Spontaneous expression of mirror self-recognition in monkeys after learning precise visual-proprioceptive association for mirror images

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Mirror self-recognition (MSR) is generally considered to be an intrinsic cognitive ability found only in humans and a few species of great apes. Rhesus monkeys do not spontaneously show MSR, but they have the ability to use a mirror as an instrument to find hidden objects. The mechanism underlying the transition from simple mirror use to MSR remains unclear. Here we show that rhesus monkeys could show MSR after learning precise visual-proprioceptive association for mirror images. We trained head-fixed monkeys on a chair in front of a mirror to touch with spatiotemporal precision a laser pointer light spot on an adjacent board that could only be seen in the mirror. After several weeks of training, when the same laser pointer light was projected to the monkey's face, a location not used in training, all three trained monkeys successfully touched the face area marked by the light spot in front of a mirror. All trained monkeys passed the standard face mark test for MSR both on the monkey chair and in their home cage. Importantly, distinct from untrained control monkeys, the trained monkeys showed typical mirror-induced self-directed behaviors in their home cage, such as using the mirror to explore normally unseen body parts. Thus, bodily self-consciousness may be a cognitive ability present in many more species than previously thought, and acquisition of precise visual-proprioceptive association for the images in the mirror is critical for revealing the MSR ability of the animal.

mirror self-recognition | rhesus monkey | bodily self-consciousness | visual-proprioceptive association | instrumental mirror use

Self-awareness reflects a form of higher intelligence that could be revealed by mirror self-recognition (MSR) in humans. Testing MSR has become the main approach in studying self-recognition in animals, and only a few species (1–8) have passed the test. In the standard face mark test for demonstrating MSR, an odorless nonirritant dye is placed on the face of the subject (without the subject's awareness) that can only be seen in the mirror. Humans and several species of great apes could pass the test by touching the dye mark after seeing themselves in the mirror. However, it remains unclear whether failing the MSR test is a result of the lack of an animal's self-recognition ability or the inadequacy of the mirror test to reveal this ability (9). Previous studies on several species of monkeys have shown that although monkeys could not pass the mark test, they were capable of using the mirror as an instrument to find hidden objects with or without training (10–15). This has led to the view that instrumental mirror use and MSR represent two distinct levels of cognitive abilities. In our previous study, we found that some rhesus monkeys could pass various forms of the mark test after visual-somatosensory training, indicating the monkey's ability to learn MSR. This led to the present study of the mechanism underlying the transition from the simple instrumental use of the mirror to MSR in rhesus monkeys. We found that mirror-induced self-directed behaviors, a sign of bodily self-consciousness, spontaneously appeared in the rhesus monkey after training for precise visual-proprioceptive association for the mirror images.

This also explains the acquisition of MSR after visual-somatosensory training in our previous study (16).

Results

Training of Visual-Proprioceptive Association for Mirror Images.

Three young male rhesus monkeys (3–4 y old; M1, M2, and M3) were chosen for this training, together with three control male monkeys of a similar age. All monkeys underwent a period of mirror habituation (30 min daily for 7 d) on a mirror-facing head-fixation chair that allowed free arm movements. After the habituation period, face mark tests (using nonirritant laser pointer light or odorless dye mark of various colors) were performed, and all monkeys showed no face mark touching behaviors on the chair in front of the mirror, as reported by a previous study (16). Three control monkeys were similarly head-fixed on the chair and went through the same mirror exposure throughout the habituation and testing periods as the experimental monkeys, but did not go through the training protocol.

