

The Mirror Test

Gordon G. Gallup, Jr., James R. Anderson, and Daniel J. Shillito

Can animals recognize themselves in mirrors? Gallup (1970) conducted an experimental test of this question using a relatively simple approach. Individually housed chimpanzees were confronted with a full-length mirror outside their cages for a period of 10 days. The chimpanzees initially reacted as if they were seeing another chimpanzee and engaged in a variety of social displays directed toward the reflection. These social responses waned after the first few days. Rather than continue to respond to the mirror as such, the chimpanzees began using the mirror to respond to themselves by engaging in mirror-mediated facial and bodily movements and self-directed responses such as grooming parts of the body only visible in the mirror. The transition from social to self-oriented responding gave the impression that the chimpanzees had learned to recognize themselves; i.e., that they had come to realize that their behavior was the source of the behavior being depicted in the mirror. To assess this possibility Gallup devised the mark test. Each chimpanzee was anesthetized and, while unconscious, a red mark was applied to the brow above one eye and the top half of the opposite ear. A nonodorous, nonirritant dye was used, so that upon recovery from the anesthetic the chimpanzees would have no knowledge of the marks. Observations in the absence of the mirror confirmed this as the chimpanzees rarely touched the marks. When the mirror was reinstated, however, the effect was dramatic: the chimpanzees looked at their reflection and guided their fingers to the marks on their faces that could only be seen in the mirror. In addition to touching the marks repeatedly and looking at their fingers, some even smelled their fingers.

Comparative Data on Self-Recognition

Gallup's (1970) initial study was comparative in the sense that the same procedures were carried out with three different species of monkeys: stumptailed, rhesus, and cynomolgus macaques. The monkeys' initial reactions to the reflection were also social, but in contrast to chimpanzees, the tendency to respond as if in the presence of another monkey persisted. Even after three weeks of mirror exposure, none of the monkeys showed any mirror-aided self-directed behaviors, nor did they use the mirror to investigate the marks during the mark test. The major implications of the study were not only that chimpanzees shared with humans the capacity for self-recognition, but that the capacity might be limited to those primates most closely related to humans, namely the great apes (family *Pongidae*).

In the three decades since this study a substantial literature has accumulated concerning the phylogenetic distribution of self-recognition. Studies involving dozens of species and scores of individual prosimians and monkeys have been conducted to determine to what extent other primates might show any of the criterion behaviors for self-recognition (spontaneous mirror-guided self-exploration and mark-directed responses on the mark test). Primates tested for mirror-image reactions include lemurs and bushbabies (prosimians), squirrel monkeys and several species of marmosets, tamarins, and capuchin monkeys (New World monkeys), several species of baboons and guenons (African Old World monkeys) and numerous species of macaques (Asian Old World monkeys). Even gibbons (Asiatic apes of the family *Hylobatidae*) have been assessed. Some studies have been carefully designed to replicate Gallup's original

mirror exposure and mark test regime, while others have systematically manipulated other variables in an effort to increase the likelihood of getting monkeys to make the transition from a socially oriented to a self-oriented perception of their reflection. Experimental manipulations have ranged from giving monkeys many months or even years of almost continuous exposure to their reflections, starting mirror-image experience at a very young age, and providing mirrors of various shapes and sizes and at various angles and degrees of accessibility. Other attempts to find self-recognition have included training monkeys to attend explicitly to their reflections, training them to use the reflected environmental information as a cue to find otherwise invisible objects, or adapting marking procedures in an effort to improve the animals' responsiveness to the change to their normal physical appearance (Anderson 1984; Anderson and Gallup 1999; Gallup 1987; Gallup 1994).

The collective contribution of all of these studies is that we can now eliminate several potential explanations for the failure of most primates to show any signs of self-recognition. They do not fail because they need earlier or longer experience with mirrors or because they cannot grasp the correspondence between the reflected and the real environments. Non-self-recognizing species do not fail to show mirror-mediated mark-directed responses because of a simple lack of attention or motivation. A control procedure introduced by Gallup et al. (1980) shows that individuals who exhibit no responses to marks in critical body regions during mark tests will respond to body marks that are directly visible without a mirror, such as the wrist or the belly (see also Shillito et al. 1999). Nor do they fail to understand the source of the reflection because of an aversion to making eye contact with their image. When two mirrors are arranged at an angle so that eye-to-eye contact with the reflection is impossible, social responses may diminish, but they

are not replaced by patterns of self-directed responding (Anderson and Roeder 1989; also Shillito et al. 1999).

