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An Analysis of Behavior Directed toward Foreign Marks on the Body in Rhesus Macaques (*Macaca mulatta)*: Salience and Motivation Underlie Response

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An abstract of
A thesis submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
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Abstract

Self-awareness is essential for social cognition and there is a continuing debate over which primates possess self-awareness. The most common view is that self-awareness only exists in humans and apes, all other primates do not appear to be self-aware. This conclusion is based primarily upon the results from the mark test, a test of mirror self-recognition developed by Gordon Gallup (1970). However, passing the mark test requires both understanding the contingencies of mirrors and a motivation to inspect foreign marks on the body. If either of these requirements is not met, then failing the mark test does not demonstrate an absence of mirror self-recognition or self-awareness. In order to assess how motivated rhesus monkeys are to inspect marks, we analyzed self-directed behavior of twelve juvenile rhesus macaques towards five different foreign marks placed in plain view on their bodies: touch area, shaved area, finger paint, peanut butter, and sticker. These marks varied in salience and it was predicted that high salience marks, such as peanut butter would be attended to compared to low salience marks such as a shave mark. Mark-directed behaviors were significantly influenced by the type of mark. Finger paint, a mark similar to the marks typically used in the mark test, was not touched more frequently than chance and did not differ significantly from touch-only and shave marks. Peanut butter elicited significantly more self-directed behaviors than expected by chance and than any other mark. These results suggest that not only does the salience of a mark influences the frequency and duration of self-investigative behaviors of a foreign mark placed on the body, but also that the types of marks generally used when testing for mirror self-recognition may not be salient enough to elicit self-investigative behaviors in rhesus monkeys. Species differences that have been observed in performances on the mark test may be attributed to species differences in motivation to inspect marks on their bodies and not to a qualitative difference in mirror self-recognition or self-awareness.

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Introduction

Self-awareness can be considered the first step in the development of a more complex theory of mind, which is the capability to understand one’s own mental state and to attribute mental states to others for interaction in a social environment (Boyson & Hymes, 1999; Premack & Woodruff 1978). There is debate on whether self-awareness is common across species, whether it is limited to a subset of species, or whether it occurs only in humans (Povinelli & Preuss, 1995). This debate has resulted in comparative studies of self-awareness using a variety of techniques. Since in nonhumans it is not possible to rely on self report, the primary tool in studies of human self-awareness, indirect techniques have been proposed for studies in animals. Recognizing oneself in the mirror is considered an indicator of self-awareness, and such beliefs about mirror self-recognition and self-awareness as well as the difficulty of directly testing self-awareness in preverbal humans and nonhuman animals have resulted in the development of a test for mirror self-recognition that has been used on a variety of species (Gallup 1970, Gallup 1976, Anderson, 1983; Brooks-Gun & Lewis, 1984). The mark test for mirror self-recognition, in which, unbeknownst to the subject, a mark is placed on the body in a position that can be visually accessed only by using a mirror, has become the primary tool for assessing mirror self-recognition and self-awareness in nonhumans. An individual passes the mark test if he exhibits self-investigative or self-directed behaviors towards the mark that has been placed on his body only when looking in a mirror. Failures on the mark test by nonhumans have been taken as evidence for the absence of self-awareness, and this idea that nonhumans lack self-awareness has subsequently been used to explain the discrepancy in social and cognitive abilities between humans and nonhumans. What traits and capabilities, including self-awareness, theory of mind, and mirror self-recognition, nonhuman primates share with humans is unresolved. Therefore, it is important to understand what is demonstrated by the mark test for mirror self-recognition before drawing conclusions about other animals' capacities for self-awareness, or theory of mind. In order to reach that point, there are significant challenges to overcome. Most importantly, factors that could affect or even predetermine performance on the mark test, such as an individual's inherent motivation to be sensitive to changes in physical appearance as assessed by the levels of self-directed behavior, should be explored.

In the 1960's and 1970's, Gordon Gallup performed the first mark test for mirror self-recognition on several nonhuman primate species and concluded that while chimpanzees were capable of recognizing themselves in a mirror, rhesus macaques and other species of monkey were not (Gallup, 1970; Gallup, 1976). Since these initial studies in nonhuman primates were conducted, Gallup's mark test has since gained enormous popularity and has led to the investigation of many nonhuman species' performances on the mark test. Over the past 40 years, it has been argued that not only do humans and some species of great ape possess this capability but so do dolphins (Tobach et al, 1997), elephants (Plotnik et al, 2006), and magpies (Prior et al, 2008). Despite many attempts, rhesus macaques and several other species of monkey have consistently failed to show mirror self-recognition as assessed by Gallup's mark test (Gallup, 1970; Gallup, 1976; Hauser, 2001; Macellini et al, 2010; Posada, 2005; Roma et al, 2007). Recently, however, striking evidence that rhesus monkeys recognize themselves in a mirror, although they fail Gallup's mark test, has called into question what the mark test actually measures (Rajala et al, 2010).

Despite their consistent failures at the mark test, recent evidence suggests that rhesus macaques possess the capacity for mirror self-recognition. While observing five adult rhesus macaques who were a part of a larger project for which they had received head-mounted platforms for electrophysiological experiments, Rajala and colleagues (2010) noticed that the monkeys were using mirrors hanging in their cages to groom and inspect areas of their bodies, including the area around the head platform, which would otherwise be hidden from view without a mirror. The rates of self-directed behaviors that the monkeys exhibited were significantly higher, nearly tenfold greater, when in the presence of a mirror than when in the presence of a mirror on which the reflective surface was covered with black plastic (Rajala et al, 2010). Such self-directed behaviors combined with this type of mirror use had not previously been reported in rhesus monkeys (Gallop, 1976; Posada & Colell, 2005; Paukner, Anderson, & Fukita, 2004). In fact, quite the opposite has been published. According to a meta-analysis of the behavioral responses of several species of nonhuman primate to their mirror images (Inoue-Nakamura, 1997), the only species to exhibit any type of self-directed behavior when faced with their mirror image are the great apes, whereas prosimians, new world monkeys, old world monkeys, and lesser apes consistently fail to show self-directed responses.

Although Rajala et al (2010) presented convincing evidence that their rhesus macaques possessed mirror self-recognition capabilities based on their self-directed responses when looking at a mirror image, all of their monkeys failed Gallup's mark test for mirror self-recognition. While the monkeys in this experiment showed convincing evidence for mirror-guided self-directed behavior, hesitation to believe that they have the capacity for mirror self-recognition remains due to their failures on this mark test. Ironically, the developer of the mark test of mirror self-recognition has argued that the essential property of the mark test is that it demonstrates mirror-mediation of self-directed behavior (Gallup, 1994). The data presented by Rajala et al (2010) should be accepted by Gallup and other skeptics as evidence for mirror self-recognition in rhesus macaques. However, this is not the case. Thus it is necessary to investigate what it is about the mark test that results in a species that demonstrates mirror-self-recognition failing the mark test.

Rajala and colleagues (2010) discuss the possibility that the marks typically used in the mark test for mirror self-recognition, dye marks, are not salient enough to motivate the monkeys to elicit self-directed behaviors towards the marks, thus resulting in failures on the standard mark test. They argue that the presence of the head platforms provided the motivation to use the mirror to groom the skin surrounding the head platform and thus allowed the monkeys to demonstrate their capacity for mirror self-recognition. Although increasing the salience of the mark has been previously attempted by using more extensive dye markings these changes did not alter the monkey’s lack of response (Hauser et al, 2008). The responses of the monkeys to the head platform but not to the dye marks suggest that, at least in rhesus monkeys, something more relevant than a dye mark needs to be used to elicit mirror-guided self-directed behaviors. In the original studies, Gallup (1970) used red dye and it was assumed that this mark would be salient due to the biological significance of the color red. However, Gallup did not provide any evidence for the salience of the mark and it is possible that his assumption was invalid. Resolution of this issue requires performing a more rigorous test of what kinds of marks specific species are motivated to inspect before subjecting individuals to a mirror mark test.

Although attempts at increasing the salience of marks have been made, why an animal would be interested in inspecting a mark on its body, regardless of the fact that it is something that was not present before, remains unanswered. Most animals are not particularly fastidious and it is not clear that marks on their body have much salience. In fact, it is quite striking that some animals, chimpanzees in particular, seem to care about marks on their bodies. There is no a priori reason to assume that an animal would necessarily care about the presence of a mark. Missing in the research conducted thus far is a controlled experiment to determine if a nonhuman primate, specifically the species of monkey that fail the mark test, would increase self-directed and exploratory behavior towards a mark on the body that is visible without a mirror. If macaques do not show increased interest in plainly visible marks on their bodies, it would strongly suggest that they fail the mark test because body marks are of little significance to them and so they simply ignore them.

