ARTICLE IN PRESS

PERGAMON

Neuropsychologia 1493 (2002) 1–6

NEUROPSYCHOLOGIA

www.elsevier.com/locate/neuropsychologia

An 8-year longitudinal study of mirror self-recognition in chimpanzees (*Pan troglodytes*)

Monique W. de Veer [a,1], Gordon G. Gallup Jr. [b,2], Laura A. Theall [c], Ruud van den Bos [a,1], Daniel J. Povinelli [c,*]

[a] *Animal Welfare Centre, Faculty of Veterinary Medicine, Utrecht University, Utrecht, The Netherlands*
[b] *Department of Psychology, State University of New York at Albany, Albany, NY 12222, USA*
[c] *Cognitive Evolution Group, University of Louisiana at Lafayette, 4401 W. Admiral Doyle Drive, New Iberia, LA 70560 USA*

Received 28 March 2002; accepted 2 June 2002

Abstract

In a previous cross-sectional study of mirror self-recognition involving 92 chimpanzees, Povinelli et al. [Journal of Comparative Psychology 107 (1993) 347] reported a peak in the proportion of animals exhibiting self-recognition in the adolescent/young adult sample (8–15 years), with 75% being classified as positive. In contrast, only 26% of the older animals (16–39 years) were classified as positive, suggesting a marked decline in self-recognition in middle to late adulthood. In the present study, all of the chimpanzees from the 8–15-year-old group in the Povinelli et al. study ($n = 12$) were again tested for self-recognition, 8 years later. Using the same criteria, 67% of the animals were classified the same. Although a higher proportion of the adult animals in this study (50%) exhibited self-recognition than would be inferred on the basis of the previous study (25%), all changes in self-recognition status were in the negative direction. These results show that mirror self-recognition is a highly stable trait in many chimpanzees, but may be subject to decline with age. Connections with human research are briefly discussed.

Keywords: Mirror self-recognition; *Pan troglodytes*; Human research

1. Introduction

Gallup [6] demonstrated that chimpanzees (*Pan troglodytes*) are capable of what has been termed self-recognition in mirrors. Typically, chimpanzees initially react to their mirror image as if it were another chimpanzee, but after a period ranging from a few minutes to several days (see [11]), they use the mirror to explore otherwise difficult to view parts of their bodies. To validate the impression of self-recognition that arose from observing the animals engaging in self-exploratory behaviors, Gallup [6] designed a test where the animals were sedated and marked on the right eyebrow ridge and upper left ear. After recovery, the chimpanzees showed clear and selective attempts to touch and investigate these marks while in front of the mirror (for evidence of the specificity of these touches, see [12]).

In a cross-sectional study involving a sample of 92 chimpanzees, Povinelli et al. ([11], Exp. 1) obtained evidence that self-recognition typically emerges in young adolescence; relatively few animals younger than 8 years of age displayed compelling instances of self-exploratory behavior, whereas 75% of the subjects aged 8–15 years ($n = 12$) did so. Povinelli et al. also reported the surprising finding that only 26% of the older adults (16–39 years, $n = 35$) exhibited evidence of mirror-mediated patterns of self-exploration. Humans begin to show mirror self-recognition between 18 and 24 months of age (e.g. [1]) and do not typically lose the capacity until they enter the advanced stages of senility (for a review see [7]). Thus, on the basis of the Povinelli et al. sample, the onset of self-recognition in chimpanzees would appear to be delayed relative to humans, and the loss of self-recognition in later life by chimpanzees may be accelerated.

Povinelli et al. [11] also provided evidence for a dissociation between the two primary measures of mirror self-recognition: spontaneous self-exploratory behaviors and the results of mark tests. Thirty-six subjects who had been coded as either self-recognition positive (SR+, $n = 18$), negative (SR−, $n = 12$) or ambiguous (SR?, $n = 6$) on the basis of their spontaneous patterns of mirror-mediated self-exploratory behavior, were administered mark tests.

* Corresponding author. Tel.: +1-337-482-0265; fax: +1-337-373-0057.
E-mail address: ceg@louisiana.edu (D.J. Povinelli).
[1] Tel.: +31-302-53-4851; fax: +31-302-53-7727.
[2] Tel.: +1-518-442-4852; fax: +1-518-442-4867.