The failure to find self-recognition in monkeys is not due to poor problem solving skills. Although many species use tools (Beck 1980), experiments with tool-using macaque and capuchin monkeys have revealed no relationship between tool use and self-recognition (Anderson and Marchal 1994). Claims of incipient self-recognition in monkeys or protorecognition have appeared over the years, but in each case the evidence is flawed, inconclusive, or has proven impossible to replicate (see Anderson and Gallup 1999 for a general review). Along with the growing list of failures to find self-recognition in monkeys are studies that have shown similarities in the effectiveness of live conspecifics and mirror-image stimulation for eliciting a variety of social behaviors, reinforcing the view that monkeys perceive their reflection as some kind of conspecific (Anderson 1994).

Thus, Gallup's (1970) suggestion that self-recognition might be limited to the great apes has held up well. Numerous studies have confirmed self-recognition in chimpanzees and there is now information regarding the importance of early social experience (Gallup et al. 1971), along with data on developmental trends and individual differences (Lin et al. 1992; Povinelli et al. 1993). What about other species of great apes? Self-recognition in orangutans is well established (Suarez and Gallup 1981), and several individuals in two captive groups of bonobos have shown mirror-mediated self-exploration (Hyatt and Hopkins 1994; Walraven et al. 1995) indicative of self-recognition. On the other hand, most studies have failed to find convincing evidence in gorillas, in spite of modifications to the original mirror and mark test procedure (Suarez and Gallup 1981; Shillito et al. 1999). There is one claim of positive evidence for a gorilla (Patterson

and Cohn 1994) which has had extensive contact with humans from an early age. It has been hypothesized that under normal circumstances the capacity for self-recognition may not develop in gorillas, but that enculturation in the form of early and extensive rearing by humans may result in the formation of critical neural connections required for the expression of this capacity (Povinelli 1994).

Attempts to Discredit the Mirror Test

The existence of such decisive phyletic differences has been disconcerting to people who are committed to the idea that species differences are a matter of degree rather than kind (Tomasello and Call 1997). People have adopted a number of tactics in an attempt to discredit the mirror test findings and salvage the intellectual continuity hypothesis. Some have tried to modify the criteria for self-recognition. For example, Hauser et al. (1995) claim that when the mark's saliency was increased by applying it to species-significant morphological features (hair-tufts on the subjects' heads), they found positive evidence of mirror self-recognition in cotton-top tamarins. Hauser et al. contend that increased viewing time during the mirror-present condition compared to the mirror-absent condition of the mark test constitutes evidence that the tamarins recognized their image. Given that monkeys view their reflections as conspecifics (see Anderson 1994 for a review), it is not surprising that Hauser's subjects exhibited an increase in viewing time when confronted with what appeared to be another monkey with bright purple hair tufts (especially given the importance of these tufts to the species). Furthermore, a review of Hauser's videotaped mirror tests reveals that the subjects' mark-directed responses were not attempts to investigate

the marks. Indeed they do not even touch the marks. Rather, subjects appear to be scratching an irritation (in fact, they even used their hind legs to do this in a manner similar to a dog scratching at fleas). More importantly, Hauser and his colleagues now concede that despite several attempts, they have been unable to replicate their original findings of self-recognition in tamarins (Hauser et al. in press).

Epstein and colleagues (1981) have argued that self-awareness does not exist and apparent self-aware acts are byproducts of environmental contingencies. Epstein et al. used an extensive training regimen to engineer positive mark test results with pigeons. Not only have these findings proven difficult, if not impossible to replicate (Thompson and Contie 1994), but the logic behind their approach is seriously flawed. In their zeal to discredit the mirror test, Epstein et al. (1981) missed the point. The mark test was devised as a means of verifying impressions based upon observations of chimpanzees using mirrors to inspect and manipulate otherwise invisible body parts. Training an animal to respond to marks on its body, without collateral evidence of self-recognition indicates more about the achievements of the researchers who designed the training procedures than any underlying ability of the animal (Gallup and Suarez 1986). If training pigeons to peck at marks on their bodies was equivalent to what chimpanzees do, then as a by-product of such training, the pigeons ought to engage in other indicators of self-recognition such as mirror-mediated self-preening behavior. They do not. Furthermore, instead of training the prerequisite responses and then administering the mark test, Epstein et al. trained their pigeons to emit the criterion response (i.e., pecking the mark). This is equivalent to teaching human subjects the correct answers on an IQ test; granted their scores would improve, but such results would reveal nothing about their cognitive abilities. In a recent article on the

pitfalls of radical behaviorism, Frans de Waal describes the Epstein et al. paper as "one of the greatest travesties in behavioral science" (DeWaal 1999: B6).