There have been several unsuccessful and poorly controlled attempts at using a plainly visible mark as a control when testing for mirror self-recognition. In two infant apes, an orangutan and a chimpanzee, Robert (1986) placed dye marks on the toes of the subjects to measure their mark-directed behavior to plainly visible marks. Robert (1986), without presenting any data or statistical analysis, claimed that the apes showed considerable interest in their marked toes although they failed to show any mark-directed behavior towards the mark on their foreheads during the experiment. A similar control was used with a gorilla who showed such interest in the marks that he removed them from himself before any formal observations could be made (Posada & Colelli, 2007). Hauser (2001) utilized a similar control in cotton-top tamarins in which the arm of the tamarin was dyed as well as the head hair tuft. The tamarins failed to show any mark-directed behavior to either the arm or the head (Hauser, 2001). Similar controls have been used in other mirror self-recognition studies, but the degree to which the subject pays attention to the mark as well as how much self-directed behavior is exhibited towards the same area when the mark is not present is never reported and these controls are usually presented as anecdotes making interpretation of the findings impossible. The performance on these control tasks are usually expressed as whether the animal did or did not inspect the mark visible without a mirror (Boccia, 1994; Galup, 1970). It is possible that the mark inspection that is anecdotally reported has been misinterpreted and is in fact not a sign of interest or motivation to touch foreign marks, let alone statistically significant.

The mark test has been treated as the gold standard for determining which species are capable of mirror self-recognition. However, evidence suggests that there is considerable variation in performance on the mark test within species, which further supports the idea that some factor other than mirror self-recognition, possibly motivation, is influencing performance on the mark test. Swartz and Evans (1991) tested 11 chimpanzees on the standard mark test and found that only one individual showed more self-directed behaviors towards a mark when in the presence of a mirror than when without a mirror. The chimpanzees in this experiment were given multiple mark tests at different time points in their mirror exposure (ranging from two to 80 hours of mirror exposure) in order to investigate how much mirror exposure is required to induce mirror self-recognition, as it was expected that all chimpanzees would eventually show mirror self-recognition. Although several other studies have had higher success rates in chimpanzees, it is common for one or more individuals to fail the mark test (Povinelli et al, 1993; de Veer et al, 2003). Failures on the mark test have been linked to failures to demonstrate self-exploratory or self-directed behavior in general (Povinelli et al, 1993). This variation indicates inherent differences in motivation to self-explore, but individuals who fail to self-explore are still referred to as lacking self-recognition. It is highly unlikely that there is such a qualitative difference in self-recognition between individuals within a species, and that it would be better explained by some other factor, namely, motivation to attend to a mark on the body.

Similarly, in humans, variations in performance on the mark test exist between cultures. It has been demonstrated that mirror self-recognition can be reliably demonstrated by the mark test in infants by approximately twenty months of age (Amsterdam, 1971). However, through cross-cultural analyses of 18-20 month old infants' performances on the mark test, it was discovered that while the majority of Greek, Costa Rican, and German children passed the mark test, less than four percent of Cameroonian children passed (Keller et al, 2004). Furthermore, other cultural differences have been observed between Western children and children from non-Western communities such as Kenya, Saint Lucia, Grenada, and Peru (Broesch et al, 2009). In these experiments, a significantly smaller percentage of the non-Western children passed the mark test for mirror self-recognition. The performance of these children on the mark test has not been, nor would it be correct to be, taken as evidence that they lack self-recognition capabilities but rather that some cultural factors have influenced how the children construe the task (Broesch et al, 2009).

Variation is not only seen between individuals but it has also been documented within individuals. de Veer and colleagues (2003) performed a longitudinal study on the mirror self-recognition behaviors of chimpanzees. Chimpanzees were given a mark test in 1992, and then again eight years later, and while nine out of twelve chimpanzees passed the mark test in 1992, only six of the same twelve chimpanzees passed the test in 2000 (de Veer et al, 2003). Although the difference in the number of chimpanzees who passed the test between 1992 and 2000 was not statistically significant, the fact that three individuals who once passed the mark test failed to do so eight years later is striking. One possible explanation given by the authors is that aging results in the loss of the capacity for mirror self-recognition (de Veer et al, 2003), however this seems unlikely as the chimpanzees who failed were no older, and in some cases younger, than the chimpanzees who passed both times. It is much more likely that the individual's motivation for self-inspection vary over time and not that inherent capacity for self-recognition changes.

Considering all of the studies of mirror self-recognition it is apparent that not only is it possible that individuals failing the mark possess mirror self-recognition, but also puts in doubt one major assumption of the mark test that individuals are comparably motivated to inspect a mark on their body. It has been assumed that not only is this motivation present but also that it does not fluctuate over time. While attempts have been made to determine if an individual would be motivated to touch a mark on his body that is visible without a mirror, they were either poorly controlled or the results of such controls have not been rigorously analyzed. Thus, after more than 30 years of study, the issue of a subject's motivation to attend to a mark on its body remains unresolved.

A first step towards addressing the role of motivation to self-inspect is to investigate the amount of self-directed behavior rhesus monkeys exhibit towards plainly visible marks on their bodies. To directly address the issue of the subject's motivation to attend to a mark we employed five different types of marks varying in salience to the subject. Salience ranged from a shaved patch of hair, hypothesized to be of low salience, to a dab of peanut butter, excepted to be of high salience. It was hypothesized that the amount of mark-specific, self-directed behaviors would be higher when the mark was highly salient to the subject and that subjects would essentially ignore low-salience marks

Methods

Subjects

Subjects were twelve (six male, six female) juvenile (age range 18-34 months) rhesus macaques. All subjects were living in 50-100 member social groups with species-typical social organization at the Yerkes National Primate Research Center in Lawrenceville, Georgia. These subjects have spent the majority of their lives in outdoor compounds with attached indoor quarters and thus engage in social interactions 24 hours per day. One subject spent the majority of the six months prior to testing individually housed due to health complications.

Apparatus and Procedures

Subjects were tested in a (26.5 x 22.5 x 32.5 in) cage with a clear Plexiglass side and modified to have a movable back panel to allow subject immobilization. Subject behavior was recorded with a Canon FS10 digital camera.

Each of the 12 subjects experienced five testing sessions. No subject experienced more than one test session per day. Testing sessions consisted of two, thirty-minute trials during which the behavior of the subjects was continuously recorded. At the start of each session, the experimenter transferred the subject into the modified testing cage and left the testing room for the duration of the trial. After 30 minutes, the experimenter returned and the subjects were administered one of five possible marks. Using the modified back panel of the testing cage, the experimenter pulled the subject forward so that he or she was immobilized to allow the experimenter to safely access one of the subject’s arms. The arm that was marked was alternated throughout the testing sessions for each subject.

Once access to the arm was gained, the experimenter held the hand of the subject and applied the mark, in full view of the subject, to an area on the forearm beginning at the wrist and extending approximately one inch above the wrist. The subject was released after marking and given free range of the cage. The experimenter left the testing room and the subject’s behavior was recorded for another 30 minutes.

The marking condition in the first test session for all subjects was touch-only (TT). In this condition, the experimenter gained access to the arm, held the hand, and rubbed the target area four times. In the second test session all subjects were marked with black, nontoxic, washable finger paint (FP, Crayola LLC.). A dab of paint was applied to the arm and then blotted with a small piece of gauze so that the remaining mark was as dry as possible and rubbed into the fur as opposed to a raised dab of paint.

For the third test session, the target area of the arm was shaved with an electric razor (SH). For the fourth test session half of the subjects had the arm area shaved and then marked with a blue, smiley-face paper sticker (ST). The other half of the subjects had their arms shaved and then marked with a dab of creamy peanut butter (PB) (Kroger Co.). These marking conditions were then reversed for the fifth test session.

Analysis

All videos were coded using Windows Media Player and WinOBS (CBN, Atlanta, GA). The frequencies and durations of all self-directed behaviors were scored. See Table 1 for the complete ethogram and description of each subset of self-directed behavior. For the first trial of each test session, the area of the body on which the mark would be placed in the second trial was labeled the "unmarked target area". In the second trial this area was marked and referred to as the "marked target area". Types of self-directed behavior as well as if the behavior was directed towards the unmarked target area (trial one), marked target area (trial two), or other areas of the body ("other-directed behavior") were coded.

