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Report

Mirror-Induced Self-Directed Behaviors in Rhesus Monkeys after Visual-Somatosensory Training

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Summary

Mirror self-recognition is a hallmark of higher intelligence in humans. Most children recognize themselves in the mirror by 2 years of age [1]. In contrast to human and some great apes, monkeys have consistently failed the standard mark test for mirror self-recognition in all previous studies [2–10]. Here, we show that rhesus monkeys could acquire mirror-induced self-directed behaviors resembling mirror self-recognition following training with visual-somatosensory association. Monkeys were trained on a monkey chair in front of a mirror to touch a light spot on their faces produced by a laser light that elicited an irritant sensation. After 2–5 weeks of training, monkeys had learned to touch a face area marked by a non-irritant light spot or odorless dye in front of a mirror and by a virtual face mark on the mirroring video image on a video screen. Furthermore, in the home cage, five out of seven trained monkeys showed typical mirror-induced self-directed behaviors, such as touching the mark on the face or ear and then looking at and/or smelling their fingers, as well as spontaneously using the mirror to explore normally unseen body parts. Four control monkeys of a similar age that went through mirror habituation but had no training of visual-somatosensory association did not pass any mark tests and did not exhibit mirror-induced self-directed behaviors. These results shed light on the origin of mirror self-recognition and suggest a new approach to studying its neural mechanism.

Results and Discussion

In the standard mark test used for detecting mirror self-recognition [11], an odorless non-irritant dye is placed on the subject's face that can only be seen in the mirror. Subjects pass the test if they touch the dye mark after seeing themselves in the mirror, but not in the absence of the mirror. Based on the mark test or other mirror-induced self-directed behaviors, some chimpanzees [11], orangutans [12], bonobos [13], and gorillas [14, 15] were reported to exhibit mirror self-recognition. Monkeys have consistently failed the mark test [3, 4], despite efforts in prolonging the mirror exposure [5], starting mirror stimulation at a young age [6], changing mirror sizes and shapes [7], prior training for touching visible marks on the body [8] or using the mirror as an instrument [9], and increasing the saliency of the mark [10]. Using a new training strategy involving visual-somatosensory association, we show here that some rhesus monkeys could pass various forms of the mark test and spontaneously use the mirror to explore normally unseen body parts. Thus, rhesus monkeys can acquire through training the capability of mirror-induced self-directed behaviors resembling self-recognition.

The first set of experiments involved visual-somatosensory training of three young male rhesus monkeys (M1, M2, and M3). One year later, four additional male monkeys (M4–M7) were trained, together with four control male monkeys that were similarly mirror habituated but received no training. Habituation was performed on a mirror-facing head-fixation chair (7 days, 30 min/day) to reduce stress and social responses to the mirror image. Two pre-training mark tests included the use of water-soluble odorless dye applied to the cheek or eyebrow of awake monkeys at positions unlikely to be visible to them without the mirror and a low-power laser light (5–20 mW, for 3 s duration) projected from the side to the monkey's face at random locations, and the mark touching was counted before and after a mirror was placed in front of them. Consistent with previous studies, all 11 monkeys did not touch the dye mark or the light spot on their faces, regardless of whether the mirror was present.

The monkeys were then trained on the same chair in front of a mirror with a high-power red-color laser light (250 mW, 1–3 s) projected to random locations on either side of the monkey's face (Figure 1A). This caused apparent irritant sensation, inducing the monkey to touch the projected area with a reliability of >95% (Movie S1, part 1). Food reward was given when the monkey touched the illuminated area during the light exposure. Each day after training (50–240 trials), the high-power laser was substituted with a low-power non-irritant laser of the same color to assess whether the monkey has learned the association between the light spot in the mirror and the face area by touching the correct area in the absence of somatosensation. Food reward was provided to motivate the monkey's behavior. We found that all seven monkeys successfully learned the association after 12–38 (22 ± 3) days of training, with correct face touching within 3 s in >95% of all trials (Movie S1, part 2). The possibility that the low-power laser still produced some somatosensation was excluded by the finding that trained monkeys responded to a virtual face mark (a red-point cursor generated at random locations on the mirrored video face image), with a high percentage of correct face touching among all trials (M1, 86%; M2, 99%; M3, 94%; Movie S1, part 3).