More recently, Heyes (1994) championed an "anesthesia hypothesis" in still another attempt to discredit the mirror test. Heyes claimed that the increase shown by chimpanzees in mark-directed touches after the introduction of the mirror is an artifact of incomplete recovery from anesthesia. Heyes contended that during the mirror-absent condition of the mark test, subjects are still feeling the effects of the anesthetic agent and consequently their ambient level of self-touching behavior is suppressed. As subjects continue to recover from anesthesia during the subsequent mirror-present condition, their normal level of autogrooming returns, accounting for an increased number of coincidental mark touches during this period. In the same vein Heyes argued that the species differences on the mirror test are due to differences in rates of nonspecific, ambient face touching rather than cognitive distinctions between species.

However, had Heyes conducted a thorough review of the literature it would have been clear from the outset that her concerns were untenable (Gallup et al. 1995). Most researchers wait until their subjects have fully recovered from the anesthesia (at times waiting over 24 hours) before administering the mark test. In fact, some studies have surreptitiously marked chimpanzees without the use of anesthesia using sham-marking protocols and have obtained positive results on the mark test (e.g., Calhoun and Thompson 1988).

Furthermore, the chronology of subjects responses during the mirror test also shows that Heyes' argument was flawed. The anesthesia hypothesis predicts that subjects should exhibit a gradual increase in mark touches throughout the mirror-present condition as the motorically inhibiting effects of the anesthetic diminish. However, results from mirror tests do not follow this

pattern (Povinelli et al. 1997). Rather, self-recognizing subjects exhibit a pronounced interest in their marks immediately after the mirror is introduced, but this interest is short-lived. Once chimpanzees discover that the marks are inconsequential their attention rapidly wanes (as indicated by decreased mark contacts).

Results from a recent experiment examining the temporal pattern and topography of chimpanzees' mark touches further invalidate Heyes' position. Povinelli and colleagues (1997) recorded the duration and number of times subjects touched their marked eyebrow and ear as well as their corresponding unmarked brow and ear. Contrary to Heyes, mark-directed behavior was conditional upon seeing themselves in the mirror and chimpanzees focused their attention almost exclusively on their marked facial features rather than their unmarked eyebrow and ear. Thus mark touches clearly represent attempts to investigate the marks that can only be seen in the mirror, rather than random contacts brought on by increased activity levels

Self-Recognition in Humans

In parallel with the comparative studies of nonhuman primates, developmental psychologists have tried to map the ontogeny of self-recognition in children, and elucidate the relationship between self-recognition and other aspects of the developing sense of self. The modern era of self-recognition studies on humans began when Amsterdam (1972) observed the reactions of young infants and toddlers to a mirror and devised a less rigorous version of the mark test that involved applying rouge to the child's nose (see Gallup 1994 for a critique). Children toward the end of the first year of life show mostly social responses to their reflection (e.g., smiling,

vocalizing). These sometimes persist into the second year, when coy reactions and avoidance are also observed. Not until around 18 months do some infants use the reflection to investigate the mark on their nose, the majority doing so by two years of age. One study reported a positive relationship between performance on tasks related to self-recognition and tasks related to object permanence (Bertenthal and Fischer 1978), but age as a covariate can rarely be ruled out in such studies. In an attempt to establish more precise age-norms, subsequent research has used video techniques to demonstrate the importance of contingency cues in the infant's developing understanding of its own image (Johnson 1982; for a review see Anderson 1984).

The existence of individual differences in self-recognition among chimpanzees is also well documented among humans. Mentally retarded persons sometimes fail to learn to recognize themselves in mirrors (Harris 1977). Among autistic children, self-recognition is developmentally delayed and can remain absent in as many as 30 percent of the cases (Spiker and Ricks 1984). People diagnosed with schizophrenia often experience a disassociation with their image in mirrors and come to respond to the reflection as if in the presence of another person (Gallup et al. in press). At the other end of the life-span, some people with Alzheimer's disease lose the ability to recognize themselves in mirrors (Biringer and Anderson 1993).