0028-3932/02/$ – see front matter © 2002 Published by Elsevier Science Ltd.
PII: S0028-3932(02)00153-7

Positive results on the mark test came almost exclusively from animals that had been diagnosed as SR+ (82%, 9/11 cases), and animals the were coded as SR? or SR− exhibited only rare instances of passing the mark test (11%, 2/18 cases). However, only half of the SR+ animals passed the mark test (50%, 9/18 cases). These data add confidence to the scheme developed by Povinelli et al. for coding the spontaneous behavioral reactions of chimpanzees to their mirror images (see Section 2), by showing that the coding system does not lead to a substantial number of false negatives (i.e. SR− diagnosis based on spontaneous behavioral reactions to mirror, but SR+ diagnosis on mark test).

The main purpose of the present study was to examine the long-term stability of one of the measures of mirror self-recognition (self-exploratory behavior) in the adolescent subjects of Povinelli et al. [11]. To do so, we used a longitudinal design and re-tested the 12 chimpanzees from the 8–15-year-old group in the Povinelli et al. [11] study 8 years after the original study. These data can help to determine whether the apparent decline in mirror-mediated self-exploratory behavior among adult chimpanzees indicated by the cross-sectional data of Povinelli et al. is a robust phenomenon. A secondary objective was to re-examine data from the original study to further explore the relationship between measures of spontaneous self-exploratory behavior (the measure used here) and the results of the mark tests.

2. Method

2.1. Subjects

Subjects were 12 chimpanzees (*Pan troglodytes*) housed in social groups (range = 6–9 animals) at the University of Louisiana (enclosure dimensions: exterior, 8 m × 5.5 m × 4 m; interior, 4.5 m × 5.5 m × 3 m). Eight years earlier, when they were between 8 and 15 years of age (see Table 1), these subjects had participated in the mirror self-recognition experiments of Povinelli et al. [11]. At the time of the present tests, the subjects ranged in age from 16 to 23 years.

Table 1
Subject information

Subject	Gender	Age		1992 classification
		1992	2000	
Cindy	F	8 (5)	16 (3)	SR+
Chakema	F	9 (7)	18 (1)	SR+
Angela	F	10 (1)	18 (11)	SR+
Keetah	F	10 (6)	18 (1)	SR+
Misty	F	10 (10)	18 (8)	SR+
Christy	F	10 (10)	18 (8)	SR+
Gilda	F	11 (11)	19 (9)	SR+
Lisa	F	12 (10)	20 (7)	SR+
Schulman	F	15 (4)	23 (1)	SR+
Liz	F	15 (11)	23 (9)	SR?
Abby	F	10 (5)	18 (2)	SR−
Christine	F	11 (1)	18 (11)	SR−

The values in parentheses are number of animals.

2.2. Materials

For testing, a one-way mirror (47 cm × 43 cm) was mounted in front of a window cut into the top half of a wooden box. A video camera positioned on a tripod was placed directly behind the mirror inside the box. The camera was covered by a cloth to prevent light from entering the box behind the mirror. This arrangement made it possible to obtain high-quality video footage of the chimpanzees as they looked in the mirror. This procedure differed slightly from the study conducted by Povinelli et al. [11] who used trained observers to code the behaviors as they occurred. Methodological advances in the interim, however, suggested using this more reliable method (see [4]). The apparatus was placed in front of the enclosure, as close to the mesh as possible, but out of reach of the chimpanzees.

2.3. Procedure

The 12 animals from the Povinelli et al. study were housed with a variety of other animals in different enclosures. Each of these groups were exposed to the mirror for 6 days. Each day, two groups were tested; one group was filmed twice a day for 2 h (2 h in the morning and 2 h in the late afternoon) and one group was filmed once for 2 h in the early afternoon. After filming, the apparatus was removed and another mirror was placed at the same location and left there for the rest of the day. The order and time of testing was counterbalanced across days.