One coder scored 100% of the videos and a coder blind to the hypotheses scored 10% of the same videos to assess inter-rater reliability. For this experiment, reliability = (% agreement - % chance)/ (1-% chance). The % agreement, or the proportion of behaviors coded in agreement by the two observers, was calculated by dividing the total number of behaviors coded in agreement between the observers by the total number of behaviors coded. The % chance values were calculated by finding the sum of the products of each coder's totals for each type of behavior and dividing that value by the square of the total number of behaviors coded. The coders were found to be 88.6% reliable.

Difference scores were calculated in order to assess not only the change that occurred in self-directed behavior as a result of the marking procedure but also to compare the pattern of differences between the types of self-directed behavior within and between trials across all mark types. The difference scores for frequency and duration of marked-target-directed behavior and other-directed behavior were calculated by subtracting the values for other-directed behavior in the second trial from the values for marked-target-directed behavior. The difference scores for marked-target-directed behavior and unmarked-target-directed behavior were calculated by subtracting the latter from the former.

Repeated measures analyses of variance were calculated to compare the difference scores as well as the frequency and duration of marked-target-directed behavior, unmarked-target-directed behavior, and other-directed behavior across all mark types and trials. If any violations of Mauchley's test for sphericity were found, degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity. Between subjects analysis with repeated measures ANOVA was conducted to assess possible interactions of session with sex and age. Significant differences found with the repeated measures ANOVA were further examined with Bonferroni post-hoc pairwise comparisons. A criterion of $p < 0.05$ was set for statistical significance for all statistical tests, and all tests were carried out using PASW Statistics 18 (formerly SPSS) for Windows (IBM Corp).

Results

Comparison of Other-Directed Behavior in Trials One and Two

The frequencies and durations of other-directed behavior in trials one and two were compared across all mark types. No main effects of mark type F (2.20, 24.18) = 2.68, $P = 0.08$, trial F (1, 11) = 0.006, $P = .94$, or of the interaction between mark type and trial F (2.096, 23.05) = 0.45, $P = 0.77$ on other-directed behavior were found. See Figure 1 and Figure 2 for average frequencies and durations of other-directed behaviors in trials one and two. Mauchly's test of sphericity was violated in this analysis and degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity.

Comparison of Unmarked-Target-Directed Behavior and Other-Directed Behavior

A main effect of location (unmarked-target area vs. other areas) on frequencies of self-directed behavior was found, and the frequencies of unmarked-target-directed behavior were significantly smaller than other-directed behavior F (1, 11) = 14.31, $P = 0.003$, $\eta_p = 0.57$. See Figure 1 for average frequencies of unmarked-target-directed behavior and other-directed behavior. No main effects of mark type or the interaction between mark type and location on self-directed behaviors were found (all *P's* > 0.05). A main effect of location on the durations of self-directed behavior was found, with the durations of unmarked-target-directed behavior shorter than those of other-directed behavior F (1, 11) = 10.46, $P = 0.008$, $\eta_p = 0.49$. See Figure 2 for average durations of unmarked-target-directed behavior and other-directed behavior. Mauchly's test of sphericity was violated in the duration analysis and degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity.

Comparison of Marked-Target-Directed Behavior and Other-Directed Behavior (Trial Two)

Figure 1 presents the the average frequencies of marked-target-directed behavior and other-directed behavior in trial two. A main effect of mark type on the frequencies of self-directed behavior was found F (4, 44) = 7.13, $P = 0.001$, $\eta_p = 0.11$. No main effect of location (marked-target area and other areas) was found ($P > 0.05$). The interaction between location (marked-target area and other areas) and mark type was significant F (4, 44) = 5.23, $P = 0.002$, $\eta_p = .32$. The frequency of marked-target-directed behavior was higher than the frequency of other-directed behavior only when the mark was PB, and this result was significantly different only from the TT mark ($P = 0.002$). .

A main effect of mark type on the durations of self-directed behavior was found F (4, 44) = 4.32, $P = 0.005$, $\eta_p = 0.28$. The interaction between location (marked-target area vs. other areas) and mark type was also significant $F = 10.85$, $P < 0.001$, $\eta_p = 0.50$. The duration of marked-target-directed behavior was higher than other-directed behavior only when the mark was PB, and this pattern differed significantly only from that of TT ($P = 0.04$). See Figure 2 for the average durations of marked-target-directed behavior and other-directed behavior in trial two.

To more clearly illustrate the effects of mark type on target-directed behavior we calculated the difference between marked-target-directed behavior and other-directed behavior in the second trial for each mark type and compared these difference scores across all sessions. Figure 3 illustrates that the frequency difference scores were greater for marked-target directed behavior only in the PB condition, for all other marks they were either the same as or less than other-directed behavior. A main effect of mark type on the difference between marked-target-directed behavior frequency and other-directed behavior frequency was found F (4, 44) = 5.23 $P = 0.002$ $\eta_p = 0.32$. The difference score for PB was significantly different from the scores for TT ($P = 0.04$) and SH ($P = 0.008$). The averages of the difference scores indicate that, on average, the frequency of other-directed behavior was higher than marked-target-directed behavior for all marks but PB ($M = 2.32$, SD = 3.85) and ST ($M = 0.08$ SD = 2.75 Difference scores were also calculated for the durations of these behaviors (Figure 4) and compared across all sessions. A main effect of mark type on the difference between marked-target-directed behavior duration and other-target-directed behavior duration was found F (4, 44) = 10.85 $P < 0.001$ $\eta_p = 0.50$. PB elicited a significantly different pattern of behavior than TT ($P = 0.002$), FP ($P = 0.01$), SH ($P = 0.001$), and ST ($P = 0.07$).

Comparison of Marked-Target-Directed Behavior and Unmarked-Target-Directed Behavior

Figure 1 presents the average frequencies of marked-target-directed behavior (trial 2) and unmarked-target-directed behavior (trial 1). A main effect of trial on target-directed behavior was found F (1, 11) = 43.113, $P < 0.001$, $\eta_p = 0.80$. A main effect of mark type on target-directed behavior was also found F (4, 44) = 14.82, $P < 0.001$, $\eta_p = 0.57$. The interaction between trial and mark type on target-directed behavior was also significant F (4, 44) = 17.51, $P < 0.001$, $\eta_p = 0.61$. The behaviors directed towards TT and SH were not significantly different. Frequencies of behavior directed to FP were significantly more frequent than those directed towards TT ($P = 0.016$). The behaviors directed towards PB were significantly greater than those directed towards TT ($P = 0.001$), FP ($P = 0.037$), and SH ($P = 0.006$). No significant differences were found in the frequency of marked-target-directed behaviors between FP and SH, FP and ST, SH and ST, or PB and ST (all *P's* > 0.05).

Figure 2 presents the average durations of marked-target-directed behavior (trial 2) and unmarked-target-directed behavior (trial 1). A main effect of trial on the duration of target-directed behavior was found $F\ (1, 11) = 19.42$, $P = 0.001$, $\eta_p = 0.64$. A main effect of mark type on target-directed behavior was also found $F\ (1.49, 16.35) = 15.78$, $P < 0.001$, $\eta_p = 0.59$. The interaction between mark type and trial on the durations of self-directed behavior was also significant $F\ (1.48, 16.23) = 15.71$, $P < 0.001$, $\eta_p = 0.59$. The duration of marked-target-directed behavior for PB was significantly longer than those for TT ($P = 0.006$), FP ($P = 0.004$), and SH ($P = 0.011$). The durations of marked-target-directed behavior for ST were also significantly longer than those for TT ($P = 0.015$). Mauchly's test of sphericity was violated in the duration analysis and degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity.

To control for the unmarked-target directed behavior we calculated the difference between the frequencies of marked-target-directed behavior and unmarked-target-directed behavior for each mark type and these difference scores (Figure 5) were compared across all marks. A main effect of mark type on the difference between marked-target-directed behavior frequency and unmarked-target-directed behavior frequency was found $F\ (4, 44) = 17.51$ $P < 0.001$ $\eta_p = 0.71$. The difference score for PB was found to be significantly different from the scores for TT ($P < 0.001$), FP ($P = 0.01$), and SH ($P < 0.001$). The difference score for ST was significantly different from that of TT ($P = 0.012$). No significant differences were found between the difference scores for TT, FP, and SH or between the scores for ST, FP, and SH, or ST and PB. The averages of the difference scores indicate that, on average, frequency of marked-target-directed behavior was higher than unmarked-target-directed behavior for all marks but TT (M = -0.83 SD = 0.29).