Self-Recognition, Self-Awareness, and Mental State Attribution

If the species and individual differences in self-recognition are real, are they important? Mirror self-recognition is an indicator of self-awareness (Gallup 1979). In its most rudimentary form self-awareness is the ability to become the object of your own attention. When you see yourself in

a mirror, you are literally the object of your own attention, but most organisms respond to themselves in mirrors as if confronted by another organism. The ability to correctly infer the identity of the image in the mirror requires a pre-existing sense of self on the part of the organism making that inference. Without a sense of self, how would you know who you were seeing when confronted with your reflection in a mirror? Recent neuropsychological evidence is highly consistent with the proposition that self-recognition taps into the ability to conceive of oneself. Patients with damage to the frontal cortex are not only impaired in their ability to recognize their own faces, but they show corollary deficits in self-evaluation and autobiographical memory (Keenan and Wheeler in press).

As an extension of this line of reasoning, it has been argued that the ability to infer the existence of mental states in others (known as theory of mind, or mental state attribution) is a byproduct of being self-aware (Gallup 1982). The rationale for postulating a connection between self-recognition and mental state attribution is simple. If you are self-aware then you are in a position to use your experience to model the existence of comparable experiences in others. For example, when you see someone who is carrying a large box approach a door, you might be prompted to walk ahead of them and hold the door open. This is based on a set of inferences you make as a consequence of having found yourself in comparable situations. Based on the direction they are walking and their proximity to the door you make an attribution about their intention to leave the building, coupled with a corollary attribution about their inability to open the door because their hands are full. Thus, making inferences about states of mind in others is a logical extension of your experience with your own mental states. Knowledge of self is an inductive springboard for an inferential knowledge of others.

According to this model, species that fail to recognize themselves in mirrors should likewise fail to show evidence of introspectively based social strategies. Because of their inability to take into account what other individuals may know, want, or intend to do, intentional instances of deception, gratitude, grudging, sympathy, and empathy, should be absent in organisms that are not self-aware. Monkeys, for example, which fail to show self-recognition, seem incapable of taking into account mental states in other monkeys (Cheney and Seyfarth 1990). The same holds true for humans. People who fail to recognize themselves in mirrors are often deficient in their ability to infer what other people are thinking. For instance, it is only after children learn to recognize themselves that evidence of being able to take into account what other people are feeling or seeing begins to become evident (Carruthers and Smith 1996). Both embarrassment and the use of personal pronouns, as well as the development of an autobiographical memory, also only appear after children show evidence of self-recognition (Howe and Courage 1997; Lewis et al. 1989). In contrast to normal children, autistic children (who show self-recognition impairment) are deficient in their ability to make inferences about what other people are thinking (Baron-Cohen 2000). Schizophrenics also show mental state attribution deficits, and schizophrenic patients often respond to themselves in mirrors as though they were seeing other people (for details see Gallup et al. in press).

Other developmental studies also bear on the hypothesis that self-recognition is related to the ability to infer mental states in others. Johnson (1982) found that mirror self-recognition in 18-24-month-olds was positively related to the likelihood of altruistic or prosocial intervention (e.g., helping, comforting) when the mother feigned distress. Asendorpf and Baudonnière (1993) classified infants as self-recognizers or non-self-recognizers and paired them in the presence of

objects. Long phases of synchronic imitation (both infants acting similarly on identical objects while monitoring each other) were most characteristic of dyads composed of self-recognizers, and the authors relate self-recognition to the development of perspective-taking skills.

