

The monkey in the mirror: Hardly a stranger

Frans B. M. de Waal^{*†}, Marietta Dindo^{*}, Cassiopeia A. Freeman^{*}, and Marisa J. Hall^{*}

^{*}Living Links Center, Yerkes National Primate Research Center, and [†]Department of Psychology, Emory University, Atlanta, GA 30322

This contribution is part of the special series of Inaugural Articles by members of the National Academy of Sciences elected on April 20, 2004.

Contributed by Frans B. M. de Waal, June 9, 2005

It is widely assumed that monkeys see a stranger in the mirror, whereas apes and humans recognize themselves. In this study, we question the former assumption by using a detailed comparison of how monkeys respond to mirrors versus live individuals. Eight adult female and six adult male brown capuchin monkeys (*Cebus apella*) were exposed twice to three conditions: (i) a familiar same-sex partner, (ii) an unfamiliar same-sex partner, and (iii) a mirror. Females showed more eye contact and friendly behavior and fewer signs of anxiety in front of a mirror than they did when exposed to an unfamiliar partner. Males showed greater ambiguity, but they too reacted differently to mirrors and strangers. Discrimination between conditions was immediate, and blind coders were able to tell the difference between monkeys under the three conditions. Capuchins thus seem to recognize their reflection in the mirror as special, and they may not confuse it with an actual conspecific. Possibly, they reach a level of self–other distinction intermediate between seeing their mirror image as other and recognizing it as self.

primate | self-awareness | empathy | development

Our species has always been fascinated with reflective surfaces because they make us literally reflect on ourselves (1, 2). This fascination has been translated into a long tradition of research on self-identification of the specular image, known as mirror self-recognition (MSR). Comparisons with other species have been part of this tradition ever since it was shown that apes respond in a more complex fashion to mirrors than do other animals. Apes show every sign of recognizing self-contingency with the mirror (3, 4), going so far as embellishing themselves in front of it (5). Gallup (6) was the first to formally test mirror understanding by applying a so-called “mark test” to monkeys and apes, confirming MSR in the latter but not in the former.

The mark test has become the standard in comparative mirror studies as well as a lightning rod for those opposed to cognitive Rubicons, such as the implied contrast in self-awareness. The mark test consists of placing odorless paint on the face at a location invisible to the subject without assistance of a mirror. If the subject then selectively inspects the painted spot guided by a mirror, it is considered to possess MSR. The current consensus is that all anthropoid apes (i.e., chimpanzees, bonobos, gorillas, and orangutans) are capable of passing the mark test, even though by no means every individual ape does, and that, apart from humans, no other primates possess this capacity (7, 8).

Mirrors and Empathy

Mirror responses *per se* are of little interest to the biologist as they seem functionally irrelevant. Primates do encounter their mirror image under natural conditions (Fig. 1), but it is hard to imagine natural selection for self-recognition. The importance of MSR resides rather in its cognitive correlates. A sharper distinction between the social environment and the self may allow for more advanced forms of intersubjectivity in which a subject connects with an object’s emotional state, such as distress, without losing sight of who actually is in the situation that caused this state. Instead of blending its own and the other’s emotions, the two can be kept apart. Thus, MSR has been called a “marker of mind” along with empathy and attribution (9).

In human ontogeny, the emergence of higher forms of empathy, in which children adopt the perspective of others, indeed coincides with the first signs of MSR (10, 11). de Waal (12) has suggested a similar connection during phylogeny, i.e., humans and apes, which possess MSR, show more complex expressions of empathy than do monkeys, which lack MSR. This distinction is not to deny emotional connectedness in monkeys, but empathy in these animals may not go beyond so-called emotional contagion, i.e., matching of another’s emotional state (13).

The literature offers striking descriptions of cognitive empathy and aiding behavior among apes (4, 12, 14–18). The only other animals for which a similar array of helping responses is known are dolphins and elephants (19–22). Remarkably, the only nonhominoid for which there is compelling MSR evidence is the bottlenose dolphin (23). One study failed to find MSR in elephants (24), but more research is needed before elephants can be considered an exception to the hypothesized connection between MSR and empathy.

Systematic differences have been found in the primate order with respect to the alleviation of others’ distress. Consolation, defined as reassuring contact (e.g., putting an arm around the other’s shoulders) by an uninvolved bystander to a victim of aggression, has been demonstrated in chimpanzees, but thus far not in monkeys (25–28).

The large hominoids thus differ empirically from other primates on two fronts in that they show MSR as well as consolation and targeted helping. That apes go further in their expressions of empathy likely rests on the same increased distinction between self and other thought to underlie the shift from “personal distress” to “empathic concern” (or “sympathy”) during human ontogeny (29, 30).

Continuity

It becomes important to establish where the interspecific continuities end and the differences begin. With regard to empathy, Preston and de Waal (31–33) discuss various levels as well as fundamental features shared across the mammalian order. The first forms of empathy probably arose along with parental care (34, 35), starting with state-matching based on shared representations of action and perception and internalization of the object’s state (31). Neurological evidence for this so-called perception–action mechanism has grown rapidly over recent years (36–39). More advanced capacities evolved around this core mechanism until the entire set of intersubjectivity levels began to resemble a multilayered Russian doll (40).

One expects similar continuity and levels of complexity with regards to mirror responses. But here there are two schools of thought. One school, prevalent in comparative psychology, draws a sharp boundary: self-recognition of one’s mirror image implies a concept of self (6), hence species devoid of MSR lack this concept. Self-awareness is thus seen as an all-or-nothing phenomenon. The other school, prevalent in developmental

Abbreviation: MSR, mirror self-recognition.

See accompanying Profile on page 11137.

[†]To whom correspondence should be addressed. E-mail: dewaal@emory.edu.

© 2005 by The National Academy of Sciences of the USA



Fig. 1. Juvenile chimpanzee playing with his own reflection in the water. Apes are known to connect their reflections with themselves. [Photograph by F.B.M.d.W. and reproduced with permission (Copyright, F. B. M. de Waal).]

psychology, looks at the self concept as the endpoint of gradual change: the concept does exist before MSR but is not yet developed enough to be detectable by the mark test (41): “Mirror-recognition is a phenomenon well worth studying, but it is deeply misleading as an index of self-awareness” (42).

The sharp boundary in comparative psychology has led to a lumping of all animals without MSR as representing a single cognitive stage, from fish and small-brained birds (e.g., a robin’s never-abating attacks on its image in a window pane) to animals such as dogs and monkeys (43). Rochat classified monkeys at level 0 of self-awareness, i.e., confusion between mirror and reality (44). The literature variously describes what a monkey sees in the mirror as “another individual” (1), “another animal of equal circumstances as him/herself” (45), or a “strange conspecific” (46).