Difference scores were also calculated for the durations of these behaviors and compared across marks (Figure 6). A main effect of test mark type on the difference between marked-target-directed behavior duration and unmarked-target-directed behavior duration was found F (4, 44) = 15.71 $P < 0.001$ $\eta_p = 0.59$. Post-hoc analyses revealed that the difference score of marked-target-directed behavior and unmarked-target-directed behavior for PB was significantly different from the difference scores from TT (P = 0.006) FP (P = 0.003), and SH (P = 0.01). The difference score for ST was significantly different from the scores for TT (P = 0.05), and SH (P = 0.04). No significant differences were found between the difference scores for TT, FP, and SH, or FP and ST.

Between-Subject Factors: Sex and Age

There was no evidence that either sex or age affected unmarked-target-directed behavior or marked-target-directed behavior with regard to frequency or duration ($P >$ 0.05). There were significant interactions between trial, sex, and mark type on the frequency of other-directed behavior F(4, 40) = 3.08, P = 0.03, $\eta_p = 0.24$. When the mark was TT, males and females behaved the same, but for FP, SH, and PB, the average other-directed behavior in the second trial was higher than the average of other-directed behavior in the first in females. Males showed more other-directed behavior in the first trial when the mark was TT, FP, SH, and PB. For ST, females showed more other-directed behavior in the first trial, whereas males showed more other-directed behavior in the second trial. See Figure 7 for the average frequencies of other-directed behaviors in trials one and two for males and females.

Individual Differences in Marked-Target-Directed Behavior

Results from Cochran's test indicate that the types of marks differ in their effectiveness in eliciting self-directed behavior towards those marks N = 12 $Q = 99.66$ $P < 0.001$. Only 1/12 monkeys showed any marked-target-directed behavior towards TT. Comparatively, 11/12 monkeys exhibited marked-target-directed behavior towards the FP mark and 5/12 directed behavior towards SH. All of the monkeys directed behavior towards PB and ST at least once. In addition, 10/12 monkeys showed no change in target-directed behavior between trials with TT, 7/12 monkeys did not change when SH mark was applied, 4/12 monkeys showed no change with FP, and 2/12 monkeys remained unchanged when marked with ST. All twelve of the monkeys exhibited more behaviors towards the target area once the peanut butter was applied in the second trial than in the first trial.

Discussion

Prior to this experiment, no controlled analysis of the amount of self-directed behaviors that rhesus monkeys exhibit towards foreign marks placed on the body had been conducted. Without this information, it is impossible to interpret performances on the mark test for mirror self-recognition. The possibility that motivation underlies performance on the mark test was addressed in this study, and the results suggest that not only does motivation influence self-directed behavior, but that the levels of motivation to investigate a mark vary with the mark's salience. Previous work suggests that the salience of a mark cannot be increased simply by increasing the marks size or brightness

(Hauser, 2008), but by making a mark more relevant for the species in question it may be possible to tap into natural displays of self-investigative and self-directed behaviors (Rajala, 2010).

Five marks of varying predicted salience were used in this experiment in order to evaluate what mark characteristics might be salient enough to elicit self-directed behaviors. However, the levels of behaviors directed towards the target areas were not the only behaviors of interest. One concern with the design of the experiment was that all of the subjects would be awake during the marking procedure. In many of the previous mark test experiments with nonhuman primates, the subjects were anesthetized so that they were unaware of the marks until faced with a mirror (Gallup, 1970, Gallup, 1976, Heyes, 1994). Time and safety constraints on the subjects used in the present study prevented the use of anesthesia for marking. While there may be some concern that self-directed behavior would be influenced by the opportunity the monkeys had to witness the marking procedure, several control procedures and analyses were carried out to alleviate this concern. In order to determine if the handling during the marking procedure would influence self-directed behavior, an analysis of the frequencies and durations of behaviors directed towards other parts of the body (not the target area) was completed. Not only was there no main effect of trial on the amount of other-directed behavior, but there were also no significant differences in the frequencies and durations of other-directed behavior across session and mark type. This suggests that not only did the marking procedure not influence self-directed behavior in general, but also that self-directed behavior was not influenced by the amount of experience that the subjects had in the testing environment or with the testing procedures. Similarly, there was not a significant increase in the frequency or duration of target-directed behavior from trial one to trial two when the mark was touch-only. This type of control mark allowed us to conclude that the handling procedures and the ability of the monkeys to witness the marking procedure alone do not influence self-directed behaviors. As a result, any changes in target-directed behavior observed with other mark types can accurately be attributed to the mark itself and not to other uncontrolled factors.

In addition, this experiment did not utilize any kind of mirror test. In Gallup's mirror mark tests, subjects are anesthetized to prevent them from having any experience with the mark before facing a mirror in order to assess mirror-guided mark-directed behaviors (Gallup, 1970, Heyes, 1994). In this study, however, the purpose of the marking procedure was to assess how motivated monkeys are to investigate foreign marks on the body. Because the behavior of the subjects was continuously recorded and the measure of interest was any interaction with the mark, the monkeys' abilities to immediately interact with the mark after application was not an issue. The only benefits to using anesthesia in a study like the present one would be to minimize dangers associated with direct contact with alert rhesus macaques as well as allowing for some marks, like the finger paint, time to dry so that olfactory and tactile cues that result from the application of the mark would be eliminated (this point will be discussed in more detail later).

The marks used in this study were chosen based on their predicted levels of salience. As mentioned previously, the touch mark was chosen to act as a control mark in order to assess how the handling procedures affected target-directed behavior. The shave mark was chosen because it is a visually striking change in appearance that was predicted to have little effect on self-directed behavior. The finger paint mark is most similar to the types of marks used in mirror mark tests and was chosen to assess the possibility that failures to touch these types of marks on the mirror mark test may be attributed to low levels of motivation to investigate the marks rather than an absence of mirror self-recognition. The sticker mark was chosen because it was thought to be moderately salient to the monkeys: the stickiness of the backing and the weight of the paper both provide tactile cues to the monkeys and could also be minimally uncomfortable (if the sticker pulls at the hair), and thus possibly increasing the motivation the monkeys would have to remove it. Peanut butter was chosen to act as the most salient mark because it is edible and it was predicted that the monkeys would be very motivated to remove the mark and eat it.

Target-directed behavior was assessed in two ways: it was compared across trials as well as compared to other-directed behavior within the same trial. Comparisons of unmarked-target-directed behavior (in trial one) and other-directed behavior (in trial one) revealed that the frequencies and durations of other-directed behaviors were higher than those for unmarked-target-directed behavior. This finding is not surprising: more opportunities (more body parts) for other-directed behavior exist than for target-directed behavior (one area) and therefore it makes sense that, when a mark is not yet present, the monkeys would self-direct more towards areas other than the target area. Along the same lines as the controls previously discussed, the difference between unmarked-target-directed behavior and other-directed behavior in the first trial did not vary significantly across the different mark types. This finding supports the conclusion that experiential factors other than the presence of a mark did not influence levels of self-directed behavior.

Comparing the frequencies and durations of marked-target-directed behavior and other-directed behavior in trial two allowed us to get a better picture of the pattern of self-directed behavior elicited by specific marks. The pattern of these behaviors only significantly differed between the highest and least salient marks (PB and TT), with the frequency and duration of marked-target-directed behavior exceeding other-directed behaviors with peanut butter only. As seen in Figure 3, the difference between marked-target-directed behaviors and other-directed behaviors decreases as the salience of the mark increases, suggesting that as more attention is paid to the mark, the less attention is paid to other parts of the body (as a factor of mark salience).

Analyzing the difference scores of marked-target-directed behavior and unmarked-target-directed behavior allowed us to have a pure measure of how the presence of a certain mark influenced target-directed behavior by taking into account the amount of behaviors that would be normally directed towards the target area by chance. A main effect of mark type on these difference scores was found. With regard to frequency, peanut butter elicited significantly more self-directed behavior than the touch, finger paint, and shave marks. Similarly, peanut butter elicited longer self-directed behaviors than touch, finger paint, or shave marks. The finger paint mark did not differ significantly in the frequency of elicited marked-target-directed behavior from touch or shave marks or from the sticker mark. The sticker mark did not elicit significantly fewer marked-target-directed behavior than peanut butter. These data suggest that salience ranks of the marks (as defined by the levels of self-directed behavior elicited by the marks) are (from lowest to highest): touch, shave, finger paint, sticker, and peanut butter.