Neuropsychological Correlates of Self-Recognition

There is growing evidence that self-recognition can be localized in the human brain. For instance, Keenan and colleagues (Keenan et al. 1999) found that there were no differences in reaction time required to identify familiar faces as opposed to their own face when people responded with their right hand. However, when required to press keys with their left hand, subjects identified their own faces faster than faces of other people. As a consequence of contralateral control, the left-hand advantage suggests that self-recognition is related to processing of information in the right cerebral hemisphere. Keenan et al. (2001) report another intriguing case of hemispheric lateralization of self-recognition involving epileptic patients undergoing preoperative evaluation using the application of intracarotid amobarbital, known as the WADA test. These patients were shown a morphed picture consisting of their own face and that of a famous person while either the right or left hemisphere was anesthetized. Upon recovery from anesthesia they remembered seeing their own faces when the left hemisphere was anesthetized, but only the faces of familiar people when the right hemisphere was anesthetized. Thus, it is possible to literally turn self-recognition on and off by selectively deactivating different parts of the brain. There are also reports of brain damaged patients who fail to recognize themselves in mirrors. Breen (1999) describes a patient with damage restricted to the right prefrontal cortex that could identify other

people with a mirror, but insisted that his own reflection was not himself. Keenan and Wheeler (in press) review a number of other studies that implicate both right hemispheric lateralization and localization of self-recognition in the prefrontal cortex. In support of the idea that self-recognition is a byproduct of self-awareness, other studies have shown that self-evaluation and autobiographical memories are also localized in the right prefrontal region.

The same part of the brain that appears to be responsible for self-recognition is also crucial for making inferences about what other people are thinking. For example, Stone and colleagues (1998) report that patients with right frontal cortex damage have difficulty representing mental states in other people. Likewise, Happe et al. (1999) found that patients with right hemisphere damage were impaired in their ability to interpret mental state attribution narratives, and fail to appreciate humor that requires understanding the mental state of different characters. More recently, Stuss et al. (2001) found that in contrast to patients with brain damage elsewhere, those with lesions restricted to the right frontal lobes were deficient in visual perspective taking and in their ability to detect instances of deception.

Thus, the neuropsychological evidence bolsters the proposition that self-recognition is an indicator of self-awareness, and that mental state attribution is a byproduct of self-awareness (Gallup 1982). The frontal cortex (particularly the right prefrontal cortex) appears to be involved in self-recognition, self-evaluation, episodic (autobiographical) memory, introspection, humor, and mental state attribution. Furthermore, deficits in mirror self-recognition and mental state attribution are characteristic of a number of psychiatric disorders (see Gallup et al. in press).

Finally, in light of what we now know about the neuroanatomical correlates of self-awareness in humans, it is important to return to a comparative perspective because

preliminary data may shed new light on the gorilla's peculiar inability to recognize itself in a mirror. Relative to the other great apes which show self-recognition, gorillas appear to have a smaller, less well developed frontal cortex (Semendeferi 1999). Indeed, gorilla brains are not only smaller in areas that have been implicated in social intelligence, but they are also less structurally/anatomically lateralized than those of their chimpanzees and orangutan counterparts (LeMay and Geschwind 1975).

References

Amsterdam, B. (1972). Mirror self-image reactions before the age of two. *Developmental Psychobiology* 5: 297-305.

Anderson, J. R. (1984). Monkeys with mirrors: some questions for primate psychology. *International Journal of Primatology* 5: 81-98.

Anderson, J. R. (1994). The monkey in the mirror: The strange conspecific. In *Self-awareness in animals and humans: Developmental perspectives*, ed. R. W. Mitchell, S.T. Parker, and M.L. Boccia, pp. 315-329. New York: Cambridge University Press.

Anderson, J. R., and Gallup, G. G., Jr. (1999). Self-recognition in non-human primates: past and future challenges. In *Animal models of human emotion and cognition*, ed. M. Haug and R. E. Whalen, pp. 175-194. Washington DC: American Psychological Association.

Anderson, J. R., and Marchal, P. (1994). Capuchin monkeys and confrontations with mirrors. In *Current Primatology: Social Development, Learning and Behaviour*, ed. J.-J. Roeder and B. Thierry and J. R. Anderson and N. Herrenschildt, pp. 371-380. Strasbourg: University Louis Pasteur.

Anderson, J. R., and Roeder, J.-J. (1989). Responses of capuchin monkeys (*Cebus apella*) to different conditions of mirror stimulation. *Primates* 30: 581-587.

Asendorpf, J. B., and Baudonnière, P.-M. (1993). Self-awareness and other-awareness: mirror self-recognition and synchronic imitation among unfamiliar peers. *Developmental Psychobiology* 29: 88-95.

Baron-Cohen, S. (2000). The cognitive neuroscience of autism: Evolutionary approaches. In *The New Cognitive Neurosciences (2nd ed.)*, ed. M. Gazzaniga, pp. 1249-1257. Cambridge, MA: MIT press.