Instead of assuming that self-awareness appeared with a Big Bang, though, should not students of animal behavior adopt the gradualist framework of developmental psychologists? The latter makes more evolutionary sense. The search for continuity has taken many forms, from challenges to the validity of the mark test (ref. 47 countered by ref. 48; ref. 49 countered by ref. 50) and questions about the confounding role of attention and motivation (51, 52) to innovative approaches that circumvent mirrors altogether (53, 54). Indeed, it has been argued that some level of self-awareness must be present in every animal (55, 56).

Given the large number of failed attempts to demonstrate MSR in nonhominoids (8), we here accept the fundamental difference in mirror response between monkeys and apes. Instead, we examine a curiously neglected issue: the assumption that monkeys see a stranger in the mirror. The few studies that have compared the reactions of monkeys to a mirror versus their reaction to a conspecific hint at differentiation. For example, Itakura (57) reports that the heart rate of macaques confronted with a stranger rises at first, then drops, whereas the heart rate

drops immediately upon exposure to a mirror. A calming effect of one’s own reflection is also suggested anecdotally for wild baboons (58), and signs of discrimination between one’s reflection and an unfamiliar peer were noted in macaques (46). It should not be taken for granted, therefore, that monkeys mistake their mirror image for an actual conspecific (7, 59).

However, macaques reared in front of a mirror resumed social responses as soon as their mirror was either relocated or removed and brought back (60, 61). These monkeys understood mirror surfaces (e.g., turned around to look at people detected in the mirror) but seemed oblivious to the source of what they saw when looking at themselves. Yet, even if monkeys do not recognize themselves in the mirror, does this really mean that they are as confused as fish and small-brained birds?

Developmental psychologists recognize two levels of mirror understanding intermediate between mirror/other confusion (level 0) and MSR (level 3) (44). Level 1 is differentiation between the mirror image’s perfect contingency with the self and other events in the environment. Level 2 is the tendency to explore this contingency, meaning that subjects connect what they see in the mirror with their own body. Given recent evidence that monkeys recognize being imitated by another (62), they should be able to reach level 1. Perhaps they react like young children, who seem to distinguish their reflection from another individual well before the emergence of MSR (63, 64). The self–other distinction of these children may have parallels in phylogeny, meaning that some non-MSR species reach levels 1 or 2 of mirror understanding.

The Present Study

The present study is the most detailed comparison to date between the responses of monkeys to mirrors and conspecific strangers. The study uses the brown or tufted capuchin monkey (*Cebus apella*), a neotropical primate that fits the non-ape pattern of lacking MSR and directing social behavior at the mirror (65–69). Capuchins are among the largest-brained, longest-lived primates, whose cognitive capacities are customarily compared to those of chimpanzees. Tool use by capuchin monkeys is impressive (70), which may be relevant in relation to mirror responses because of the suggested connection between tool use and a kinesthetic self-concept (71–73).

With regard to empathy, too, capuchins may be special. Like other monkeys, they fail to initiate consolation, but they do provide reassurance to distressed individuals seeking contact (74). Capuchin monkeys also readily share food with each other and are highly cooperative, both in the wild and in captivity (75–78).

Riviello *et al.* (68) reported “reality testing” by brown capuchins looking at their reflection as also suggested for pygmy marmosets (79) and known of pre-MSR human infants (41). One juvenile capuchin held her tail with her hands while alternately rubbing it on the mirror surface and on the floor, as if exploring the difference between a reflective and nonreflective surface. Such curiosity stands in stark contrast to its absence in fish and small-brained birds confronted with a mirror.

Methods

Subjects and Housing. Brown capuchin monkeys were housed in two separate groups at the Yerkes National Primate Research Center. One group included three adult males, six adult females, and eight immatures (i.e., under the age of 5 years). The second group included five adult males, seven adult females, and four immatures. Both enclosures had indoor and outdoor areas. An opaque divider prevented visual but not acoustic contact between the groups. Every day, the monkeys received food biscuits, fruits, vegetables, and water ad libitum.

The eight female subjects of study 1 ranged in age from 6 to an estimated 30 years. Four females had dependent offspring

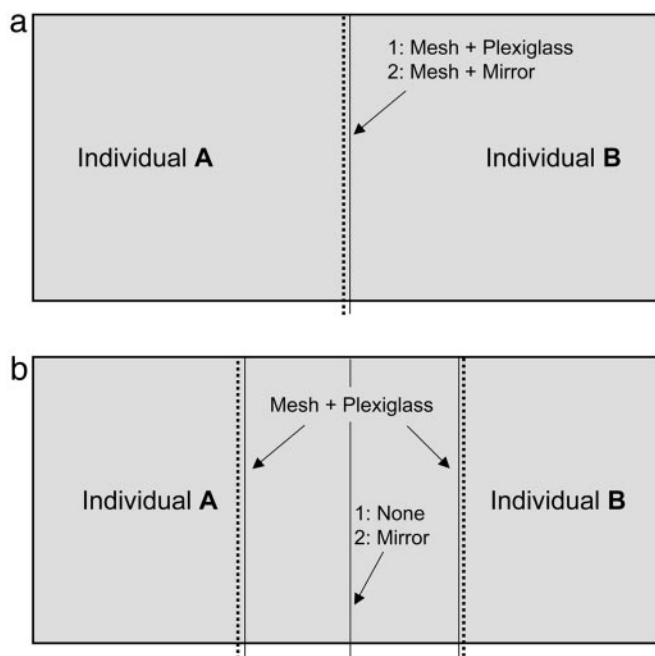


Fig. 2. Test chamber for experiments with female (a) and male (b) capuchin monkeys. Visual and tactile experiences during mirror and partner tests were held constant. Females were separated by a single partition consisting of either one layer of mesh and clear Lexan if there was a partner on the other side, or a mirror right behind a layer of mesh with no actual partner on the other side. Males were kept away from each other, with 45 cm of space between them. They either looked at a partner through mesh and Lexan on their own side as well as the same double-layer on their partner's side, or they looked through mesh and Lexan at a mirror placed in the middle thus reflecting the same double-layer with their own reflection behind it. (Reproduced with permission from the authors.)

under the age of 1 year, which accompanied their mothers (see Table 3, which is published as supporting information on the PNAS web site). Each test with a familiar female from the own group or an unfamiliar female (stranger) from the other group served as the same condition for the partner as subject. Subject pairs were chosen based on age and rank similarity. Only unrelated pairs of adult females were used.