2.4. Videotape analysis

The videotapes were coded for the presence of mirror proximity and self-exploratory behaviors using the published protocols and criteria (see Table 1 in [11]). Briefly, mirror proximity was scored when the subject was near the mirror and mirror-mediated patterns of self-exploratory behavior were scored when the animal used the fingers or hands to manipulate parts of the body otherwise not visible (e.g. facial areas and ano-genital region). To qualify as mirror-mediated, the animal had to be looking at its own image in the mirror when the behavior occurred. Following Povinelli et al. [11], a distinction was made between weak and compelling instances of self-exploratory behaviors (see Table 2).

Videotape coding occurred after all groups had been tested. To facilitate coding by a naïve rater, a time stamp was incorporated onto the video images, and each subject was tagged by editing a colored dot onto their image whenever they appeared on screen. The tapes were scored by a person who was naive to the purpose of the study. Inter-observer reliability was calculated by comparing the coding of the naive rater and the principal investigator (MdV) at 1 s intervals for 5 min samples from five of the

Table 2
Compelling vs. weak self-exploratory behaviors

Compelling self-exploratory behaviors	
	Using hands or feet to groom/pick/inspect any part of the face or teeth repetitively
	Grooming neck, shoulder or back repetitively
	Manipulating ano-genital region
Weak self-exploratory behaviors	
	Grooming or picking any part of the face (including teeth) non-repetitively
	Observing food or liquid in open mouth
	Positioning body to look at ano-genital region
	Pulling hair on any part of the body repetitively
	Rubbing or wiping any part of the face repetitively
	Touching ano-genital region
	Manipulating chewed food
	Manipulating lips
	Manipulating nipples

subjects. This analysis revealed an agreement in 93.6% of the intervals. To avoid artificially high levels of agreement due to the absence of behavior, the samples were selected by the principal investigator from animals who showed high levels of activity in front of the mirror. As an additional check, a secondary inter-laboratory coding was conducted by having a third observer (naive to the purpose of the study and situated in a different laboratory) code the same 5 min samples. The agreement with the original rater was 96.0%.

Following Povinelli et al. [11], animals that exhibited five or more compelling instances of self-exploratory behavior, totaling at least 30 s, were classified as SR+. Animals that showed from one to four instances or in total less than 30 s of compelling self-exploratory behavior were classified as SR?. Those that showed no compelling instances of self-exploratory behavior were classified as SR−.

2.5. Archival analysis

To further examine the relationship between the behavioral measures used in the present study, and the results of mark tests, we examined the archival records for all 18 subjects from the Povinelli et al. [11] study who were coded as SR+ using the behavioral criterion (see above) and who had also received mark tests (this included 7/12 of the subjects in the longitudinal study). We then examined the relationship between the number of spontaneous bouts of self-exploratory behavior they exhibited and the number of mark-directed touches they made during the testing phase of the mark test.

3. Results

The central focus of this investigation was the stability of the SR status of each animal from 1992 to 2000, and whether a substantially lower percentage of animals exhibited evidence of self-recognition from 1992 to 2000.

3.1. Trait stability

First, as can be seen in Table 3, 8/12 animals (67%) exhibited the same classification at the two time-points. Six of the nine animals classified as SR+ in 1992, still showed compelling evidence of self-recognition in 2000. Two subjects (Keetah and Lisa), who were SR+ in 1992 were diagnosed as SR? in 2000. Keetah showed three bouts of compelling self-exploratory behaviors for 22 s and Lisa engaged in three bouts of compelling self-exploratory behaviors for 27 s. One subject (Angela) who was coded as SR+ in 1992, was SR− in 2000 (although it may be important to note that she only had 4 min of mirror proximity). The two chimpanzees that were SR− in 1992 (Christine and Abby), were still SR− in 2000. Finally, one subject (Liz) who met the criterion for being SR? in 1992, showed no mirror related behaviors in 2000, and thus changed her status to SR−.

3.2. Aging effects

Another way of examining the data above is to ask whether there was a decline with age in the percentage of subjects that exhibited evidence of self-recognition. The percentage of SR+ animals declined from 75% (9/12) in 1992, to 50% (6/12) in 2000. Although the difference in the number of SR+ subjects was not statistically significant (Fisher's exact test, $P > .05$), all movement in status was in the negative direction.