Training of visual-proprioceptive association was performed on three monkeys in the head-fixation chair in three steps: First, we projected a red laser pointer light (5 mW, <5 s duration) at random positions surrounding the monkey that could be directly seen and reached by the monkey. With food reward, all three monkeys learned to touch the light spot after several days of training (50–200 trials each day). Second, the location of the light spot was gradually moved toward the rubber balls along the head-fixing rod on each side of the monkey's head that were only visible via the mirror image (Fig. 1A). After daily training

Significance

Self-awareness is a higher intelligence that can be revealed by mirror self-recognition (MSR) in humans. Testing MSR has become the main approach to examining the existence of self-recognition in animals, and only a few species have passed the test. However, it remains controversial whether failing the MSR test is a result of the lack of an animal's self-recognition ability or the inadequacy of the mirror test. We found that MSR spontaneously appeared in rhesus monkeys after training for precise visual-proprioceptive association for mirror images. Thus, bodily self-consciousness may be a cognitive ability present in many more species than previously thought, and could be revealed by MSR when the animal acquired visual-proprioceptive association for the images in the mirror.

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Fig. 1. Visual-proprioceptive training for mirror Images. (A₁) Drawing and video image depicting step 2 of the training: the head-fixed monkey was trained to touch the light spot on the two rubber balls that could be seen only via the mirror image. (A₂) Image from [Movie S1, 1](#) showing that the monkey did not touch the light spot on the face after 2–4 wk of training in the mirror use after step 2 training. (B₁) Drawing and video image depicting step 3 of the training, using the mirror for locating light spots at multiple random positions on the board. (B₂) Image from [Movie S1, 2](#) showing that the trained monkey correctly touched the light spot on the face after 3 d of step 3 training. (C) The data depict the monkeys' performance during the course of step 2 and step 3 training and during face mark tests after each step of training. Step 2 training was performed every day, and representative data from 6 d were shown. Face mark tests after step 2 and step 3 were performed after 2 wk of continuing training, when the monkey had acquired 100% success in touching the light spot on the ball or board.

(50–200 trials per day) for a much longer period of 2–4 wk, all 3 monkeys learned to touch the light spot on the rubber ball with 100% success rates (with food reward) by looking at the mirror image of the light spot (Fig. 1C). This result showed that the monkey could learn to use the mirror as an instrument to locate the position of the light spot. The training continued for 2 more weeks after the monkey acquired 100% success in this task. Subsequent test of monkey's response with the laser light projected to the monkey's face (with the same food reward) showed that all three trained monkeys failed to touch the face mark point (Fig. 1A and C; [Movie S1, I](#)), consistent with the previous finding that instrumental mirror use did not lead to MSR in monkeys (10–15).

We then proceeded to the third step of training by substituting the rubber ball with a bigger flat board on each side of the monkey's head that could be seen only in the mirror. The light spot could be moved to multiple random positions in two dimensions

on the board, and more precise touching with one hand was required to obtain food reward (Fig. 1*B*). This task was more difficult, and all monkeys initially performed with a low success rate; several days of training were required to reach 100% success rate (Fig. 1*C*). Interestingly, after 2 wk of further continuous training to stabilize the performance, we found that when the light spot was projected to the monkey's face, all three monkeys correctly touched the spot position on the face with high success rates (92–100% in 60 trials; Fig. 1*B* and *C*; [Movie S1, 2](#)). These results indicate that after training of visual-proprioceptive association to locate spots precisely outside the body, the monkey has learned the association between the light spot image in the mirror and the corresponding position on his face, which is the general experimental criterion for MSR. Control monkeys were head-fixed on the chair in front of the mirror and went through similar daily sessions without training.