The six male subjects of study 2 ranged in age from 6 to 30 years (Table 3). Unfamiliar pairs had corresponding ranks within their home groups. Only maternally unrelated pairs of adult males were used, but the oldest male, Ike, is the confirmed father of Ozzie.

Previous Experience. None of the subjects had been deliberately exposed to mirrors before, but we cannot rule out nonexperimental exposures. All monkeys in our facility are familiar with reflective surfaces, such as windows, water pools, and metal panes. It is best, therefore, to consider subjects as having had intermittent exposure to mostly low-quality reflective surfaces.

Many subjects had previously been used in studies on food sharing, cooperation, and material exchange (77, 80, 81). Monkeys from different groups had not lived together for 12 years, and cohabitation from before this period applied to the oldest four females only.

Study 1: Females. A trained separation procedure was used to move subjects into a familiar test chamber placed in front of their housing area. The rest of the colony (i.e., both groups) was locked outside the building during tests. All tests were conducted in a 144 × 60 × 60 cm chamber used for over a decade for daily

tests on both groups (i.e., the chamber had collected the smells of individuals from both groups). The chamber was divided into two equal sections. In paired tests, the first subject was led into the chamber and then sat in its own section separated from the other by a combination of a mesh partition and a transparent Lexan panel (Fig. 2a) offering visual but no tactile contact with the partner. The tactile experience was the same as during mirror tests, when the mirror was placed right behind the mesh such that visually the situation resembled having a partner behind mesh. The following three conditions were tested: (i) familiar, behind mesh and Lexan sat a female from the subject's own group; (ii) stranger, behind mesh and Lexan sat a female from the other group; and (iii) mirror, directly behind mesh, a mirror faced the subject.

Before each familiar and stranger test, one monkey entered its chamber section and was videotaped from the moment the partner entered its section. In mirror tests, videotaping began when the subject entered the chamber, marking the start of exposure. All tests were 15 min long, and an experimenter was present. Each subject was run through the three test conditions above in randomized order. After all subjects had gone through the three conditions once, a second randomized test series was conducted pairing subjects with the same partners as in the first. No individual was ever tested more than once per day.

Digital videos were coded for 16 behaviors (see Table 4, which is published as supporting information on the PNAS web site) along with the minute block in which the behavior occurred. We also noted the duration of mother–infant contact (i.e., infants were coded as being either on or off mother). Before the study, behavior patterns were divided into either socially positive (i.e., patterns often used in friendly association or courtship) or socially negative (i.e., patterns expressing hostility, anxiety, or fear), a classification based on the literature (70, 82–84). “Dismantling” was classified as negative as it could potentially lead to escapes from the test chamber if monkeys managed to remove a panel (as happened in one cancelled male mirror test).

Video records showed the entire test chamber, permitting us to determine whether subjects made eye contact with partner or mirror. These videos were unsuitable for blind coding because they revealed the test condition. A third test run was conducted on the females by an uninvolved team member with a camera angle avoiding the partition in the test chamber. These tapes obscured the test condition. Twelve tests were conducted exposing four subjects to all three conditions. Two laboratory members independently watched the tapes to estimate the test condition from the subject's behavior, and then their ratings were compared with the actual test conditions.

Study 2: Males. Males were tested in the same chamber, with the differences that instead of one partition in the middle, there were two at a distance from each other, which kept subjects 45 cm apart (Fig. 2b). Each of the two partitions consisted of mesh and Lexan. In familiar and stranger tests, the subjects saw each other through both layers, whereas in the mirror test, a mirror was placed in the central slot so that the subject looked at its reflection through a layer of mesh and Lexan as well as a reflection of this layer. This chamber modification prevented close proximity between stranger males, which can be extremely hostile.

The males too went through all three conditions in randomized order in one round, and then again in a second round. Tests were videotaped with two cameras, one of which showed only a single subject and did not reveal the test condition so that the tape could be used for blind coding.

Analysis. Analyses were limited to behaviors that occurred at least 10 times across all conditions and subjects. A repeated measures ANOVA was conducted on behavioral frequencies for individ-

ual subjects during the three conditions (i.e., familiar, stranger, and mirror) and test order. Because of differences in testing set-up, data on males and females were analyzed separately. Initially, a between-subjects factor regarding the presence of an infant (i.e., mother or nonmother) was part of the ANOVA, but it is not presented because we found no significant effects.

Results

Study 1: Females. ANOVAs across conditions (see Fig. 6 and Table 5, which are published as supporting information on the PNAS web site) showed the strongest variance for eye contact (almost exclusively directed at the mirror image) and also significant differences for friendly swaying and lip smacking (mostly toward the mirror), avoidance of eye contact (typical of the stranger condition), glancing (mostly directed at the stranger, but also at the mirror), and inspection of the partition between the test chamber halves (typical under the mirror condition). No significant effect of condition was found on the frequency of threat displays nor of self-directed behavior. Fig. 3 illustrates direct eye contact with the mirror image and gaze avoidance between strangers.

For behavioral categories that were significant in the ANOVA, we conducted paired contrasts between stranger and mirror condition. Results were significant for friendly sway and lip smacking, eye contact, and partition manipulation. When the effect of test order (i.e., first vs. second round) was inspected, a significant effect existed only for the avoidance of eye contact ($F_{1,7} = 18.61$, $P = 0.004$), mainly due to a drop in the second compared to first stranger test, and for eye contact ($F_{1,7} = 20.36$, $P = 0.003$), mainly due to a drop in the second compared to the first mirror test.

Immediate reactions were tested by comparing data on the first 5 min of the first mirror exposure with the first 5 min of the first stranger test. Significant differences existed for eye contact (paired $t = 4.05$, $df = 7$, $P = 0.005$), friendly sway ($t = 2.39$, $P = 0.048$), and partition manipulation ($t = 4.09$, $P = 0.005$), with all behaviors being more frequent under the mirror condition.

If young infants were present, the duration of mother–infant contact per subject ($n = 4$) was subjected to a repeated-measures ANOVA for the three conditions with test order added (i.e., first or second exposure) as a second variable. We found a significant effect of condition ($F_{2,6} = 6.44$, $P = 0.032$) but not test order ($F_{1,6} = 3.94$, NS). Fig. 4 shows the results per mother–infant pair arranged from left to right from the youngest to the oldest infant, all under 12 months of age. Infants stayed most in contact under the stranger condition and least under the familiar partner condition. In the presence of a mirror, the amount of mother–infant contact was intermediate.