The case of the finger paint mark is interesting to consider. While its pattern of behaviors as well as the frequency and duration of marked-target-directed behavior do not differ from those of the least salient marks, it also does not differ significantly from the moderately salient mark, the sticker. The point that the finger paint provides tactile and olfactory cues along with visual cues to the monkey was touched upon earlier. It is possible that the minimal to intermediate levels of salience seen in the data could be attributed to these extra cues. While it seems likely that, according to these data, the finger paint mark would not be salient enough to elicit a convincing pattern of self-directed behavior in a mirror mark test, it is hard to make a direct comparison with the marks used in the mirror mark tests due to the difference in sensory cues provided by the mark used in this study. An important follow up to this experiment would include the use of a clear mark that is both damp and has a scent, like the finger paint (such as vinegar or sugar water), a dry mark that is not damp but is dark like the finger paint, or the use of anesthesia during the marking procedure to ensure that the finger paint would dry before the monkeys awoke. Although these uncertainties about the finger paint mark exist, it is still possible to conclude from these data that the likelihood that a dry finger paint or dye mark would elicit self-directed behavior is very small. That the monkeys were able to witness the marking procedure and that the finger paint mark provided tactile, olfactory, and visual cues but yet the monkeys still failed to show statistically significant patterns of behavior towards this mark compared to touch only and shave marks is very striking.

In the absence of these extra cues, the pattern of behaviors may look more like those elicited by the touch and shave marks.

While it was predicted that the shave mark would be minimally salient, the fact that it is so similar to the touch mark is slightly surprising. The shave mark is not only visually striking but is also a physical change in the appearance of the monkey. This combined with the aversive noise and vibration of the razor could be enough to change the patterns of self-directed behavior either by an increase or a decrease. This was not seen in the data, however, indicating that these monkeys may have very low levels of motivation to be fastidious observers and maintainers of their appearance.

With all marks except the peanut butter mark, at least one individual failed to show an increase in target-directed behavior once the mark was applied. This apparent absence of motivation in some individuals to investigate certain types of mark places an even greater importance on the use of a control like this one in future mark tests for mirror self-recognition. For example, although the finger paint mark may have been minimally salient to eight of the twelve individuals tested, it was not sufficient to elicit an increase in self-directed behavior in four of the individuals. If we were to conduct a mirror mark test with these same subjects, we would be remiss to choose a mark that has clearly not been shown to be salient enough to motivate self-investigative behaviors and then make claims about the mirror self-recognition capability of those four individuals.

The interaction of sex, trial, and mark type on the difference scores of other-directed behavior that was found, though interesting, is difficult to interpret. The pattern of results suggests that females generally groomed more in the second half of a test session whereas males groomed more in the first half. This difference in activity pattern was not seen in any other behavioral category, however. No sex differences in the amount of self-manipulation have been observed in free ranging rhesus monkeys (Draper, 1966), however, it is possible that a sex difference does exist in not necessarily the frequency of self-manipulative or self-directed behavior but rather in the pattern of these behaviors.

It is apparent from this data that the amount of behavior directed towards a mark on the body varies with the salience of the mark in question. In the standard mirror mark test, the mark generally used is a dye or paint mark, similar to the finger paint mark used in this study. It appears that while rhesus monkeys may pay minimal interest to this type of mark, there are individual differences in the amount of interest paid. It is also unclear if the finger paint mark would be salient enough to elicit responses if the subjects are faced with a mirror. That the monkeys behave more similarly to the touch and shave conditions in the finger paint condition than in the peanut butter and sticker conditions suggests that while this type of mark may be minimally salient to some individuals, it is not nearly salient enough to rest the decision about mirror self-recognition properties of the individual on the amount of interest paid to that mark. Perhaps when faced with a mirror, the amount of distracting objects and situations increases so that any minimal salience that would be attributed to a dye or paint mark would be lost.

Not only should a control like this study be used in all mirror mark tests before making assumptions about an animal's interest in a mark, but it is apparent that marks need to be chosen that not only seems salient to the researchers but also holds salience with the animal in question. It is evident that simple changes in appearance, whether shave marks or dye marks, are not salient enough to induce self-directed behavior in rhesus macaques although the monkeys are quite capable of producing self-directed behaviors, and the assumption that a rhesus macaque would pay attention to such a mark when faced with a mirror is misguided. The idea that rhesus macaques lack mirror self-recognition because they fail the mirror mark test should be revisited because their failure may very likely be attributed to a lack of motivation to inspect the marks in the first place. Failures on the mark test should not be attributed to species differences in mirror self-recognition capabilities, but rather to species and possibly individual differences in motivation.

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Table 1

Ethogram

Behavior	**Description**
Self-Bite	Any type of vigorous, self-directed behavior (slapping, biting, mutilation, hair pulling)
Self-Groom	Deliberate, concentrated self-directed behavior (lick, pick, rub, touch, sniff, etc.). Head orientation towards area may be combined with these behaviors but is not necessary.
Scratch	Scratching with hands or feet that is quick and crude; quicker than a self-groom of the area
Removal of Mark	Active removal of the mark (either by picking and dropping or ingestion)
Accidental Mark Removal	Mark removal that occurs when the subject rubs up against or bumps into the caging or if the mark simply falls off of the body.
Interaction with Mark Post Removal	Interaction that happens with the mark after the mark is removed. This would include taking the mark out of the mouth and placing it back in the mouth, picking it up off of caging, or rubbing the mark off with the other hand and then interacting with that hand.

Figure Captions

Figure 1. The average total frequencies of unmarked-target-directed behavior (labeled TargetBehavior for the graph for trial 1), marked-target-directed behavior (labeled TargetBehavior for the graph for trial 2), and other-directed behavior in trials 1 and 2. The dark bars (blue) represent target-directed behavior and the lighter bars (green) represent other-directed behavior. The bar graph on the top corresponds to trial 1 and the bar graph on the bottom corresponds to trial 2. Error bars represent 1 standard error from the mean.

Figure 2. The average total durations of unmarked-target-directed behavior (labeled Target_D for the graph for trial 1), marked-target-directed behavior (labeled Target_D for the graph for trial 2), and other-directed behavior in trials 1 and 2. The dark bars (blue) represent target-directed behavior and the lighter bars (green) represent other-directed behavior. The bar graph on the top corresponds to trial 1 and the bar graph on the bottom corresponds to trial 2. Error bars represent 1 standard error from the mean.

Figure 3. The difference scores for the frequency of marked-target-directed behavior and other-directed behavior (trial 2). The bars represent the average difference scores for the frequency of marked-target-directed behavior and other-directed behavior for each mark type on the X-axis. Error bars represent 1 standard error from the mean.

Figure 4. The difference scores for the duration of marked-target-directed behavior and other-directed behavior (trial 2). The bars represent the average difference scores for the

duration of marked-target-directed behavior and other-directed behavior for each mark type on the X-axis. Error bars represent 1 standard error from the mean.

Figure 5. The difference scores for the frequency of marked-target-directed behavior and unmarked-target-directed behavior. The bars represent the average difference scores for the frequency of marked-target-directed behavior and unmarked-target-directed behavior for each mark type on the X-axis. Error bars represent 1 standard error from the mean.

Figure 6. The difference scores for the duration of marked-target-directed behavior and unmarked-target-directed behavior. The bars represent the average difference scores for the duration of marked-target-directed behavior and unmarked-target-directed behavior for each mark type on the X-axis. Error bars represent 1 standard error from the mean.

Figure 7. The average total frequencies of other-directed behavior for males and females. The dark bars (blue) represent males and the light bars (green) represent females. The top graph represents data from trial 1 and the bottom graph represents data from trial 2. Error bars represent 1 standard error from the mean.