Fig. 2. Mark tests on trained monkeys. (A₁) Video images showing correct touching of face point marked by a red or violet laser pointer light by a head-fixed monkey in front of a mirror without food reward after step 3 training of precise visual-proprioceptive association. (A₂) Data depicting the percentage of correct touching for all three trained monkeys for 60 trials of light projections each before ("–") and after ("+") placing the mirror. Colored lines connect data from tests with laser light of the corresponding color. The differences between "–" and "+" were highly significant for all colors ($P < 0.001$, t test). (B₁) Video images showing the touching of the face mark using the red and black dye in front of a mirror without food reward. (B₂) Data depicting the total number of correct face mark touching for all three trained monkeys before (for 15 min) and after (for 15 min) placing the mirror. Colored lines connect data from tests using dyes of corresponding colors. Trained monkeys showed face dye mark touching in front of the mirror, but no touching without the mirror. The differences were significant in all tests ($P < 0.05$, t test). (C) Video image from [Movie S2, 1](#) showing that the trained monkey in the home cage touched the face point produced by a laser light spot in front of a mirror without food reward. Data on the right are presented as in A₂ ($P < 0.001$, t test, for all cases). (D) Video image from [Movie S2, 2](#), showing that the trained monkey in the home cage touched the face mark produced by the dye. Data on the right are presented as in B₂, including data from ear mark test with the red dye ($P < 0.05$, t test, for all cases).

but showed complete failure in our tests of touching the light spot on the ball, board, or face.

Mark Tests on Trained Monkeys. During the above training and posttraining tests, the monkeys were given food reward for each successful light spot touching. We then performed the face mark test without food reward, using laser lights of three different colors (red, green, and violet). For 60 such trials, all three monkeys showed high percentages of correct face mark touching in front of the mirror, but no face mark touching in the absence of the mirror (Fig. 2A). Furthermore, we performed a traditional face mark test by applying the water-soluble odorless dye of red, black, or green color to the cheek or eyebrow of the monkeys, at positions unlikely to be visible to them without the mirror (*Materials and Methods*). After the marking, we found that all three monkeys exhibited face mark touching during the 15-min observation period in front of the mirror, but not during the 15-min period before the mirror placement (Fig. 2B). We have also examined mirror-induced self-directed behaviors of these trained

monkeys in the unrestrained condition of their home cages. First, we performed laser light-spot mark test (on the face) and conventional dye mark test (on either face or ear) in front of a wall-size mirror without food reward, and found that all three monkeys passed the test with high success rates (Fig. 2C and D; [Movie S2](#)). During the dye mark test, the monkeys exhibited typical mirror self-recognition behaviors, including face or ear mark touching, followed by looking and/or smelling at their fingers, consistent with previous observations on rhesus monkeys that underwent visual-somatosensory training (16) and on chimpanzees that had been exposed to the mirror for some time (1). In contrast to the trained monkeys, all three untrained control monkeys showed no face point touching when the two types of mark test were performed in the home cage.

Self-Specificity in Mirror-Induced Mark Touching. To address the critical issue of whether the trained monkeys were really recognizing themselves in the mirror or simply learned a rule of touching the corresponding point on their own faces when seeing

Fig. 3. Face mark test using monkey pairs and spontaneous mirror-induced self-directed behaviors. (**A₁**) Drawing and video image from [Movie S3](#) showing that the trained monkey (red collared) performed correct self light mark touching in front of the mirror when the light spot was projected to his face or body. (**A₂**) Drawing and video image from [Movie S3](#) showing that the trained monkey touched the face light mark on a cohoused naïve monkey (green collared) when the light spot was projected on the latter's face or body. (**B₁**) Video image showing social behaviors of the trained and naïve monkey separated by a transparent glass wall. (**B₂**) A table showing the total number of face mark touching in all three trained monkeys, during each of the six observation cycles (each with 15-min glass and 15-min mirror). (**C** and **D**) Summary of results showing that trained monkeys exhibited more GR (**C**) and GU (**D**) behaviors than control monkeys. See also Table 1 and [Movie S4](#).

any monkey image with a face mark, we cohoused an untrained naïve (control) monkey with the trained monkey in the same home cage and performed 60 trials of red light spot projections

to either the trained or naïve monkey. When the light spot was on the face or body of the trained monkey, all trained monkeys showed correct light point touching with nearly 100% success

Table 1. Spontaneous mirror-induced self-directed behaviors in rhesus monkeys after precise visual-proprioceptive association training