3.3. Relation between behavioral coding and mark test

Although it was not possible to perform mark tests on the subjects during the present study, it is reasonable to explore the exact relationship between being coded SR+ using the

Table 3
Results of behavioral measures and self-recognition status at 2000 time-point

Subject	SR status		Behavioral measures		
	1992	2000	Proximity (min)	Weak SE (s)	Compelling SE (s)
Schulman	+	+	277	61	2413
Misty	+	+	226	157	160
Christy	+	+	140	172	249
Chakema	+	+	112	32	57
Gilda	+	+	41	88	243
Cindy	+	+	36	19	100
Keetah	+	?	71	16	22
Lisa	+	?	32	9	27
Angela	+	−	4	0	0
Liz	?	−	80	0	0
Christine	−	−	76	47	0
Abby	−	−	9	0	0

See text and Table 2 for definitions of behavioral measures.

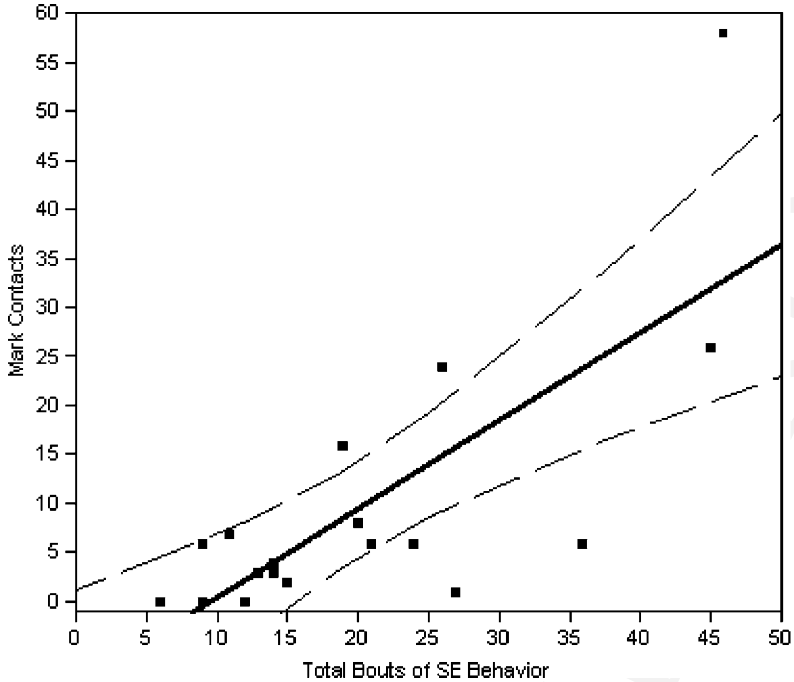

Fig. 1. Linear correlation (plus 95% confidence intervals) between total number of spontaneous bouts of self-exploratory behavior during 5 days of mirror exposure, and total number of contacts to marked regions of the face during test phase of the mark test for 18 subjects who were classified as SR+ and who were given a mark test (data derived from Tables 4 and 5 of [11] and archived records).

behavioral criterion used by Povinelli et al. [11] and also used here, and the results of mark tests. Although Povinelli et al. reported mark tests for 36 SR+, SR−, and SR? animals, and showed that positive mark test results came almost exclusively from the SR+ group (see Section 1), no further attempt was made to assess the relation between the amount of spontaneous self-exploratory behavior and the results of the marks tests. Thus, using archived data, we tabulated the total number of compelling bouts of self-exploratory behavior that each SR+ subject exhibited and explored the relationship in question in several ways.

First, a *t*-test (for unrelated samples) revealed that animals who passed the mark test ($n = 9$) exhibited significantly higher number of self-exploratory bouts ($M = 26.22$, S.D. $= 13.53$) than those ($n = 9$) that failed the test ($M = 14.56$, S.D. $= 6.23$), $t(16) = 2.35$, $P < 0.032$). Second, a point biserial correlation between the total number of bouts of self-exploratory behavior and success or failure on the mark test revealed a significant positive correlation ($r_{pb} = 0.506$, $d.f. = 16$, $P < 0.05$), indicating that the number of bouts of self-exploratory behavior accounted for approximately 25% of the variance in the pass/fail mark test results. Furthermore, as shown in Fig. 1, there was a highly significant linear correlation between the total number of contacts to the marked regions of the face (data derived from [11], Tables 4 and 5) and the total number of spontaneous bouts of self-exploration, Pearson's $r = 0.749$, $d.f. = 16$, $P < 0.0004$.