After training, we performed the mark tests (same as in pre-training tests) with non-irritant laser and odorless dye marks *without* the food reward. For non-irritant laser tests using red laser, all seven monkeys showed a high percentage of correct touching of the face point in all trials (77% ± 8%) during 60 projections but essentially no face point touching during 60 control projections in the absence of the mirror (Figure 1C; Movie S2, part 1). Interestingly, this learned association extended to laser light of other colors (Figure 1C; Movie S2, part 1) and to conventional face marks using odorless red, green, and black dyes (Figure 1D; Movie S2, part 2), for which the frequency of mark touching was significantly higher with the mirror than without the mirror.

We then examined monkeys' behaviors in their home cages. First, we performed 30 trials (60 face points) of the mark test in

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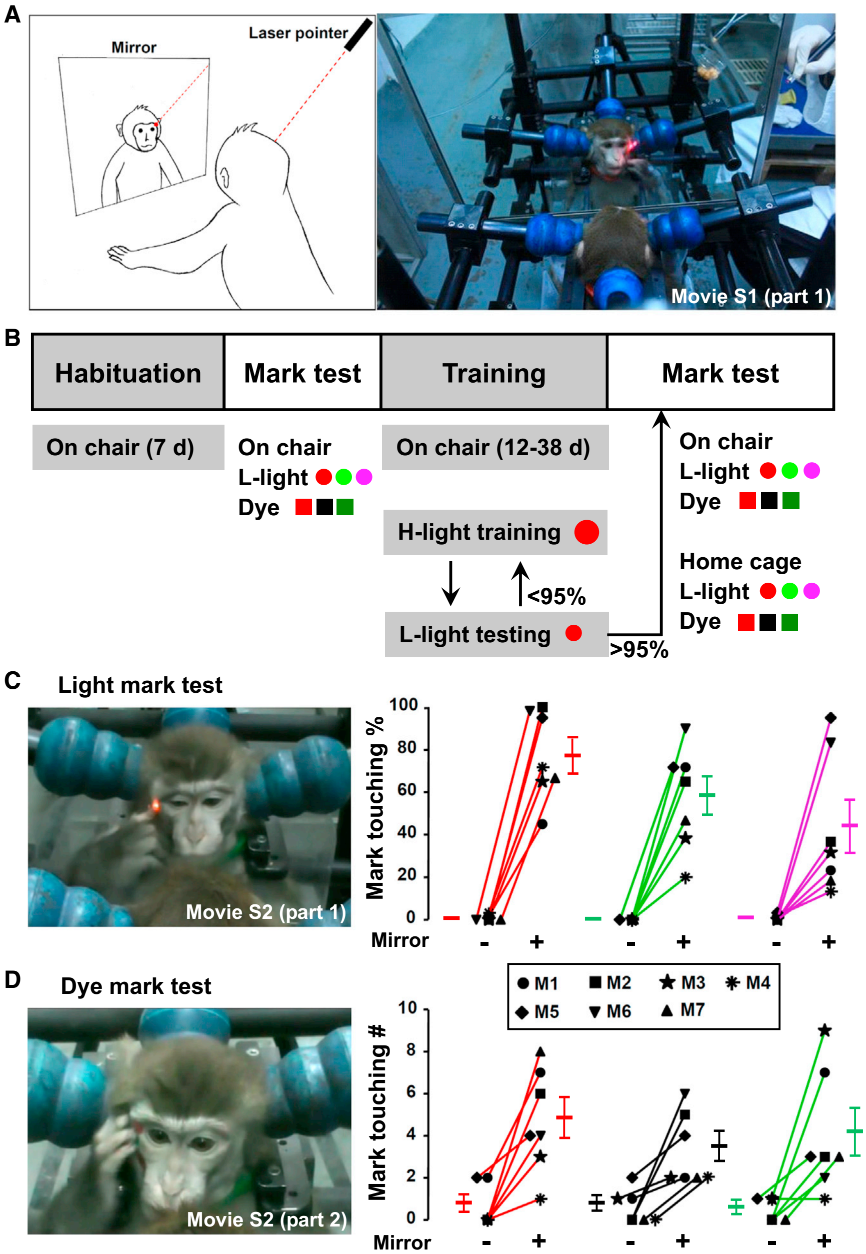

Figure 1. Visual-Somatosensory Training and Mark Tests on Monkey Chair

(A) Schematic drawing of the training setup and image of a monkey in a head-fixation training chair in front of a mirror.

(B) Summary of the experimental procedure. Colored round circles and squares represent different types of mark tests, using laser light and odorless dye of different colors, respectively.

