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Constraints on Problem Solving and Inhibition: Object Retrieval in Cotton-Top Tamarins (*Saguinus oedipus oedipus*)

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Problem solving relies on a combination of the capacity to generate appropriate solutions and the ability to inhibit prepotent inappropriate responses. Often, problems with the latter prevent some animals from performing well on problem-solving tasks. The authors used the object retrieval task to examine inhibition in cotton-top tamarins (*Saguinus oedipus oedipus*). They found that, like human infants, tamarins had difficulty retrieving a reward from inside a transparent box when the opening was on the side because they could not inhibit the tendency to reach straight into the solid face of the box. However, subjects trained with an opaque box prior to testing on the transparent box performed perfectly. These results suggest that although the inability to inhibit prepotent biases prevents individuals from acquiring an initial strategy, sufficient training on an effective strategy may allow animals to overcome their initial difficulties with tasks requiring inhibition.

Problem solving in the social and technical domains often relies on the capacity to inhibit certain prepotent responses. For example, a subordinate individual may have to forage in a lower quality area if a dominant individual is feeding in the true higher quality patch. This decision to override one's natural preference for feeding on high-quality food requires some ability to inhibit. Developmental studies have revealed that infants and even young children often fail to solve problems in part because of difficulties with inhibition rather than conceptual comprehension (e.g., Diamond, 1990, 1991a, 1991b). Some have argued that the underlying cause of this developmental pattern is maturational, in large part the result of the relative immaturity of the prefrontal cortex in the first few years of life. Supporting this view are studies with macaques and marmosets demonstrating that lesions of the prefrontal cortex cause problems with the inhibition of prepotent responses (Diamond, 1990; Diamond & Goldman-Rakic, 1989; Dias, Robbins, & Roberts, 1996). Together, these results indicate that our understanding of cognitive processes is greatly enhanced by adopting a comparative perspective, one emphasizing neurocognitive factors that change during development and evolution (Gibson & Petersen, 1991).

One well-known paradigm that relies in part on the capacity to inhibit prepotent response biases is the A-not-B task, Piaget's (1954) classic test of object permanence. In this task, an infant sits on his or her mother's lap and watches as a desired object (e.g., a toy) is hidden in one of two identical wells. The well in which the object is first placed is referred to as the *A well;* the other is known as the *B well.* The infant is allowed to reach into the A well and obtain the object. In the next trial, the infant sees the object placed into the B well and again attempts to retrieve the object. Infants between the ages of 7 and 9 months typically fail at this task (Diamond, 1985; Piaget, 1954). Although they are able to find the object inside the A well, when the object is hidden in the B well, they mistakenly search for it in A, even though they have just witnessed the object being placed inside B. Piaget believed that this A-not-B error demonstrated that young infants fail to understand the permanence of objects.

However, recent research using a slightly different methodology, the expectancy violation procedure, has shown that human infants can in fact represent objects behind barriers. Using duration of looking as an indicator of knowledge, developmental psychologists have shown that infants possess a number of expectations about the physical properties and movements of occluded objects (Baillargeon, 1995; Baillargeon, Graber, DeVos, & Black, 1990; Baillargeon, Spelke, & Wasserman, 1985; Spelke, 1991, 1994). Such results suggest that infants' failures in the A-not-B task are the result not of a lack of conceptual understanding but rather of an additional requirement of the task. Specifically, to succeed in the A-not-B task, infants must be able to inhibit the prepotent tendency to reach into the well where the object was originally placed. Diamond (1991a, 1991b)

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proposed that it is their inability to meet this additional requirement, inhibiting a prepotent action tendency when choosing between two alternative action patterns, that in part causes infants to fail the task. This explanation is supported by two findings: First, infants do sometimes fail the task even when object permanence is not involved; when transparent covers are used in this task, infants sometimes reach to the wrong location even though they can actually see the object in the new location (Butterworth, 1977). Second, infants on occasion search at the wrong location while fixating their gaze on the correct location (Diamond, 1991b; Hofstadter & Reznick, 1996). This result suggests that infants do in fact understand where the object is but reach incorrectly because they are unable to inhibit the action tendency to search in the original location.

Problem-solving failures that stem from prepotent response biases have also been reported in nonhuman animals. Boysen and her colleagues (Boysen & Berntson, 1995; Boysen, Berntson, Hannan, & Cacioppo, 1995) demonstrated this kind of failure in a group of captive chimpanzees (*Pan troglodytes*) that were tested in an experiment investigating numerical abilities. In this task, subjects were required to choose the smaller of two candy arrays to obtain the larger array. When actual food items were used in the task, the researchers found that chimpanzees preferentially chose the larger array, thereby receiving the smaller reward. This inefficient response continued even after repeated training on the task. However, when Arabic numerals were substituted for the two food rewards, subjects performed much better; the same subjects were then able to choose the smaller Arabic numeral to gain a larger food reward. Boysen suggested that chimpanzees fail this task with real food stimuli because, as in human infants in the A-not-B task, their predisposition toward one salient response—namely, choosing the larger of two food rewards—prevents them from succeeding, even though they are capable of detecting the quantity differences.

Similar problem-solving failures that stem from prepotent response biases have been reported in capuchin monkeys (Visalberghi & Limongelli, 1994). Capuchins were tested in a task in which they had to insert a stick into a tube to push out a food object. The side in which the tube was inserted determined whether the reward was pushed out of the tube or into a trap in the tube. To solve the task, the subjects needed to learn a simple associative rule, namely to push the food from the farthest distance away. However, all but 1 out of 4 individuals failed to learn this simple rule. One reason the capuchins may have failed to learn this rule is because consistently succeeding on this task required them to detach themselves perceptually from the food items, namely to push the stick from the side farthest from the food item to avoid the trap. The predisposition to push from the side closest to the food object may have prevented some individuals from performing well on this task.

