Gallup, G. G., Jr. 1986. Face touching in primates: a closer look. *Neuropsychologia*, **24,** 597–600.

Thompson, R. L. & Boatright-Horowitz, S. L. 1994. The question of mirror-mediated self-recognition in apes and monkeys: some new results and reservations. In: *Self-awareness in Animals and Humans* (Ed. by S. T. Parker, R. W. Mitchell & M. L. Boccia), pp. 330–349. New York: Cambridge University Press.