(C) Left: image from Movie S2 (part 1) showing monkey touching the correct face point following projection of a low-power laser in front of a mirror without food reward. Right: the percentage of projections with correct touching for all seven trained monkeys, for 60 projections before ("−") and 60 projections after ("+") placing the mirror. Colored lines connect data points for tests using non-irritant low-power laser of the corresponding color. The differences were highly significant in all tests ($p < 0.001$, t test).

(D) Left: image from Movie S2 (part 2) showing the touching of the face mark produced by odorless dyes of three different colors in front of a mirror without food reward. Right: the total number of correct face mark touching for all seven trained monkeys during a 15-min period before and 15-min period after placing the mirror. Colored lines connect data points for tests using odorless dye of the corresponding color. Trained monkeys showed significantly more face mark touching in front of the mirror than in the absence of the mirror. The differences were significant in all tests ($p < 0.05$, t test).

See also Movies S1 and S2.

front of a wall-size mirror *without* food reward, using non-irritant lasers successively projected to two random locations on the face. All seven trained monkeys showed high percentages of correct face point touching in front of the mirror and showed no such touching without the mirror (Figures 2A1 and 2A2; Movie S3, part 1). They moved their hands along the movement of the projected light, showing location specificity in monkeys' face touching (Figure 2A3; Movie S3, part 1). Monkey M1, M2, M5, M6, and M7 also successfully passed the conventional mark tests (with odorless red, black, or green dye) in their home cage, as shown by the number of correct face mark touching before and after the mirror placement (Figures 2B1 and 2B3; Movie S3, part 2). The difference remained statistically significant even if the data for M3 and M4 (that failed the mark test) were also included in the analysis ($p < 0.05$ for all cases; Figure 2B3). Interestingly, monkeys that passed the mark test all exhibited the same typical behaviors, including touching the marks and then looking at or smelling their fingers (Figure 2B2; Movie S3, part 2), similar to those of chimpanzees [11], and nearly all face mark touching occurred while these monkeys were looking at the mirror (Figures 2B4 and S1). By contrast, M3 and M4 did not show any face mark touching in front of the mirror, despite the appearance of mirror looking. Furthermore, identical tests on four untrained control monkeys showed no face point touching induced by either laser or dye marks in the home cage, indicating that these behaviors were specific to the trained monkeys.

Two additional tests were performed on M1 and M2 to address the critical issue of whether the face touching reflects responses to the mark on the mirror image of the trained monkey rather than simple conditioned responses to the mark on the face of any monkey. First, the trained monkey without any mark, when co-housed in a mirrored cage with a naive monkey with a red-dye face mark, did not touch his own face. Instead, M2 twice licked and touched the face mark on the naive monkey for 2 min during a period of 30 min (Figure 3A; Movie S4, part 1). By contrast, on the following day, when the face mark was put on the trained monkey instead of the co-housed naive monkey, M1 and M2 touched the face mark in front of the mirror for four and two times (in 30 min), respectively (Movie S4, part 1). Second, we introduced the naive