Figure 1

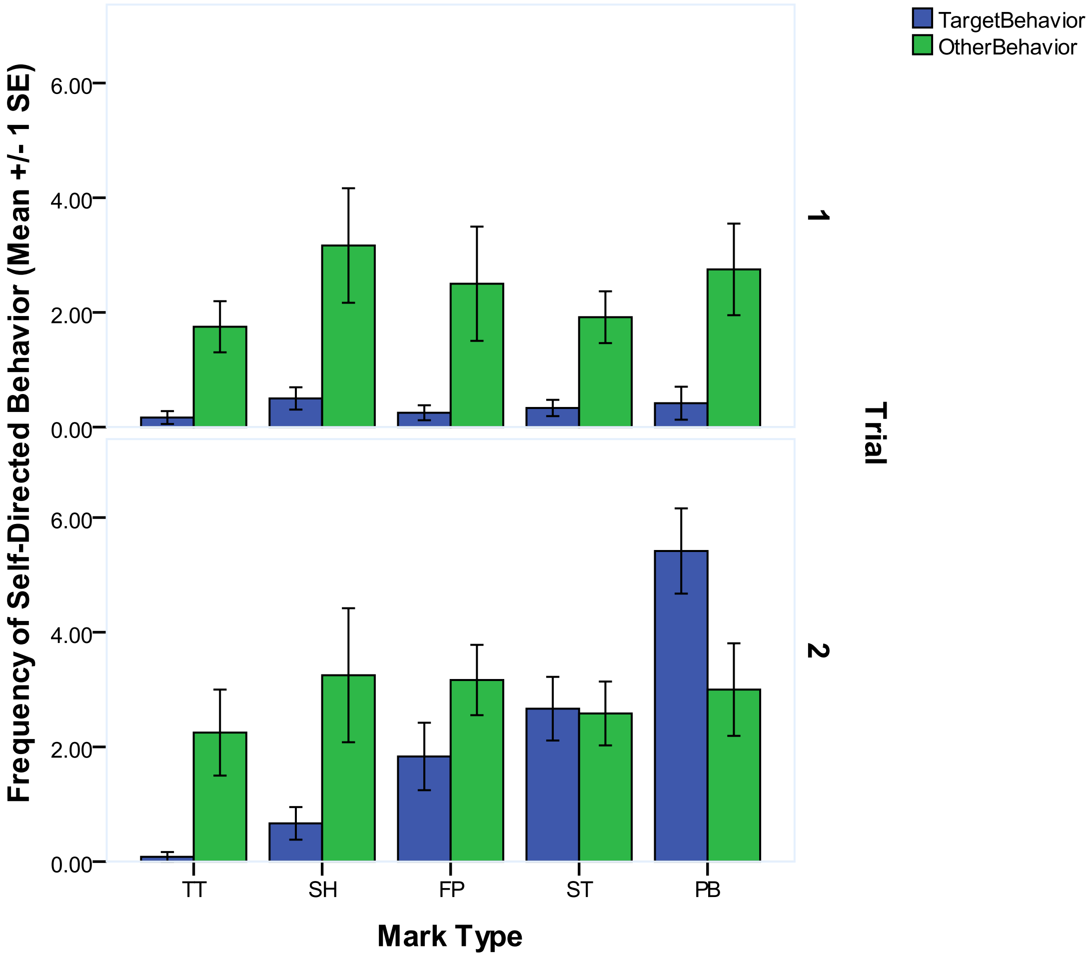

TargetBehavior
OtherBehavior
Frequency of Self-Directed Behavior (Mean +/- 1 SE)
6.00
4.00
2.00
0.00
1
2
Trial
TT
SH
FP
ST
PB
Mark Type

Figure 2

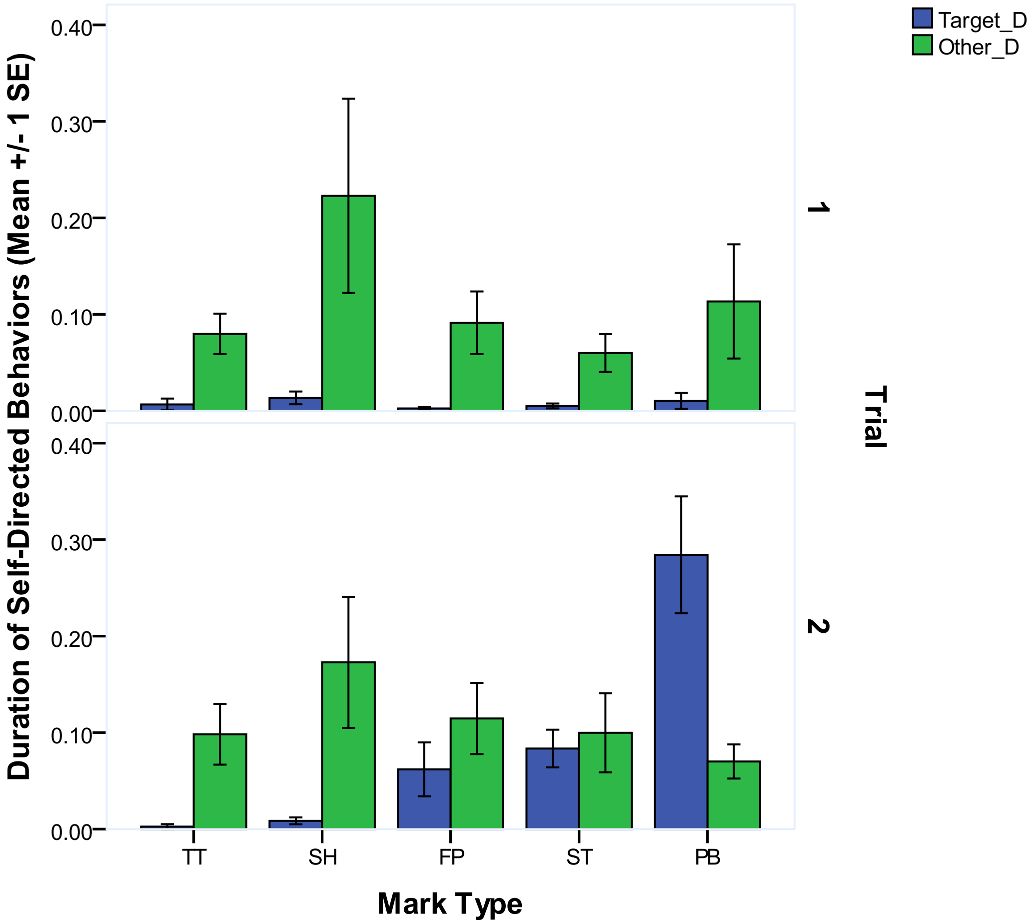

Target_D
Other_D
Duration of Self-Directed Behaviors (Mean +/- 1 SE)
0.40
0.30
0.20
0.10
0.00
Trial
1
2
TT
SH
FP
ST
PB
Mark Type