Study 2: Males. By far the strongest variance was again found for eye contact (almost exclusively directed at the mirror), and further differences existed for the bunny sit, friendly swaying, squealing, and curling up (mostly toward the mirror), and eyebrow raise and threat display (typical of the stranger condition). See Fig. 7 and Table 6, which are published as supporting information on the PNAS web site.

For behavioral categories with a significant overall ANOVA, we conducted paired contrasts between stranger and mirror condition, which were significant for eye contact, squealing, and threat display. The effect of test order was significant for eyebrow raise ($F_{1,5} = 9.12$, $P = 0.009$) and threat display ($F_{1,5} = 21.44$, $P = 0.006$) due to drops in second compared to first exposure per condition.

Comparing data on the first 5 min of the first mirror exposure with the first 5 min of the first stranger test, three behaviors were significantly different: eye contact (paired $t = 4.11$, $df = 5$, $P = 0.005$), threat display ($t = 4.72$, $P = 0.005$), and squealing ($t = 2.91$, $P = 0.034$). Eye contact and squealing were more frequent

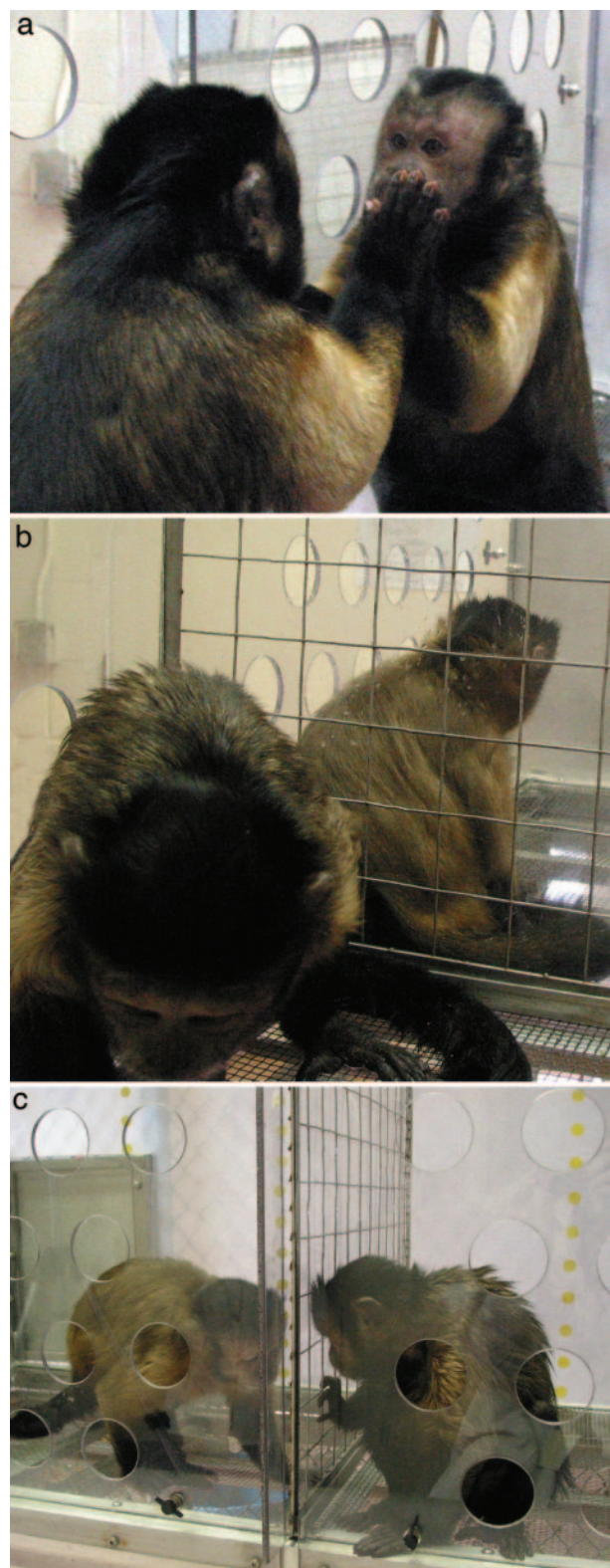


Fig. 3. Photographs showing typical reactions to each condition. (a) Mirrors elicited unwavering eye contact in both sexes. [The young adult male shown here has been photographed in direct contact with a mirror and without mesh, unlike the actual experimental condition (Fig. 2b).] (b) Strangers engaged in “cut-off” reactions and mutual “denial” of the other’s presence by staring at the floor or turning their backs at each other. Two females are shown. (c) Familiar partners were relaxed, showing little social behavior, and moving around freely. Two females are shown. (Photographs by M.D. and reproduced with permission from the authors.)

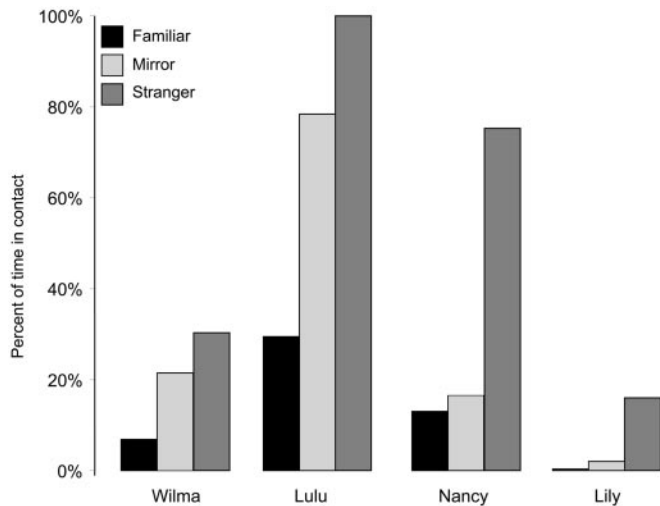


Fig. 4. Percent of time mothers and newborns were in body contact under the three conditions, arranged from left to right from the female with the youngest to the one with the oldest infant, all under 1 year of age. (Reproduced with permission from the authors.)

with the mirror, and threats were more frequent toward the stranger.

Positive vs. Negative Behavior. Behavior patterns were classified as positive or negative before the study (Table 4). We calculated for each subject and each condition a PN index between positive (pos) and negative (neg) behavior: $PN = (pos - neg)/(pos + neg)$. Because of low behavioral frequencies under the familiar condition, this condition was dropped from analysis. PN indices for males and females were subjected to a single repeated-measures ANOVA with sex as between-subjects factor and two conditions (i.e., mirror and stranger) as within-subjects factor. Significant effects concerned condition ($F_{1,12} = 54.78, P < 0.001$) as well as interaction between condition and sex ($F_{1,12} = 19.36, P = 0.001$).