4. Discussion

Consistent with the possibility of an apparent decline with age, all of the changes in self-recognition status from the previous study [11] were in the negative direction. Two of the three chimpanzees that were SR+ in 1992 tested SR? in 2000, and the other tested SR−. Another animal moved from SR? to SR−. Finally, and of great interest concerning the stability of the trait, none of the animals that failed to show evidence of self-recognition in 1992 tested SR+ or SR? in 2000.

On the other hand, the apparent decline in self-recognition as a function of age in the present sample was more modest than what might be inferred from the cross-sectional data collected by Povinelli et al. [11]. Whereas only 9/35 (26%) of the older animals tested SR+ in 1992, 6/12 (50%) of the chimpanzees that were re-tested were SR+. Further, of the animals that tested positive in 1992, 6/9 (67%) continued to test positive in 2000. Thus, two-thirds of the adolescent chimpanzees that showed self-recognition in 1992 continued to show robust evidence for self-recognition as adults 8 years later, despite the fact that they received little or no mirror exposure during the interim. This extends a previous account of retention of self-recognition by a chimpanzee for 1 year [3] to a retention interval that spans almost a decade. In the majority of instances, therefore, self-recognition in chimpanzees appears to be a persistent, highly reliable trait—at least from adolescence to mid-adulthood. It is equally important to emphasize that no animals (0/3) changed from SR− or SR? status, to SR+.

Although the present results suggest that if animals change their self-recognition status from adolescence/young adulthood to mid- to late-adulthood, it will be in the negative direction, it should also be emphasized that the present longitudinal design yielded a much higher level of self-recognition in older animals than the previous cross-sectional design (50% versus 26%, respectively). The original sample used by Povinelli et al. included some chimpanzees that were much older (25–39 years of age), but they found no correlation between self-recognition and age in adults (>16 years of age). However, in the Povinelli et al. [11] study, 33/35 (94%) of the animals aged 16–39 years were wild-born, while all 12 of the chimpanzees in the present study were captive-born. Although the samples are not strictly comparable, it is of interest to note that 1/2 (50%) of the captive-born adults from the original study were SR+, which is the same proportion as the current sample. Thus, although this study cannot directly address the effects of early experience on the expression of self-recognition, contrary to the notion that being born in captivity negatively affects the expression of this trait due to purported impoverished or restricted rearing conditions (e.g. [13]), in this instance, being reared in captivity was associated with a positive classification for self-recognition. Although this may be due to the effects of prior exposure to mirrors (which the current captive-born subjects received, but not the wild-born subjects tested by Povinelli et al., it would nonetheless be of great interest to follow these captive-born subjects into their late adulthood.

The present data set does not allow for definitive conclusions regarding the four chimpanzees who changed their self-recognition status from 1992 to 2000. The two that moved from SR+ to SR?, showed several compelling instances of mirror-mediated self-exploratory behavior and perhaps with more exposure would have met the criterion for SR+. However, it should be noted that based upon the nature of the association between the behavioral criterion and mark test results (see Section 1), the behavioral criterion is unlikely to yield a substantial number of false negatives. If anything, it is likely to lead to false positives (for empirical data on this issue, see [4]). Another mitigating factor is that some animals may have had greater access to the mirror than others. Indeed, in some instances (e.g. Lisa and Angela) access to the mirror was monopolized by more dominant cage mates who were often not part of the study. However, access alone is not likely to be a sufficient explanation, as two of the SR− animals (Christine and Liz) exhibited high levels of mirror proximity (see Table 3). In this regard, it should be noted that Povinelli et al. [11] found no correlation between time spent viewing the mirror and whether the subjects exhibited compelling bouts of self-exploratory behavior.