Figure 3

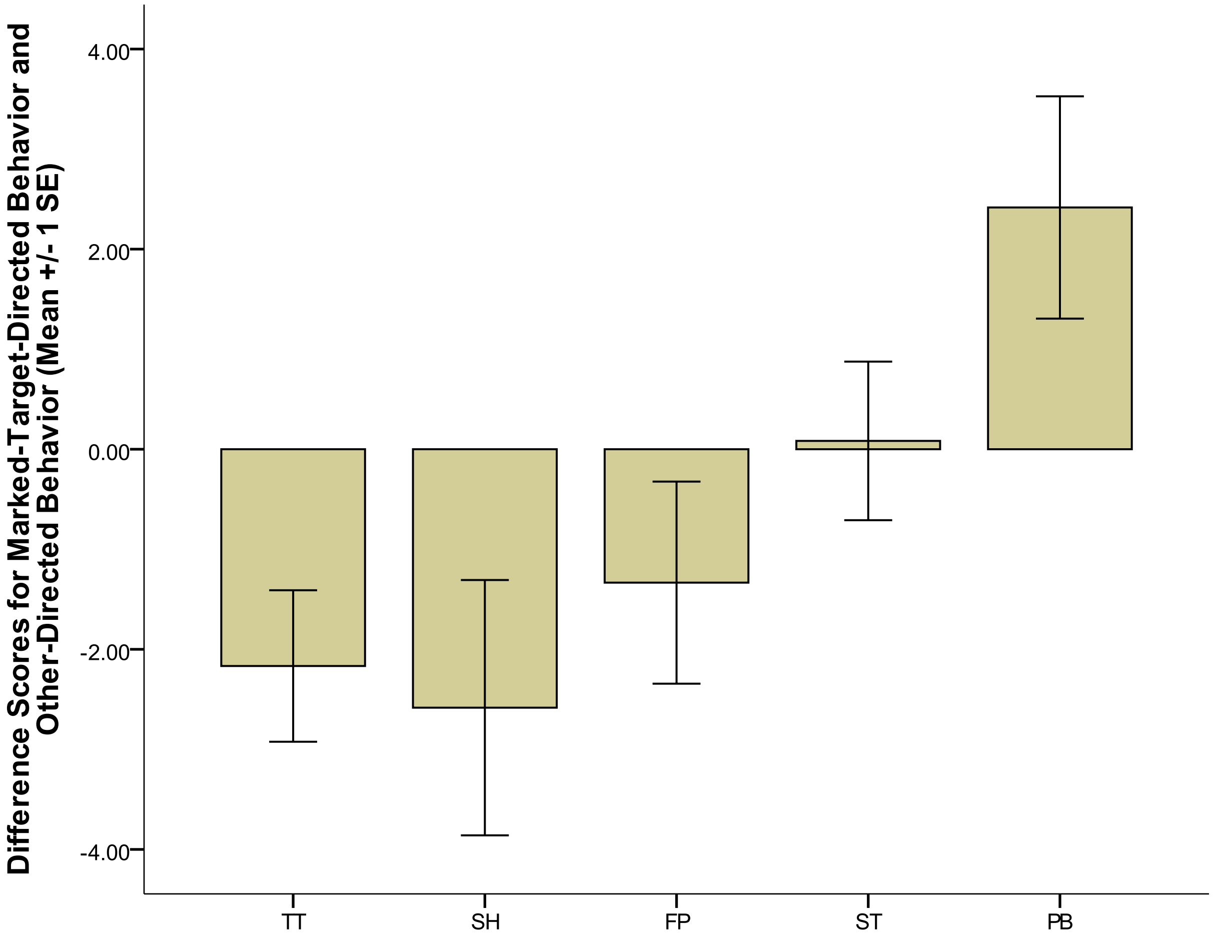

Difference Scores for Marked-Target-Directed Behavior and Other-Directed Behavior (Mean +/- 1 SE)
4.00
2.00
0.00
-2.00
-4.00
TT
SH
FP
ST
PB

Figure 4

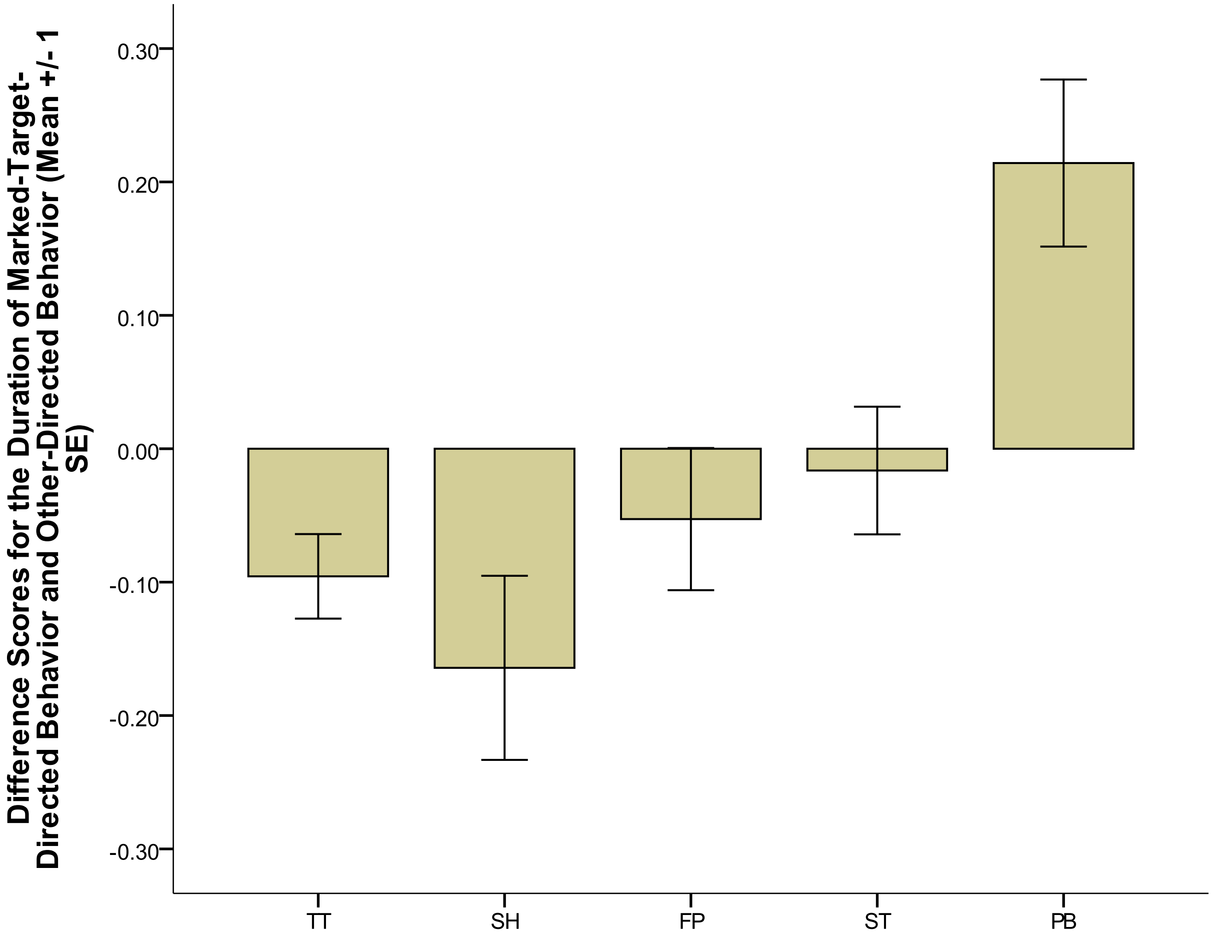

Difference Scores for the Duration of Marked-Target-Directed Behavior and Other-Directed Behavior (Mean +/- 1 SE)
0.30
0.20
0.10
0.00
-0.10
-0.20
-0.30
TT
SH
FP
ST
PB

Figure 5

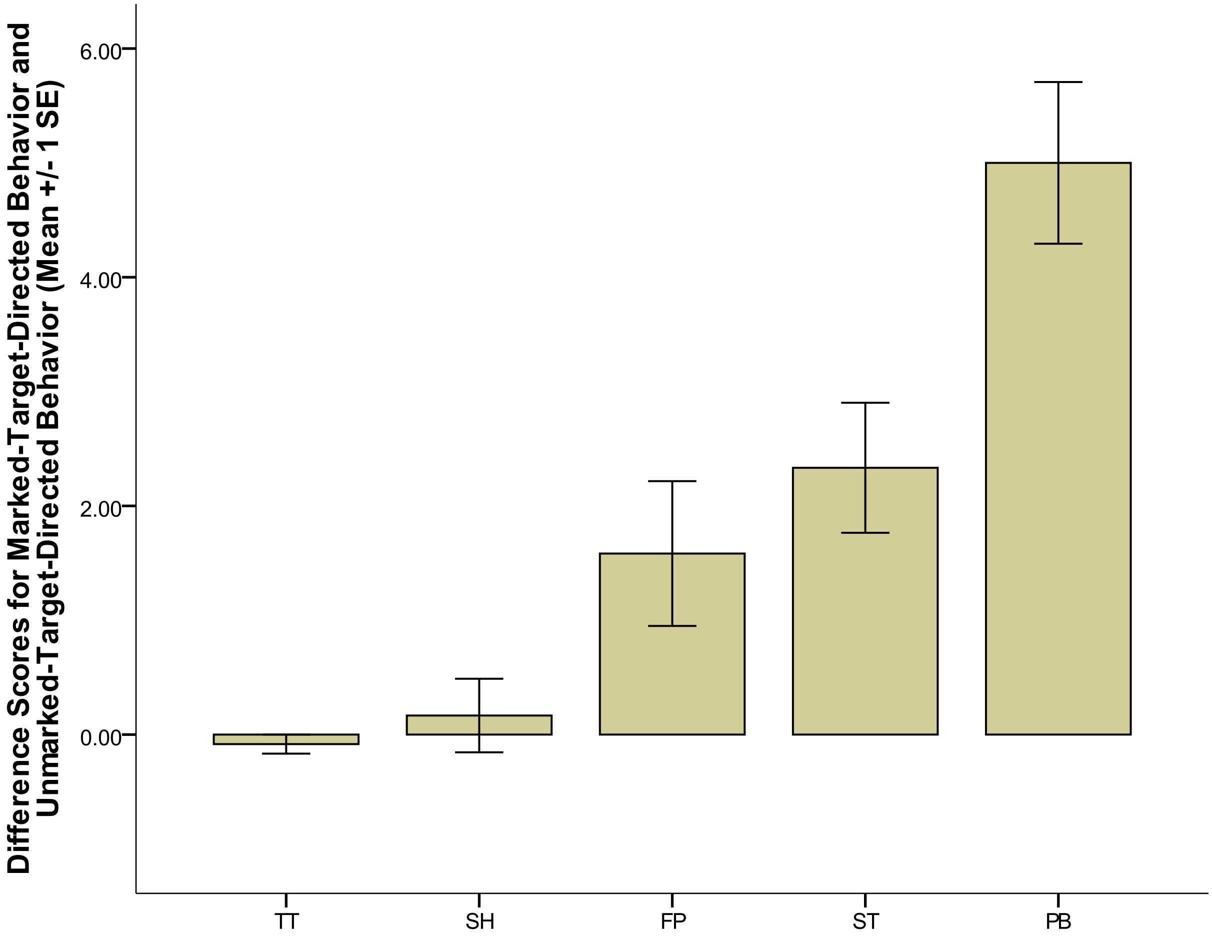

Difference Scores for Marked-Target-Directed Behavior and Unmarked-Target-Directed Behavior (Mean +/- 1 SE)
6.00
4.00
2.00
0.00
TT
SH
FP
ST
PB