Fig. 5 illustrates the data for positive and negative behavior, separately. In both sexes, positive responses peaked under the mirror condition, whereas negative responses peaked under the stranger condition. Familiar individuals aroused little response: almost no reaction in females and relatively low rates in males. The main sex difference was that whereas females showed a sharp contrast in their reaction to mirrors and strangers (i.e., pronounced imbalances in opposite directions between positive and negative behavior), males seemed more ambivalent in that the rates of both positive and negative behavior were elevated even if differently balanced.

Qualitative Descriptions. At no point did observers have the impression that capuchin monkeys recognize themselves in the mirror. They neither showed self-contingent behavior nor inspection of normally invisible body parts (e.g., inside of mouth). We did notice great curiosity in the monkeys about the mirror, however.

When Lulu first saw her reflection, she was face to face with the mirror and then started backing up. She made plenty of eye contact, unlike the way she acted with conspecifics. When she was introduced to the stranger female, Lulu kept her head down and only stole glances at the other. She made no friendly gestures, such as the bunny sit or eyebrow raising. She did observe the other closely but only if the other was looking in the opposite direction.

Lily had more eye contact with the mirror than most females.

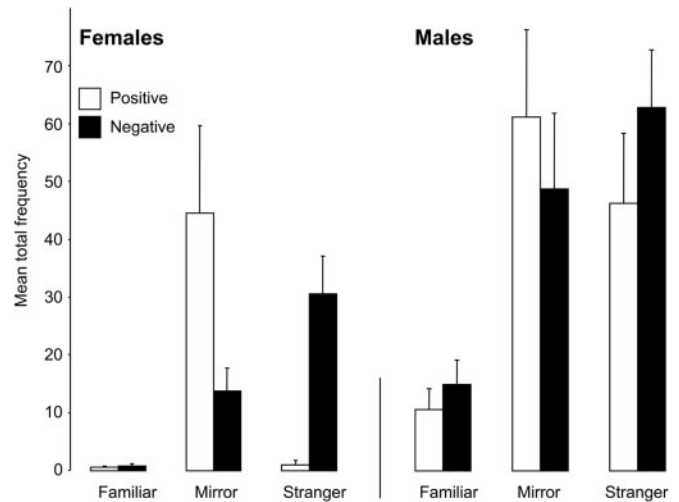


Fig. 5. Aggregate positive behavior directed at the partner or mirror compared with aggregate negative behavior. The positive category included friendly signals such as lip smacking, direct eye contact, swaying, and bunny sitting. The negative category included threatening signals, signs of distress or submission (e.g., squealing), and signs of high anxiety (e.g., glancing or curling up). The graph shows the mean (+ SEM) total frequency of positive or negative behavior per subject during both tests per condition. (Reproduced with permission from the authors.)

Upon arrival in the test chamber, she looked at the mirror and then immediately behind her. Was she checking who was in the reflection or had she recognized her infant, who was on her back? It is known that capuchins can locate hidden objects with the help of a mirror (85). In another mirror test, Nancy looked twice back and forth between the reflection of her infant and her actual infant.

Females showed great interest in the partition during mirror tests. They seemed interested in the mirror's physical properties. This mirror bias was less prominent in the males, but then the males were never in direct contact with the mirror (Fig. 2*b*). Males reacted more intensely to the mirror than the females did. Frequently, a male would make eye contact with the mirror image, followed by a series consisting of the eyebrow raise, the bunny sit, and loud squealing. Then the male would curl up on the floor while softly squealing intermittently. Males appeared confused and distraught by their reflections (*cf.* 68): they often tried to escape from the test chamber, and once a male actually did get out. In the months after the experiments reported here, our highest ranking males, who before used to compete over who could enter the test chamber, became reluctant to enter the chamber if any objects looking like a mirror were nearby.

When both alpha males were in the test chamber together, their responses were quite different from mirror exposures. These males knew each other's voices and were fiercely territorial in their home enclosures, but Ozzie and Drella seemed to ignore each other's presence. For minutes they looked down at the floor and were completely passive. The observer noticed wandering of the eyes to glance at the other, however. Both males seemed to try not to look at the other, similar to "cut-off" behavior (86). During the same tests, these males sometimes alternated between threatening poses and friendly eyebrow raising.

Interobserver Reliability and Blind Coding. Two experimenters independently coded six videotaped tests representing three conditions each with a subject of either gender. Of a total of 326 entries, the proportion scored by both raters was 87.7%. For those entries, the Kappa coefficient of agreement was 0.96 (87).

Table 1. Four observers blindly coded 12 videotapes showing the behavior of a subject without revealing the experimental condition

Condition shown	Chosen condition		
	Familiar	Mirror	Stranger
Familiar	11	0	5
Mirror	0	13	3
Stranger	1	2	13

Two observers coded tapes with female subjects, and two with male subjects. Their 48 guesses regarding the condition under which the subject was tested are shown, with most guesses situated on the diagonal, meaning they were correct.

In a separate comparison, blind coders were asked to guess the test condition of videotaped subjects. These tapes were made such that they did not reveal the condition (see *Methods*). Working independently, two observers coded 12 taped tests of female subjects, and two different observers did the same for 12 taped tests of male subjects. Table 1 gives the pooled results, showing that 77.1% of guesses were correct, which was significantly above 33.3% chance ($\chi^2 = 55.13$, $df = 1$, $P < 0.001$). The four blind coders varied between 58.3% and 100% correct choices. The one error the coders never made was confusion between mirror and familiar partner conditions.

Discussion

Capuchin monkeys notice immediately that their mirror image is not a regular stranger, or perhaps no stranger at all. Females treat their reflection positively, engaging in lots of eye contact, friendly swaying, and lip smacking. They almost “flirt” with their reflection. Females seem much less anxious in front of a mirror than in the presence of a female stranger. They throw frequent oblique glances at a stranger and avoid eye contact with her, and mothers with young infants keep their offspring closer in the presence of a stranger than a mirror. In contrast, reactions to a familiar partner are marked by almost no response at all.

Male capuchins react with greater ambiguity toward both mirrors and male strangers, but they, too, make more eye contact with a mirror. Some friendly reactions, such as the bunny sit and swaying, but also signs of distress, such as squealing and curling up, are shown almost exclusively to the mirror. Strangers are threatened far more than the mirror so that the males’ balance between positive and negative signals is positive toward the mirror and negative toward a stranger. Familiar partners elicit few responses.