It is also relevant that our retrospective analysis of the relationship between the amount of self-exploratory behavior (using the coding scheme adopted here) and the results of mark tests indicates that, to some extent, the amount of self-exploratory behavior can be used to predict success or failure on the mark test. Particularly striking is that the amount of self-exploratory behavior was correlated with, and was able to explain a significant amount of the variation in, the results the mark tests. Indeed, advances in the behavioral coding system, which take into account the particular kind of self-exploratory behaviors exhibited (teeth-picking, ano-genital explorations, etc.), when combined with existing advances in mark test techniques (see [12]), may allow for an even better ability to reliably infer mark test results solely from the animals' spontaneous reactions to mirrors.

The most conservative conclusions from the current data are that the behavioral indicators of self-recognition in chimpanzees are (a) stable across time (although, as in humans, exhibit some decline with age), and (b) suggest greater individual variation in this species than in humans. Given that a variety of lines of evidence now indicate that in humans information processing about certain aspects of the self exhibits a right hemisphere bias, and in particular, a bias in the right prefrontal cortex (e.g. [2,5,8–10]), future research should seek to clarify whether the kind of self-information that supports self-recognition in chimpanzees exhibits an homologous form of neural localization. Other research should explore where the development of the brain regions is correlated with the developmental onset of self-mirror self-recognition in both human infants and chimpanzees.

Acknowledgements

We thank James Reaux and the caretakers and staff of the New Iberia Research Center for their assistance with this study. The research was supported by a Centennial Fellowship to DJP from the James S. McDonnell Foundation and by a travel grant from the Netherlands Organization for Scientific Research (NWO) and Utrecht University to MdV. We thank James Reaux for the variety of assistance he provided the design and implementation of this study. We thank Godelieve Kranendonk, Ryan Arnold and Sarah Dunphy-Lelii for their help in videotape coding and analysis. Laura Theall is now at the Department of Psychology, McMaster University, Hamilton, ON, Canada.

References

[1] Amsterdam B. Mirror self-image reactions before age two. Developmental Psychobiology 1972;5:297–305.

[2] Breen N, Caine D, Coltheart M. Mirrored-self misidentification: two cases of focal onset dementia. Neurocase 2001;7:239–54.

[3] Calhoun S, Thompson RL. Long-term retention of self-recognition by chimpanzees. American Journal of Primatology 1988;15:361–5.

[4] Eddy TJ, Gallup Jr GG, Povinelli DJ. Age differences in the ability of chimpanzees to distinguish mirror-images of self from video-images of others. Journal of Comparative Psychology 1996;110:38–44.

[5] Fink GR, Markowitsch HJ, Reinkemeier M, Bruckbauer T, Kessler J, Heiss W-D. Cerebral representation of one's own past: neural

networks involved in autobiographical memory. The Journal of Neuroscience 1996;16:4275–82.
[6] Gallup Jr GG. Chimpanzees: self-recognition. Science 1970;167: 86–7.
[7] Gallup Jr GG, Anderson JR, Shillito DJ. The mirror test. In: Bekoff M, Allen C, Burghardt GM, editors. The Cognitive Animal. Cambridge (MA): MIT Press, in press.
[8] Keenan JP, Nelson A, O'Connor M, Pascual-Leone A. Self-recognition and the right hemisphere. Nature 2001;409:305.
[9] Keenan JP, Wheeler M, Gallup Jr GG, Pascual-Leone A. Self-recognition and the right prefrontal cortex. Trends in Cognitive Science 2000;4:338–44.
[10] Platek SM, Gallup Jr GG. Self-face recognition is affected by schizotypal personality traits. Schizophrenia Research, in press.
[11] Povinelli DJ, Rulf AB, Landau KR, Bierschwale DT. Self-recognition in chimpanzees (*Pan troglodytes*): distribution, ontogeny, and patterns of emergence. Journal of Comparative Psychology 1993;107: 347–72.
[12] Povinelli DJ, Gallup Jr GG, Eddy TJ, Bierschwale DT, Engstrom MC, Perilloux HK, Toxopeus IB. Chimpanzees recognize themselves in mirrors. Animal Behaviour 1997;53:1083–8.
[13] de Veer MW, van den Bos R. A critical review of methodology and interpretation of mirror self-recognition research in nonhuman primates. Animal Behaviour 1999;58:459–68.