Beck, B. B. (1980). *Animal tool behavior: the use and manufacture of tools by animals*. New York: Garland.

Bertenthal, B. I., and Fischer, K. W. (1978). Development of self-recognition in the infant. *Developmental Psychology* 14: 44-50.

Biringer, F. and Anderson., J.R. (1993). Self-recognition in Alzheimer's disease: Use of mirror and video techniques and enrichment. In *Recent Advances in Aging Science* (Vol. 1), ed. I. A. G. E. Beregi, and K. Rajczi, pp. 697-705. Bologna: Monduzzi Editore.

Breen, N. (1999). Misinterpreting the mirrored self. Paper presented at the *Association for the Scientific Study of Consciousness*, London, Ontario.

Calhoun, S. and Thompson., R. L. (1988). Long-term retention of self-recognition by chimpanzees. *American Journal of Primatology* 15: 361-365.

Carruthers, P. and Smith., P.K. (1996). *Theories of Theories of Mind*. Cambridge: Cambridge University Press.

Cheney, D. L. and Seyfarth, R. W. (1990). *How Monkeys see the World: Inside the Mind of Another Species*. Chicago: University of Chicago Press.

DeWaal, F. B. M. (1999). The pitfalls of not knowing the whole animal. *Chronicle of Higher Education* 26: B4-6.

Epstein, R., Lanza, R. P., and 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. (1979). *Self-recognition in chimpanzees and man: A developmental and comparative perspective*. New York: Plenum Press.

Gallup, G. G., Jr. (1982). Self-awareness and the emergence of mind in primates. *American Journal of Primatology* 2: 237-248.

Gallup, G. G., Jr. (1987). Self-awareness. In *Comparative Primate Biology, Behavior, Cognition, and Motivation* (Vol. 2B), ed. J. R. E. G. Mitchell, pp. 3-16. New York: Liss.

Gallup, G. G., Jr. (1994). Self-recognition: research strategies and experimental design. In *Self-awareness in animals and humans: developmental perspectives*, ed. S. T. Parker and R. W. Mitchell and M. L. Boccia, pp. 35-50. New York: Cambridge University Press.

Gallup, G. G., Jr., Anderson, J. R., and Platek, S. M. (in press). Self-awareness, Social Intelligence, and Schizophrenia. In *The self and schizophrenia: a neuropsychological perspective*, ed. A. S. David and T. Kircher, pp. xxx-xxx. Cambridge: Cambridge University Press.

Gallup, G. G., Jr., McClure, M. K., Hill, S. D., and Bundy, R. A. (1971). Capacity for self-recognition in differentially reared chimpanzees. *Psychological Record* 21: 69-74.

Gallup, G. G., Jr., Povinelli, D. J., Suarez, S. D., Anderson, J. R., Lethmate, J., and Menzel, E.-W. J. (1995). Further reflections on self-recognition in primates. *Animal Behaviour* 50: 1525-1532.

Gallup, G. G., Jr., and Suarez, S. D. (1986). Self-awareness and the emergence of mind in humans and other primates. In *Psychological Perspectives on the Self* (Vol. 3), ed. J. Suls and A. Greenwald, pp. 3-26. Hillsdale, N.J.: Erlbaum.

Gallup, G. G., Jr., Wallnau, L. B., and Suarez, S. D. (1980). Failure to find self-recognition in mother-infant and infant-infant rhesus monkey pairs. *Folia Primatologica* 33: 210-219.

Happe, F. G., Brownell, H., Winner, E. (1999). Acquired "theory of mind" impairments following stroke. *Cognition* 70: 211-240.

Harris, L. P. (1977). Self-recognition among institutionalized profoundly retarded males: A replication. *Bulletin of the Psychonomic Society* 9: 43-44.

Hauser, M. D., Kralik, J., Botto-Mahan, C., Garrett, M., and Oser, J. (1995). Self-recognition in primates: phylogeny and the salience of species-typical features. *Proceedings of the National Academy of Sciences, USA* 92: 10811-10814.

Hauser, M. D., Miller, C. T., Liu, K., and Gupta, R. (in press). Cotton-top tamarins (*Saguinus oedipus*) fail to show mirror-guided self exploration. *American Journal of Primatology* yy: xxx-xxx.

Heyes, C. M. (1994). Reflections on self-recognition in primates. *Animal Behaviour* 47: 909-919.