Females make about 38 times more eye contact with their mirror image than with a stranger, and males about 11 times. The response differences are, in fact, so marked that blind coders can accurately identify the condition under which a monkey has been videotaped. The different reactions to mirrors versus strangers

do not seem a product of learning, at least not learning during our experiments, because most of the differences above are measurable in the first 5 min of the first exposure.

The two main explanations for these mirror reactions will be called the “No One There” and “Puzzling Other” hypotheses (ignoring the “It’s Me” hypothesis, which assumes MSR). According to the No One There hypothesis, even though capuchin monkeys fail to identify the mirror image as themselves, they are not fooled into thinking it is another. Recognizing synchronicity with the self, they act like pre-MSR human infants, who are said to recognize the impossibility of reciprocal interaction with the mirror.

This hypothesis, however, fails to explain why high-ranking male capuchins became anxious about the mirror to the point of developing an aversion. Males hardly ever squealed or curled up in the presence of strangers, but they did so regularly in front of the mirror. They never showed friendly behavior to strangers either, which were treated with open hostility or “cut-off” reactions, whereas they did sway at and bunny sit in front of the mirror. In short, these males were socially responsive to the mirror to a degree one would not expect if they realized that there was no other monkey there. Did they see their reflection as another male whom they could not dominate?

This possibility would fit the Puzzling Other hypothesis according to which the subject sees another member of its own species but one that is confusing because it fails to “play by the rules.” The interplay with the mirror is unique. Eye contact is facilitated by the fact that the other never averts its gaze. Perhaps interaction takes place via a feedback loop. If the subject starts out with positive signals, these signals will be amplified by their reflection’s reciprocation until the whole interaction is positive. The mirror thus acts as a “superstimulus” (88). If the initial reaction is hostile, however, the feedback loop will be one of escalating hostility from which it is hard to escape because the mirror image does not accommodate attempts at disengagement.

The weakness of this hypothesis is that it predicts a gradual amplification of reactions to the mirror. In our study, however, differences in reaction were immediate. Our monkeys seemed to need only one glance to tell the difference between the mirror and a stranger. Moreover, if they really mistook the mirror for a stranger should not the “tone” of the interactive feedback loop with the mirror be set by the typical initial reaction to a stranger? Subjects should start out as if their reflection is a stranger only to engage in ever greater magnifications of this response? Because females give virtually no positive signals to strangers, how did they end up in a positive feedback loop with the mirror? And why did the males not threaten their mirror image more if threat is their typical response toward a stranger?

But why show social responses at all if the mirror image is seen as illusory? Possibly, facial expressions are impossible to suppress when looking directly into a face, whether it is one’s own or another’s face, except if one fully understand it is one’s own.

Table 2. The pros and cons of three hypotheses about the way capuchin monkeys react to mirrors

Hypothesis	Definition	Data in favor	Problematic data
Puzzling Other	Reflection is seen as an abnormally behaving stranger	Species-typical social response to mirror; high anxiety and mirror aversion in males	Immediate, substantially different reaction to mirror and stranger; mirror behavior does not follow (e.g., amplification) from response to stranger
No One There	Reflection is recognized as illusory	Immediate, substantially different reaction to mirror and stranger; curiosity about mirror surface	High anxiety and mirror aversion in males
It’s Me	Reflection is recognized as self (MSR)	Unsupported by present study	

The third hypothesis is added for completeness’ sake only.

Similar to involuntary facial mimicry (e.g., contagious yawning; ref. 89), facial interplay may be automatic. Similarly, developmental psychologists do not take the social responses by pre-MSR human infants to mean an absence of a self concept: they rather interpret such behavior as exploratory (63).

Another indicator of how the mirror is perceived is inspection of its surface. We found evidence for exploration in our monkeys. Females significantly increased manipulation of the partition if there was a mirror behind it, whereas males showed the same nonsignificant trend despite being kept away from the partition. Remember that the mirror provided the same tactile experience as the Lexan panel separating individuals, hence the difference in response indicates curiosity about the mirror's visual properties (68).

Clearly, both the No One There and the Puzzling Other hypotheses have problems (Table 2). It is obvious from our study that capuchin monkeys do discriminate between their mirror image and a stranger, reacting differently to both at first sight. Whether they see the mirror image as just an intriguing nonsocial phenomenon that involuntarily triggers social responses or as an actual member of their own species, albeit a confusing one, cannot be resolved by the present data.

Because of different traditions in different disciplines, no studies have systematically compared both hypotheses. Comparative psychologists often take an all-or-nothing view of self-awareness without considering intermediates. Because only MSR indicates a concept of self, much effort has been devoted to trying to demonstrate MSR in species that obviously lack it. Comparatively little attention has been paid to what non-MSR species exactly see in the mirror, typically summarized by the claim that they see a stranger. Developmental psychologists, on the other hand, believe in the slow emergence of a self–other distinction. They believe that the duality of the mirror is understood before MSR arises. They have as yet to demonstrate,

however, that pre-MSR infants see anything else in the mirror than a puzzling peer. In short, comparative psychologists take the Puzzling Other explanation for granted for non-MSR animals, whereas developmental psychologists take the No One There explanation for granted for all but the youngest infants.

It is time to put both hypotheses on the table for both categories of non-MSR subjects, human and nonhuman. Each hypothesis comes with a set of testable predictions. For example, one could stimulate interaction with the mirror to see how far one can push the social nature of the mirror response. One such test was conducted with scrub jays, which cache food to prevent it from being pilfered. Preliminary data indicate that these birds recache their food after a conspecific has seen the first caching, but not if a mirror took its place (90). In our own laboratory, we found that adult capuchin monkeys show little hesitation to reach with their hand through a small hole in a mirror to collect a treat (unpublished data). They are prepared to reach right through their own reflection, a behavior hardly expected if the mirror image is mistaken for another monkey.

Capuchin monkeys seem to possess a greater understanding of the mirror's illusory qualities than generally assumed even if we do not contest the claim that monkeys never achieve the mirror understanding of humans and apes.

This project would not have been possible without the assistance of Elizabeth Barrera, Kristin Bonnie, Sarah Brosnan, Hanie Elfenbein, Andrew Katz, Sandra Rothbard, David Sung, Megan van Wolken, and Megan Winton. We thank Gordon Gallup, Jr. and James Anderson for constructive feedback on an earlier version of the manuscript. We are grateful to the animal care and veterinary staff at the Yerkes National Primate Research Center for maintaining the health of our study subjects. The center is fully accredited by the American Association for Accreditation of Laboratory Animal Care (AAALAC). Research was supported by the National Science Foundation (Grant IBN-0314878) and the National Institutes of Health basegrant (RR-00165) to the Yerkes National Primate Research Center.