Spontaneous mirror-induced self-directed behaviors	C1	C2	C3	M1	M2	M3
GR						
Directing the hindquarter to the mirror and looking behind toward the mirror	3	4	4	14	2	19
First looking at the mirror, and then looking at and touching his own genital area	0	3	1	32	22	5
First looking at the mirror, and then raising a leg to examine his own genital area	0	0	0	54	10	0
Total	3	7	5	100	34	24
GU						
Looking at the mirror and touching his own face, head or teeth, or pulling his own face or head hair, and then looking at or smelling at his fingers	0	0	0	1	8	42
Looking at the mirror, then touching body parts	0	0	0	67	14	26
Total	0	0	0	68	22	68

rates in front of the mirror (Fig. 3A₁ and Movie S3). In contrast, when the light spot was on the face or body of the naive monkey, trained monkeys M1 and M2 showed no self-touching, but turned to the naive monkey and touched the light spot on the naive monkey (Fig. 3A₂ and Movie S3), whereas M3 did not touch either himself or the naive monkey. The behavior of M3 was probably a result of his lower social rank compared with that of the naive monkey. During the entire experiment, naive monkeys showed no face touching on either themselves or the trained monkeys.

We next performed the mirror/glass switching experiment (16), in which the same odorless dye face mark was applied to a trained and a naive monkey at the mirroring face location, with the two monkeys separated by either a wall-size transparent glass or a mirror (facing the trained monkey). The behavior of the trained monkey was observed for 6 cycles, each consisting of a 15-min glass separation followed by a 15-min mirror separation. As shown in Fig. 3B, typical face touching behaviors were observed only in the trained monkey during the mirror-facing period, and both trained and naive monkeys exhibited social interaction when facing each other across the glass. These results further support the notion that the trained monkey did recognize himself in the mirror.

Spontaneous Mirror-Induced Self-Directed Behaviors. Finally, we recorded the spontaneous mirror-induced self-directed behaviors of all trained and control monkeys without any mark on their body. We divided self-directed behaviors into two categories (16): First, genital-related (GR) behaviors, including directing the hindquarter to the mirror and looking behind toward the mirror, or looking at the mirror, followed by examining the genitals. Second, genital-unrelated (GU) behaviors; for example, looking at the mirror followed by touching the face, head, or teeth or by pulling face or head hair and then examining and smelling the fingers. After 1-h daily observation for consecutive 5 d, we found that all three trained monkeys exhibited frequent GR (Fig. 3C) and GU (Fig. 3D) behaviors in front of the mirror, whereas three control monkeys showed essentially no such self-directed behaviors (Table 1 and Movie S4).

Discussion

In this study, visual-proprioceptive training of rhesus monkeys to precisely locate objects outside the body has resulted in self-directed behaviors in front of a mirror. We have also observed such behaviors previously after several weeks of visual-somatosensory association training by applying an irritant laser light on the monkey's face in front of the mirror (16). Pigeons were also reported to pass the mark test for MSR after extensive training with both self-directed pecking and pecking an object using a mirror (17, 18). Notably, unlike these previous studies, our monkeys were not trained to touch themselves, and mirror-induced self-directed behaviors represent a spontaneous emergence of MSR and the realization of the monkey's own body in the mirror.

The monkeys were trained to respond to the image of a laser light seen in the mirror, and then generalize to a novel situation in which the light is moved toward the monkey's face. This generalization could represent the ability of the monkey to map the position of the light point in the mirror to the corresponding point in the proprioceptive map. Importantly, when trained monkeys were released into the home cage with a wall mirror, such ability in visual-proprioceptive mapping for the mirror images made a transition into MSR, as shown by spontaneous mirror-induced self-directed behaviors in the absence of light point stimulus. In this and previous studies, MSR in animals is operationally defined by passing the face mark test, without direct evidence for the existence of self-awareness. However, our observations of self-directed behaviors induced by the mirror do suggest the presence of bodily self-consciousness, as defined by previous studies in humans and monkeys (19–21). The similarity of spontaneous mirror-