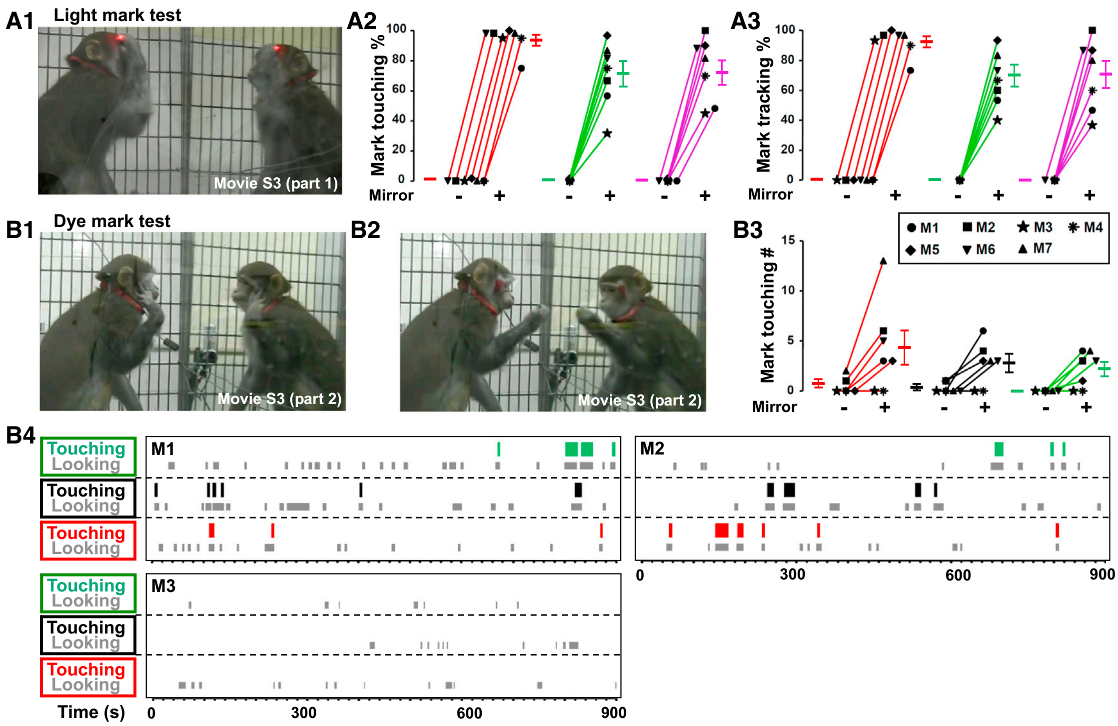

Figure 2. Mark Tests in the Home Cage

(A1) Image from Movie S3 (part 1) showing the monkey touching the face point produced by a low-power laser spot in front of a mirror without food reward.
(A2) The total percentage of projections showing correct face touching for all seven monkeys in 60 projections in the absence (−) and 60 projections in the presence (+) of a wall-size mirror. The differences were highly significant ($p < 0.001$, t test, for all cases).
(A3) The percentage of trials in which the monkey successfully tracked the movement of the light during 30 pairs in the absence and 30 pairs in the presence of the mirror. The differences were highly significant ($p < 0.001$, t test, for all cases).
(B1 and B2) Images from Movie S3 (part 2) showing the touching of the face mark produced by the odorless dye (B1), as well as the looking at and smelling of the fingers in front of a mirror without food reward (B2).
(B3) The total number of correct touching of the dye mark on the face in the absence (15 min) and presence (15 min) of the mirror. Trained monkeys showed significantly more face mark touching in front of the mirror than in the absence of the mirror ($p < 0.05$, t test, for all cases). Data on M3 and M4, who failed the face mark test in the cage, were also included.
(B4) Diagrams depict the time that trained monkeys M1–M3 were apparently looking at the mirror ("looking," gray bars) and touching the face mark ("touching," color bars) of different colors (indicated by the bar color) during the 15-min period in the presence of the mirror. Note that all face mark touching occurred when the monkey was looking at the mirror, and M3 showed no touching response when looking at the mirror.
See also Movie S3 and Figure S1.

monkey in an adjacent cage separated from the trained monkey by a wall-size mirror or transparent glass, with the same dye face mark applied to both monkeys at a mirroring face location. The monkeys' behavior was observed for six cycles, each consisting of 15 min in the presence of the glass wall, followed by 15 min of the mirror wall. During six 15-min periods in front of the glass wall, both trained and naive monkeys exhibited no face mark touching but clear social interaction when facing across the glass (Figures 3B1 and 3B2; Movie S4, part 2). By contrast, during six 15-min mirror-facing periods, both M1 and M2 exhibited the face mark touching (Figure 3B2;Movie S4, part 2). Thus, the mirror-induced face touching of trained monkeys was not simply a conditioned response induced by seeing the face mark on any monkey. We noted that most mark touching occurred during the first few mirror-facing cycles (Figure 3B2), suggesting that the monkey lost interest in the face mark with time, consistent with the finding on chimpanzees [16].

To further test whether trained monkeys could generalize the mirror recognition to regions away from the face, we first projected a low-power red laser to the wall behind the monkey or to the monkey's body parts other than the head. A trial was counted as correct when the monkey first saw the light point in the mirror and then touched the projected location. All seven trained monkeys showed very high percentages of correct touching among 60 laser projections to the wall (96% ± 2%) or to the body part (93% ± 3%; Movie S5, part 1), whereas four control untrained monkeys showed essentially no correct touching. We then applied the odorless red dye to one ear of the monkey and found that all five trained monkeys that passed the face mark test in their home cage exhibited ear-touching behaviors in front of the mirror during 15 min of observation, including scratching the marked ear, as well as looking at or smelling the fingers after touching (Figure 3C; Movie S5, part 2). No such behavior was observed prior to the mirror exposure over the same duration. The difference was statistically significant even when data on all seven monkeys were included ($p = 0.02$; Figure 3C). Four control monkeys failed to show any ear-touching responses. Thus, trained monkeys generalized the mark recognition in the mirror to regions away from the face.