- Keenan, J. P., Gallup, G. G. & Falk, D. (2003) *The Face in the Mirror* (Harper Collins, New York).
- Pendergast, M. (2003) *Mirror-Mirror: A History of the Human Love Affair with Reflection* (Basic Books, New York).
- Köhler, W. (1959) *Mentality of Apes* (Vintage, New York).
- Ladygina-Kohts, N. N. (2001) in *Infant Chimpanzee and Human Child: A Classic 1935 Comparative Study of Ape Emotions and Intelligence*, ed. de Waal, F. B. M. (Oxford Univ. Press, New York).
- Lethmate, J. & Dücker, G. (1973) *Z. Tierpsychol.* **33**, 248–269.
- Gallup, G. G., Jr. (1970) *Science* **167**, 86–87.
- Anderson, J. R. (1994) in *Self-Awareness in Animals and Humans: Developmental Perspectives*, eds. Parker, S. T., Mitchell, R. W. & Boccia, M. L. (Cambridge Univ. Press, Cambridge, U.K.), pp. 315–329.
- Anderson, J. R. & Gallup, G. G., Jr. (1999) in *Animal Models of Human Emotion and Cognition*, eds. Haug, M. & Whalen, R. E. (Am. Psychol. Assoc., Washington, DC), pp. 175–194.
- Gallup, G. G., Jr. (1982) *Am. J. Primatol.* **2**, 237–248.
- Bischof-Köhler, D. (1988) *Schweiz. Z. Psychol.* **47**, 147–159.
- Zahn-Waxler, C., Radke-Yarrow, M., Wagner, E. & Chapman, M. (1992) *Dev. Psychol.* **28**, 126–136.
- de Waal, F. B. M. (1996) *Good Natured: The Origins of Right and Wrong in Humans and Other Animals* (Harvard Univ. Press, Cambridge, MA).
- Hatfield, E., Cacioppo, J. T. & Rapson, R. L. (1993) *Curr. Dir. Psychol. Sci.* **2**, 96–99.
- Yerkes, R. M. (1925) *Almost Human* (Century, New York).
- Goodall, J. (1990) *Through a Window: My Thirty Years with the Chimpanzees of Gombe* (Houghton Mifflin, Boston).
- de Waal, F. B. M. (1998) *Chimpanzee Politics: Power and Sex Among Apes* (The Johns Hopkins Univ. Press, Baltimore).
- de Waal, F. B. M. (1997) *Bonobo: The Forgotten Ape* (Univ. of California Press, Berkeley, CA).
- O'Connell, S. M. (1995) *Primates* **36**, 397–410.
- Caldwell, M. C. & Caldwell, D. K. (1966) in *Whales, Dolphins, and Porpoises*, ed. Norris, K. S. (Univ. of California Press, Berkeley, CA), pp. 755–789.
- Connor, R. C. & Norris, K. S. (1982) *Am. Nat.* **119**, 358–372.
- Moss, C. (1988) *Elephant Memories: Thirteen Years in the Life of an Elephant Family* (Fawcett Columbine, New York).
- Payne, K. (1998) *Silent Thunder* (Simon & Schuster, New York).
- Reiss, D. & Marino, L. (2001) *Proc. Natl. Acad. Sci. USA* **98**, 5937–5942.
- Povinelli, D. J. (1989) *J. Comp. Psychol.* **103**, 122–131.
- de Waal, F. B. M. & van Roosmalen, A. (1979) *Behav. Ecol. Sociobiol.* **5**, 55–66.
- de Waal, F. B. M. & Aureli, F. (1996) in *Reaching into Thought: The Minds of the Great Apes*, eds. Russon, A. E., Bard, K. A. & Parker S. T. (Cambridge Univ. Press, Cambridge, U.K.), pp. 80–110.
- Watts, D. P., Colmenares, F. & Arnold, K. (2000) in *Natural Conflict Resolution*, eds. Aureli, F. & de Waal, F. B. M. (Univ. of California Press, Berkeley, CA), pp. 281–301.
- Schino, G., Geminiani, S., Rosati, L. & Aureli, F. (2004) *J. Comp. Psychol.* **118**, 340–346.
- Zahn-Waxler, C. & Radke-Yarrow, M. (1990) *Motiv. Emotion* **14**, 107–130.
- Eisenberg, N. (2000) in *Handbook of Emotion*, eds. Lewis, M. & Haviland-Jones, J. M. (Guilford, New York), 2nd Ed., pp. 677–691.
- Preston, S. D. & de Waal, F. B. M. (2002) *Behav. Brain Sci.* **25**, 1–72.
- Preston, S. D. & de Waal, F. B. M. (2002) in *Altruistic Love: Science, Philosophy, and Religion in Dialogue*, eds. Post, S. G., Underwood, L. G., Schloss, J. P. & Hurlbut, W. B. (Oxford Univ. Press, Oxford), pp. 284–308.
- de Waal, F. B. M. (2003) in *Feelings & Emotions: The Amsterdam Symposium*, eds. Manstead, T., Frijda, N. & Fischer, A. (Cambridge Univ. Press, Cambridge, U.K.), pp. 379–399.
- Eibl-Eibesfeldt, I. (1974) *Love and Hate* (Schocken Books, New York).
- MacLean, P. D. (1985) *Arch. Gen. Psychiatry* **42**, 405–417.
- Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C. & Lenzi, G. L. (2003) *Proc. Natl. Acad. Sci. USA* **100**, 5497–5502.
- Wicker, B., Keysers, C., Plailly, J., Royet, J. P., Gallese, V. & Rizzolatti, G. (2003) *Neuron* **40**, 655–664.
- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J. & Frith, C. D. (2004) *Science* **303**, 1157–1162.
- de Gelder, B., Snyder, J., Greve, D., Gerard, G. & Hadjikhani, N. (2004) *Proc. Natl. Acad. Sci. USA* **101**, 16701–16706.
- de Waal, F. B. M., in *Being Moved*, ed. Bråten, S. (Cambridge Univ. Press, Cambridge, U.K.), in press.
- Lewis, M. & Brooks-Gunn, J. (1979) *Social Cognition and the Acquisition of Self* (Plenum, New York).