Figure 6

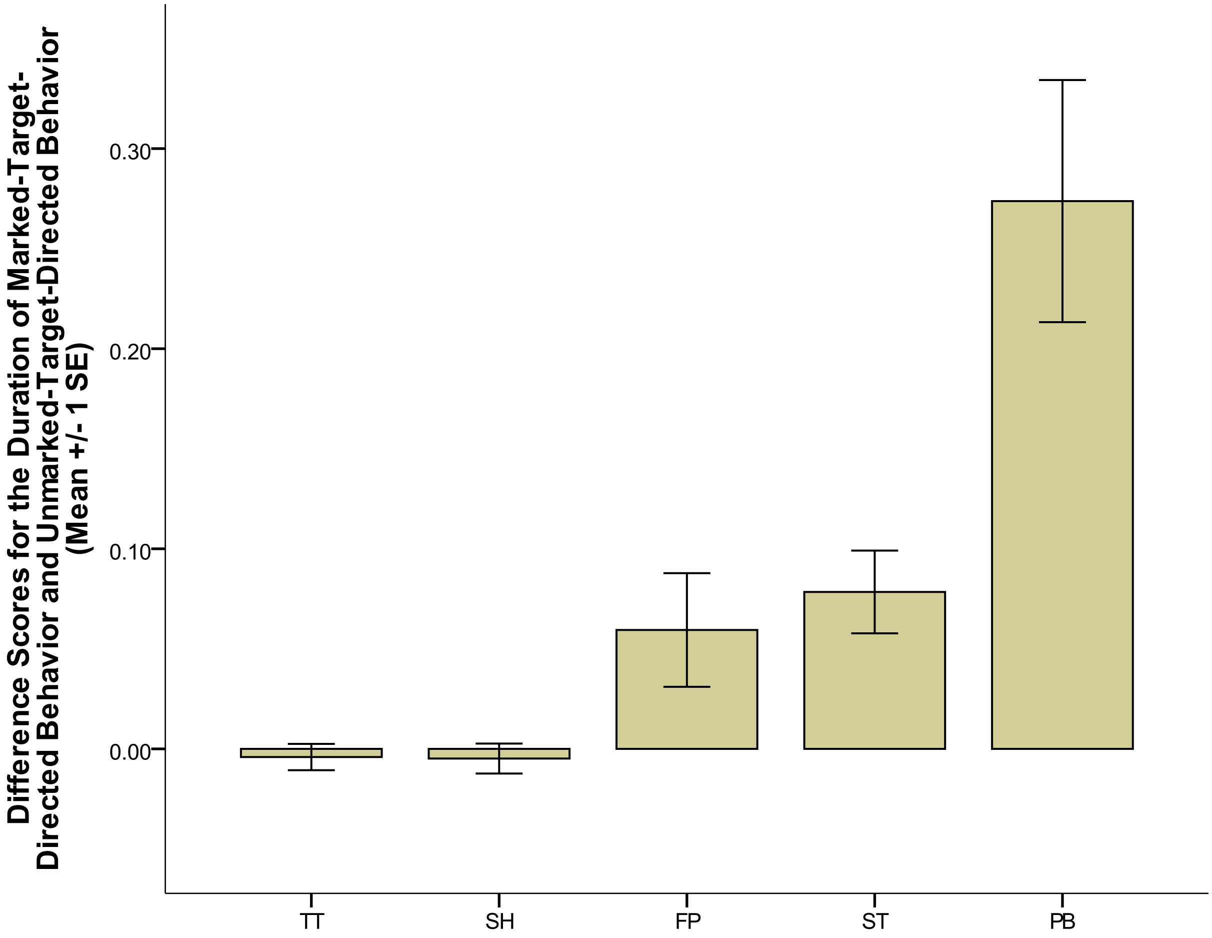
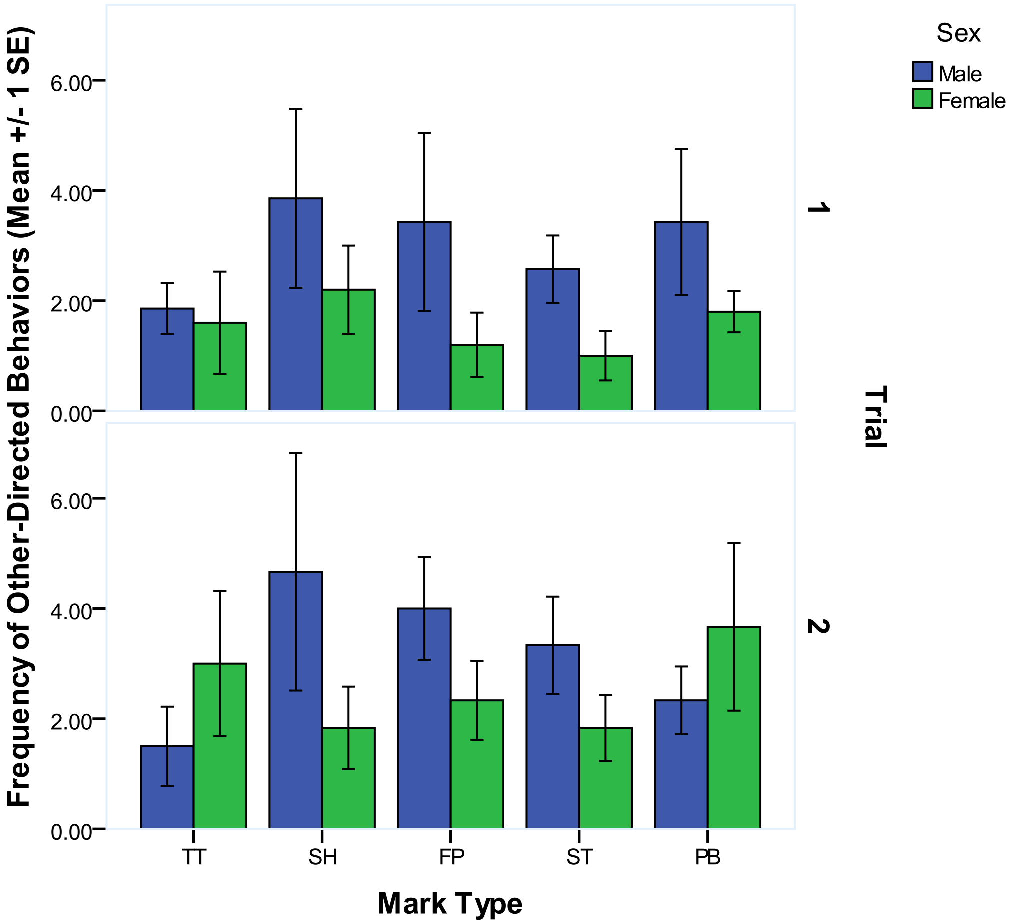

Difference Scores for the Duration of Marked-Target-Directed Behavior and Unmarked-Target-Directed Behavior (Mean +/- 1 SE)
0.30
0.20
0.10
0.00
TT
SH
FP
ST
PB

Figure 7


Frequency of Other-Directed Behaviors (Mean +/- 1 SE)
6.00
4.00
2.00
0.00
Sex
Male
Female
Trial
1
2
TT
SH
FP
ST
PB
Mark Type