Howe, M. L., and Courage, M. L. (1997). The emergence and early development of autobiographical memory. *Psychological Review* 104: 499-523.

Hyatt, C. W., and Hopkins, W. D. (1994). Self-awareness in bonobos and chimpanzees: a comparative approach. In *Self-awareness in animals and humans: developmental perspectives*, ed. S. T. Parker and R. W. Mitchell and M. L. Boccia, pp. 248-253. New York: Cambridge University Press.

Johnson, D. B. (1982). Altruistic behavior and the development of the self in infants. *Merill-Palmer-Quarterly* 28: 379-388.

Keenan, J. P., McCutcheon, B., Freund, S., Gallup, G. G., Jr., Sanders, G., and Pascual-Leone, A. (1999). Left hand advantage in a self-face recognition task. *Neuropsychologia* 37: 1421-1425.

Keenan, J. P., Nelson, A., M., O. C., and Pascual-Leone, A. (2001). Self-recognition and the right hemisphere. *Nature* 409: 305.

Keenan, J. P., and Wheeler, M. (in press). The neuropsychology of self. In *The Self and Schizophrenia: A Neuropsychological Perspective*, ed. A. S. David and T. Kircher, pp xxx-xxx. Cambridge: Cambridge University Press.

LeMay, M., and Geschwind, N. (1975). Hemispheric differences in the brains of great apes. *Brain, Behavior, and Evolution* 11: 48-52.

Lewis, M., Sullivan, M. W., Stanger, C., and Weiss, M. (1989). Self development and self-conscious emotions. *Child Development* 60: 146-156.

Lin, A. C., Bard, K. A., and Anderson, J. R. (1992). Development of self-recognition in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 106: 120-127.

Patterson, F. G. P., and Cohn, R. H. (1994). Self-recognition and self-awareness in lowland gorillas. In *Self-awareness in animals and humans: developmental perspectives*, ed. S. T. Parker and R. W. Mitchell and M. L. Boccia, pp. 273-290. New York: Cambridge University Press.

Povinelli, D. J. (1994). How to create self-recognizing gorillas (but do not try it on macaques). In *Self-awareness in animals and humans: developmental perspectives*, ed. S. T. Parker and R. W. Mitchell and M. L. Boccia, pp. 291-300. New York: Cambridge University Press.

Povinelli, D. J., Gallup, G. G., Jr., Eddy, T. J., Bierschwale, D. T., Engstrom, M. C., Perilloux, H. K., and Toxopeus, I. B. (1997). Chimpanzees recognize themselves in mirrors. *Animal Behavior* 53: 1083-1088.

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

Semendeferi, K. (1999). The frontal lobes of the great apes with a focus on the gorilla and the orangutan. In *The Mentalities of Gorillas and Orangutans*, ed. R. M. H. M. S. Parker, pp. 70-95. Cambridge: Cambridge University Press.

Shillito, D. J., Gallup, G. G., Jr, and Beck, B. B. (1999). Factors affecting mirror behavior in western lowland gorillas, *Gorilla gorilla*. *Animal Behavior* 57: 999-1004.

Spiker, D. and Ricks, M. (1984). Visual Self-recognition in autistic children: Developmental relationships. *Child Development* 55: 214-225.

Stone, V. E., Baron-Cohen, S., and Knight, R.T. (1998). Frontal lobe contributions to theory of mind. *Journal of Cognitive Neuroscience* 10: 640-656.

Stuss, D. T., Gallup, G.G., Jr., and Alexander, M.P. (2001). The frontal lobes are necessary for theory of mind. *Brain* 124:279-286.

Suarez, S., and Gallup, G. G., Jr. (1981). Self-recognition in chimpanzees and orangutans, but not gorillas. *Journal of Human Evolution* 10: 157-188.

Thompson, R. K. R., and Contie, C. L. (1994). *Further reflections on mirror usage by pigeons: Lessons from Winnie-the-Pooh and Pinocchio too*. New York: Cambridge University Press.

Tomasello, M. and Call., J. (1997). *Primate Cognition*. Oxford: Oxford University Press.

Walraven, V., van Elsacker, L., and Verheyen, R. (1995). Reactions of a group of pygmy chimpanzees (*Pan paniscus*) to their mirror images: evidence of self-recognition. *Primates* 36: 145-150.