42. Neisser, U. (1995) in *The Self in Infancy: Theory and Research*, ed. Rochat, P. (Elsevier, Amsterdam), pp. 17–34.
43. Zazzo, R. (1981) in *La Reconnaissance de son Image chez l'Enfant et l'Animal* (Delachaux & Niestlé, Neuchâtel, Switzerland), pp. 77–110.
44. Rochat, P. (2003) *Conscious. Cognit.* **12**, 717–731.
45. Neel, M. A. (1996) *Primates* **37**, 411–421.
46. Anderson, J. R. (1983) *Anim. Learn. Behav.* **11**, 139–143.
47. Epstein, R., Lanza, R. P. & Skinner, B. F. (1981) *Science* **212**, 695–696.
48. Thompson, R. K. R. & Contie, C. L. (1994) in *Self-Awareness in Animals and Humans: Developmental Perspectives*, eds. Parker, S. T., Mitchell, W. & Boccia, M. L. (Cambridge Univ. Press, Cambridge, U.K.), pp. 392–409.
49. Heyes, C. (1995) *Anim. Behav.* **50**, 1533–1542.
50. Povinelli, D. J., Gallup, G. G., Jr., Eddy, T. J., Bierschwale, D. T., Engstrom, M. C., Periloux, H. K. & Toxopeus, I. B. (1997) *Anim. Behav.* **53**, 1083–1088.
51. Parker, S. T., Mitchell, R. W. & Boccia, M. L. (1994) *Self-Awareness in Animals and Humans: Developmental Perspectives* (Cambridge Univ. Press, Cambridge, U.K.).
52. de Veer, M. W. & van den Bos, R. (1999) *Anim. Behav.* **58**, 459–468.
53. Bekoff, M. (2001) *Behav. Process.* **55**, 75–79.
54. Jorgensen, M. J., Hopkins, W. D. & Suomi, S. J. (1995) in *The Self in Infancy: Theory and Research*, ed. Rochat, P. (Elsevier, Amsterdam), pp. 243–256.
55. Cenami Spada, E., Aureli, F., Verbeek, P. & de Waal, F. B. M. (1995) in *The Self in Infancy: Theory and Research*, ed. Rochat, P. (Elsevier, Amsterdam), pp. 193–215.
56. Bekoff, M. & Sherman, P. W. (2003) *Trends Ecol. Evol.* **19**, 176–180.
57. Itakura, S. (2001) in *Primate Origins of Human Cognition and Behavior*, ed. Matsuzawa, T. (Springer, Tokyo), pp. 313–329.
58. Smuts, B. B. (2001) *J. Conscious. Stud.* **8**, 293–309.
59. Platt, M. M. & Thompson, R. L. (1985) *Primates* **26**, 300–314.
60. Suarez, S. D. & Gallup, G. G., Jr. (1986) *Am. J. Primatol.* **11**, 239–244.
61. Gallup, G. G., Jr., & Suarez, S. D. (1991) *J. Comp. Psychol.* **105**, 376–379.
62. Paukner, A., Anderson, J. R., Borelli, E., Visalberghi, E. & Ferrari, P. F. (2005) *Biol. Lett.*, **1**, 219–222.
63. Priel, B. & Zeidman, O. (1990) *J. Genet. Psychol.* **151**, 483–493.
64. Rochat, P. & Striano, T. (2002) *Child Dev.* **73**, 35–46.
65. Romanes, G. J. (1883) *Animal Intelligence* (Appleton, New York).
66. Collinge, N. E. (1989) *Zoo Biol.* **8**, 89–98.
67. Anderson, J. R. & Roeder, J. J. (1989) *Primates* **30**, 581–587.
68. Riviello, M. C., Visalberghi, E. & Blasetti, A. (1992) *Hystrix* **4**, 35–44.
69. Paukner, A., Anderson, J. R. & Fujita, K. (2004) *Behav. Process.* **66**, 1–6.
70. Frigaszy, D. M., Visalberghi, E. & Fedigan, L. M. (2004) *The Complete Capuchin: The Biology of the Genus Cebus* (Cambridge Univ. Press, Cambridge, U.K.).
71. McGrew, W. C. (1992) *Chimpanzee Material Culture: Implications for Human Evolution* (Cambridge Univ. Press, Cambridge, U.K.).
72. Povinelli, D. J. (2000) *Folk Physics for Apes* (Oxford Univ. Press, Oxford).
73. Westergaard, G. C. & Suomi, S. J. (1995) *Hum. Evol.* **10**, 217–223.
74. Verbeek, P. & de Waal, F. B. M. (1997) *Int. J. Primatol.* **18**, 703–725.
75. Perry, S. & Rose, L. (1994) *Primates* **35**, 409–415.
76. Rose, L. (1997) *Int. J. Primatol.* **18**, 727–765.
77. de Waal, F. B. M. (1997) *J. Comp. Psychol.* **111**, 370–378.
78. Mendres, K. A. & de Waal, F. B. M. (2000) *Anim. Behav.* **60**, 523–529.
79. Eglash, A. R. & Snowdon, C. T. (1983) *Am. J. Primatol.* **5**, 211–219.
80. de Waal, F. B. M. & Berger, M. L. (2000) *Nature* **404**, 563.
81. Brosnan, S.F. & de Waal, F. B.M. (2004) *Folia Primatol.* **75**, 317–330.
82. Weigel, R. M. (1979) *Behaviour* **68**, 250–276.
83. Freese, C. H. & Oppenheimer, J. R. (1981) in *Ecology and Behavior of Neotropical Primates*, eds. Coimbra-Filho, A. F. & Mittermeier, R.A. (Academia Brasileira de Ciências, Rio de Janeiro, Brazil), Vol. 1, pp. 331–390.
84. Verbeek, P. (1995) Master's thesis (Emory University, Atlanta, GA).
85. Marchal, P. & Anderson, J. (1993) *Folia Primatol.* **61**, 165–173.
86. Chance, M. R. A. (1962) *Symp. Zool. Soc. London* **8**, 71–89.
87. Bakeman, R. & Gottman, J. M. (1997) *Observing Interaction: An Introduction to Sequential Analysis* (Cambridge Univ. Press, Cambridge, U.K.), 2nd Ed.
88. Gallup, G. G., Jr. (1975) in *Socio-Ecology and Psychology of Primates*, ed. Tuttle, R. H. (Mouton, The Hague), pp. 309–342.
89. Anderson, J. R., Myowa-Yamakoshi, M. & Matsuzawa, T. (2004) *Proc. R. Soc. London B (Suppl.)* **271**, 468–470.
90. Dally, J. M. (2003) Doctoral Thesis (Univ. of Cambridge, Cambridge, U.K.).