induced self-directed behaviors between the trained monkeys in this study and those trained for visual-somatosensory association (16) points to common neural circuit modifications. During the previous study (16), visual-somatosensory training of the monkey to touch the light point on the monkey's face seen in the mirror also involves visual-proprioceptive association between the mirror image and the hand position. In future studies using brain imaging of awake monkeys, it would be of interest to compare the changes of brain circuits induced by these two training protocols. In particular, a time course study that focuses on the transition from learning to use a mirror as an instrument to mirror-induced self-directed behaviors may shed light on the neural basis of MSR and bodily self-consciousness. Mirror neurons were first discovered in macaque monkeys, and were thought to be an underlying mechanism for imitation behaviors (22). It is possible that the ability of rhesus monkeys in acquiring MSR depends on the function of mirror neurons.

Instrumental mirror use has been demonstrated in a variety of species (18, 23–28), but only a few of them exhibit MSR (18, 29). This failure, as exemplified by monkeys previously trained for instrumental mirror use (12–14), may be attributed to insufficient training of visual-proprioceptive association for the mirror images. In our study, the earlier phase of training using ball touching also failed to induce the MSR. The key feature of the later training involved more precise touching of multiple random positions on the board that require the monkey to learn efficient integration of synchronous visual and proprioceptive sensory signals, a likely prerequisite process for MSR and the mirror-induced self-directed behaviors. We note that our training may have established not only visual-proprioceptive association but also some aspects of learning of visual-motor transduction. Furthermore, the training board was placed in a “peripersonal” space, which is considered to be particularly important for bodily self-consciousness (19). However, further study is required to determine whether training within peripersonal space is necessary for inducing MSR. Consistent with the notion that MSR involves visual-proprioceptive association, we have shown previously (16) that rhesus monkeys capable of MSR after visual-somatosensory association training showed precise touching of the light point on the wall behind the monkey via seeing the mirror image, similar to the ability acquired by the present training protocol. Thus, the failure of demonstrating MSR in animals could be attributed to the lack of the ability in visual-proprioceptive association for the mirror images, rather than the absence of bodily self-consciousness. Our results also underscore the importance of developing new experimental approaches in studying self-recognition and bodily self-consciousness, which may exist in many nonprimate species.

Materials and Methods

Animal Preparation. Six young male rhesus monkeys (aged 3–4 y) were the subjects of the present study. All monkeys were purchased from Suzhou Xishan Zhongke Laboratory Animal Co., Ltd. Animal care and experimental procedures were approved by the Animal Care Committee of Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences. All efforts were made to ameliorate suffering of the animals. For behavioral training, monkeys were first seated in a front-facing, head-fixation training chair that allows free arm movement. For habituation to the mirror, the monkey was placed in the chair for 30 min in the absence and 30 min in the presence of a mirror (60 × 45 cm, placed at 10 cm in front of the monkey's face) each day for 7 d.

Mark Tests in the Training Chair. Monkeys were tested in the same head-fixation chair facing a mirror before and after the training, without any food reward. Two types of face marks were used: conventional water-soluble odorless dye and low-power laser pointer light, each of three different colors. Both the dye and the laser were apparently nonirritant to the monkey. To mark the dye on the face, awake monkeys were seated in a primate chair with both the head and arms restrained. The experimenter habituated the monkey by touching his head and face from behind for several times before an odorless dye solution was quickly placed on a random area of the monkey's cheek or eyebrow that was invisible to the monkeys themselves without the