Finally, we recorded the activity of seven trained and four control monkeys in their home cage with a wall mirror without body mark in order to observe spontaneous mirror-induced

B2

	G:Glass / M:Mirror	G	M	G	M	G	M	G	M	G	M	G	M
M1	Facing time (s)	8	39	24	11	22	62	10	21	9	5	17	47
M1	# of Touching	0	1	0	2	0	1	0	0	0	0	0	0
M2	Facing time (s)	49	32	28	48	8	20	8	33	65	56	10	15
M2	# of Touching	0	3	0	1	0	0	0	0	0	1	0	0

Time (min) 0, 30, 60, 90, 120, 150, 180

Figure 3. Further Tests on Mirror-Induced Mark Touching of Trained Monkeys

(A) Image from Movie S4 (part 1) showing that M2 (green collared) did not touch his own face when seeing the dye mark on the naive monkey (yellow collared) in the mirror but instead touched and licked the face mark on the naive monkey.

(B1) Image from Movie S4 (part 2) showing social behaviors of M2 with the naive monkey separated by a transparent glass wall.

(B2) A flow chart showing the total time (s) monkeys M1 and M2 faced a naive monkey with mirroring face mark across the glass wall or facing the mirror and the total number of face mark touching during each of the six observation cycles (with each cycle consisting of 15 min glass wall and 15 min mirror wall).

(C) Left: image from Movie S5 (part 2) showing the touching of the ear that was marked by the odorless red dye. Right: summary of results showing that trained monkeys exhibited significantly more ear mark touching behaviors in front of the mirror than in the absence of the mirror, including M3 and M4, who failed the ear mark test in the home cage ($p = 0.02$, t test).

See also Movies S4 and S5.

self-directed behaviors. In addition to behaviors that appeared to be similar to those found in normal social behaviors (e.g., genital touching, exhibiting genitals or the rear to other monkeys), we found several other mirror-induced behaviors that were not seen in control monkeys, e.g., looking at and getting closer to the mirror and then checking their own bodies or pulling their own face or head hair. Thus, we divided self-directed behaviors into two categories: genital related (GR) and genital unrelated (GU) (Figure 4; Movie S6; Table S1). After 1 hr daily observation for 5 consecutive days, we found that seven trained monkeys showed both GR (23 ± 4, total number of events in 5 days) and GU (12 ± 3) behaviors in front of the mirror, whereas four control monkeys showed only GR behaviors (7 ± 3) at a frequency significantly lower than that found in trained monkeys ($p = 0.02$; Figure 4A). These observations were made during the same 5-day period within days after training for M4–M7 but one year after training for M1–M3. Data collected after training for M1–M3 showed the same trend (not included in the above analysis). Thus, self-directed behaviors in trained monkeys persisted for at least 1year. Although GR behaviors occurred at a higher frequency in trained monkeys than in control monkeys, two trained monkeys (M3 and M4) that passed the mark test in the monkey chair, but not in the home cage, showed high frequencies of GR behaviors, suggesting that GR behaviors may not be a reliable indicator of mirror-induced self-directed behaviors. Nevertheless, GU self-directed behaviors were clearly absent in control monkeys and very low in monkeys that failed the mark test in the home cage (Figure 4B).

In this study, we have developed a new strategy for studying mirror self-recognition behaviors in rhesus monkeys. Our approach differed from that of previous studies in the use of visual-somatosensory association to train the monkey to touch the face mark. Rhesus monkeys with a head implant were reported to show self-directed genital-related behaviors in front of the mirror [17]. However, these monkeys did not pass the mark test, and the head implant could cause persistent irritant sensation near the implanted area. Our use of the virtual mark in mirroring video images excluded the possibility that face touching was induced by somatosensation. Although it remains debatable whether these monkeys have acquired the capacity of self-recognition, the results of the alternating mirror/glass wall experiment suggest that face mark touching was not induced simply by seeing any monkey with the face mark.

In addition to humans and several species of great apes, elephants [18], dolphins [19], pigeons [20], and magpies [21] have also been reported to pass the mark test, suggesting the ability of mirror self-recognition in some non-primate species, although some of these reports involve very few individuals and need to be replicated. Some species (e.g., humans, apes) show spontaneous “mirror self-recognition,” whereas pigeons reportedly passed the mark test only after extensive conditioning. Our study now demonstrates that rhesus monkeys may pass mark tests following training on visual-somatosensory association. The food reward was used during the training period to motivate the monkeys, but all mark tests were performed and self-directed behaviors were observed in the absence of food reward. Thus, five out of seven monkeys apparently made the transition from conditioned responses to mirror-induced self-directed behaviors that persisted for at least 1 year (in M1 and M2). Whether such transition might occur and persist in other species (e.g., pigeons) after training remains to be investigated. Recent studies on pigeons have

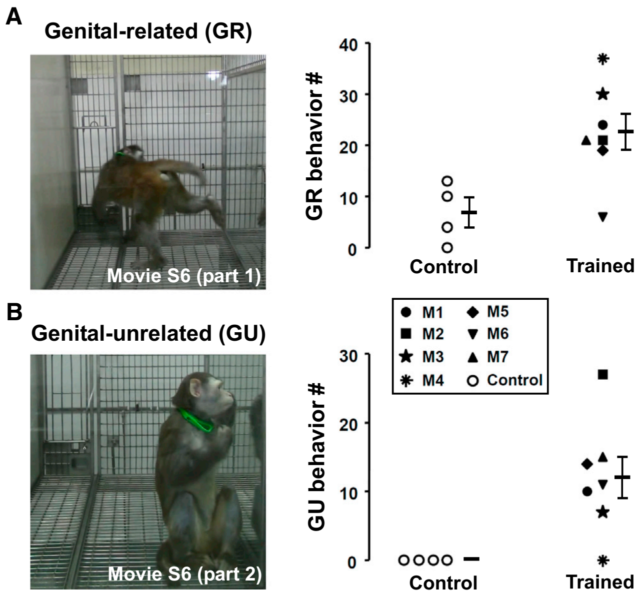

Figure 4. Spontaneous Mirror-Induced Self-Directed Behaviors

(A) Left: image from Movie S6 (part 1) showing spontaneous mirror-induced genital-related (GR) behaviors in front of a mirror. Right: summary of results showing that trained monkeys exhibited significantly more GR behaviors than control monkeys (p = 0.02, t test).

(B) Left: image from Movie S6 (part 2) showing spontaneous genital-unrelated (GU) behaviors in front of a mirror. Right: summary of results showing that trained monkeys exhibited GU self-directed behaviors while control monkeys did not (p = 0.02, t test).

See also Table S1 and Movie S6.

replicated the early finding of mark recognition [22] and provided further evidence showing discrimination of moving video images of self that suggests the acquisition of "mirror self-recognition" [23].

Our finding of the effectiveness of visual-somatosensory training supports the notion that multimodal sensory integration plays an important role in self-recognition. Studies of monkeys' responses to video images of themselves suggest that monkeys could recognize the correspondence between kinesthetic and visual information [24]. Both chimpanzees and monkeys appear to be capable of distinguishing their own hand movements from those of others [25, 26], but only chimpanzees can spontaneously recognize their own body in the mirror. The lack of self-recognition in monkeys was also indicated by the finding that mirror-experienced monkeys showed vocalizing and threatening behaviors when seeing their hand in a mirror as it approached food hidden behind an opaque barrier, as if it were the hand of another monkey [27]. It is possible that our training procedure had enhanced the capability of the monkey in multimodal sensory integration to the extent that is required for self-recognition. The fact that chimpanzees and humans require no training for mirror self-recognition suggests the existence of some fundamental underlying cognitive differences. Our training, which produces behaviors in monkeys resembling the self-recognition in humans and chimpanzees (even incomplete resemblance), may be useful in addressing the origin and neural basis of self-recognition by exploring the neural circuit changes associated with these trained behaviors.

The capacity for mirror self-recognition is impaired in many brain disorders, including mental retardation [28], autism [29], schizophrenia [30], and Alzheimer's disease [31], but the underlying neural mechanism is largely unknown. Although the impairment of self-recognition in patients implies the existence of cognitive and neurological deficits in self-processing brain mechanisms [32, 33], our finding raised the possibility that such deficits might be remedied via training. Even partial restoration of self-recognition ability could be desirable. Finally, how visual self-recognition, as shown by mark tests and spontaneous mirror-induced self-directed behaviors, is related to "self-awareness" remains to be clarified [34].

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, one figure, one table, and six movies and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.11.016.

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