mirror, whereas pure water was placed on several other face areas at the same time. These procedures were performed to avoid monkey's noticing the placement of the mark and the mark location. The monkey's forearms were released 3 min after marking, and observation of the monkey's behavior was made for 15 min before and 15 min after a mirror was placed in front of the chair. For the light mark test, low-power red (output power, 5 mw; wavelength, 650 nm; No. 3933, Deli Group Co., Ltd.), green (output power, 5 mw; wavelength, 532 nm; OX-G005, OXLasers), and violet (output power, 20 mw; wavelength, 405 nm; OX-B021, OXLasers) laser light was used. For each color, the mark test session consisted of 60 trials in the absence and 60 trials in the presence of the mirror, with the low-power laser projected from the side of the monkey to the monkey's face at random locations. The intertrial interval was 1–3 s. The side-projection of the laser was used to prevent monkey's detection of the light path, and special caution was made to avoid the possibility of exposure of the eyes to the laser. All laser points on the face could only be seen in the mirror by the monkey. The total duration for each projection was no more than 3 s, regardless of whether the monkey performed the correct touching.

Visual-Proprioceptive Association Training for Mirror Images. For the training session, food in the home cage was withdrawn, and monkeys could only obtain food in the mirror-facing head-fixation chair described here. The training involves three steps: First, the same low-power red laser light was projected at random positions surrounding the monkey that could be directly seen and reached by the monkey. Second, the location of the light spot was gradually moved from a position visible to the monkey both directly and via mirror image toward the rubber ball (7 cm diameter) along head-fixing rods on each side of the monkey, which were only visible via the mirror image (Fig. 1A). The third step of enhanced training was performed by changing the rubber ball to a flat board (10 cm × 10 cm) on each side behind the monkey, so that the light spot could be moved to multiple random positions on the board (Fig. 1B). In the ball training, the ball was as big as the monkey's hand. When the light point was projected to the ball, the monkey only needed to grasp the ball, which was counted as a successful mark touching. Thus, this test was a simple task that monkeys were only trained to use the mirror reflection to touch the ball. In the board training, the board was bigger and the light spot could be moved to multiple random positions in two dimensions on the board, and more precise hand touching was required to obtain food reward. During the whole training procedure, food reward was given when the monkey successfully touched the illuminated area

during the light exposure. For steps 2 and 3, when the 100% success rate was maintained for 14 consecutive days, the training session was terminated and further face mark tests were performed.

Mark Tests and Spontaneous Self-Directed Behaviors in the Home Cage. Each monkey was housed in a cage that was 96 × 46 × 106 cm. A wall-size mirror (73 × 85 cm) was installed vertically in the cage. The same marks as used in the mark test in the training chair were used in this test. We first performed 60 trials of the mark test without food reward, using low-power lasers of three different colors in the absence and presence of a mirror. Food reward was shown (but not given) to the monkey to attract the monkey to face the mirror. In the test using two monkeys, the same 60 trials were performed. A trial was counted as correct when the monkey first saw the light point in the mirror, and then touched the projected location. For the mark test by odorless dye in the home cage, dye was applied to the monkey's face or ear in the training chair. The monkey was released from the training chair and returned to the home cage 3 min after being marked. Observation of the monkey's behavior was made for 15 min before and 15 min after a mirror was placed in the front. The mirror-induced spontaneous self-directed behaviors were examined for 1 h per day for 5 consecutive days after the completion of all mark tests.

Data Recording and Analysis. The monkey behaviors in all training and test sessions were recorded with digital video cameras. For experiments on the training chair, the camera was placed behind the monkey to capture the monkey's image in the mirror. Independent observers (L.C. and S.Z. and other recruited volunteers) were blind to the video recording and the identity of the monkey (trained vs. untrained). They were not blind to the overall aim of the study. The interobserver reliability was obtained by calculating the Cohen's κ for time-matched events scored by two independent observers. For mark tests using a laser pointer (Figs. 1 and 2), the interobserver reliability was 0.99 (Cohen's κ). For mark test with odorless dyes (Figs. 2 and 3) and spontaneous self-directed behaviors (Fig. 3), the Cohen's κ was 0.91 and 0.84, respectively. Interobserver reliability was calculated by all data used in the figures. All observations and analyses were based on video records.

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