To better understand the problem of inhibition in human infants and nonhuman animals, Diamond and her colleagues developed a different procedure, known as the *object retrieval task* (Diamond, 1981, 1990, 1991b; Diamond & Gilbert, 1989; Diamond & Goldman-Rakic, 1986; Diamond, Zola-Morgan, & Squire, 1989). In the object retrieval task, subjects are presented with a small transparent box with an open side. During testing, this opening is placed so that it is either facing the top, facing the subject, to his left, or to his right. After the subject is exposed to the box, an experimenter places a desired object inside. The subject's task then is to reach into the opening of the box and retrieve the item. To succeed in this task when the opening is not facing forward, the subject must be able to inhibit the urge to reach directly for the object, by either reaching around to one side or on top.

Diamond (1981) found that 7- to 9-month-old infants had difficulty with the object retrieval task. In spite of immediate tactile feedback from contacting the solid transparent wall, infants continued to reach straight forward, in line with the object's location. Curiously, however, when the same infants were tested with an opaque box in which the toy could not be seen through the closed side, they performed much better (Diamond, 1981, 1990; Lockman, 1984). This counterintuitive finding suggests that part of what made the task difficult for the infants was actually seeing the goal through the closed side; the tendency to reach straight for the object had to be inhibited. It seems that the inability to inhibit the prepotent direct reach is part of the reason why young infants fail at this task.

Diamond and her colleagues hypothesized that infants' performance on inhibition tasks involving object retrieval can be linked rather directly to the maturation of the frontal cortex that takes place at the end of the first year of life (Diamond, 1990, 1991a, 1991b). They found that although adult rhesus monkeys (*Macaca mulatta*) are able to easily retrieve food items in object retrieval tasks (Diamond & Goldman-Rakic, 1989), 2- to 4-month-old monkeys and adult monkeys with lesions of the dorsolateral prefrontal cortex perform rather poorly (Diamond, 1990, 1991b; Diamond & Goldman-Rakic, 1986). Both the young and lesioned individuals show the same patterns as human infants, repetitively reaching to the transparent closed side. Similar inhibitory difficulties have been demonstrated in common marmosets (*Callithrix jacchus*) following lesions of the lateral and orbital prefrontal cortex regions (Dias et al., 1996; Roberts et al., 1991) and vervet monkeys (*Cercopithecus aethiops sabaeus*) given 1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine (MPTP) injections, which reduce the amount of dopamine in the frontal-striatal system (Taylor, Elsworth, Roth, Sladek, & Redmond, 1990; Taylor, Roth, Sladek, & Redmond, 1990). On the basis of these findings, Diamond and her colleagues argued that a fully functional prefrontal cortex is necessary for reaching tasks that require inhibition of salient action tendencies (Diamond, 1991a, 1991b; Diamond & Gilbert, 1989; Diamond & Goldman-Rakic, 1986, 1989).

If the cause of infants' failures in explicit search tasks is an inability to inhibit prepotent responses due to the immaturity of the prefrontal cortex, then one would predict that other species with more poorly developed prefrontal areas should fail at similar explicit search tasks, because they should, like infants, lack the capacity to inhibit salient action tendencies. The cotton-top tamarin (*Saguinus oedipus oedipus*) is a species that has demonstrated problems in a variety of tasks in which members were forced to inhibit salient action tendencies (Hauser, Kralik, & Botto-Mahan, 1999; Hood, Hauser, Anderson, & Santos, 1999; Santos, 1997), even though very little is actually known about the differentiation of the prefrontal regions of this species (T. Deacon, personal communication, October 1997). We therefore decided to test Diamond's hypothesis more completely by extending the work to cotton-top tamarins. To facilitate interspecific comparisons, we followed the general design of the object retrieval task used with both rhesus macaques (Diamond et al., 1989) and marmosets (Dias et al., 1996). If tamarins' failures on explicit search tasks are the result of problems with inhibiting prepotent responses, then they should show difficulty in the object retrieval task, performing at the level of human infants before 9 months of age and adult monkeys with lesions to the prefrontal cortex.

Experiment 1

Method

Subjects. Subjects were adult cotton-top tamarin monkeys (*Saguinus oedipus oedipus*), members of an arboreal New World monkey species native to the Colombian rain forests. Individual subjects were born in captivity at the New England Primate Research Center in Southborough, MA, and are now housed in a single room at the Primate Cognitive Neuroscience Lab at Harvard University. Prior to testing, all subjects had experience in experiments involving object manipulation (Hauser, 1997; Hood et al., 1999; Santos, 1997). Subjects' weights were maintained at approximately 15% less than what would be attained by ad libitum feeding and thus approximated weights obtained in the wild (A. Savage, personal communication, May 1994). Three males and 2 females (JL, NC, NQ, RM, SC), hereafter referred to as the *transparent group,* participated in Experiment 1.

Materials. During testing, subjects were placed in a transparent test box. This box (Figure 1), made entirely of Plexiglas, measured approximately 45 cm × 40 cm × 60 cm. Subjects sat inside the transparent triangular enclosure and were able to reach out of the enclosure through an opening in the front panel. This opening had two separate covers: a transparent Plexiglas screen, which prevented subjects from reaching out of the test box, and an opaque foam-core occluder, which prevented subjects both from seeing the apparatus and from reaching out of the test box. Both the Plexiglas screen and the foam-core occluder could be raised or lowered by the experimenter. Because of previous experimentation, subjects had had substantial exposure to this box and sat quiet and still inside the enclosure for 30 min at a time.

Table 1
Trial Order of Tests

Trial	Box opening	Object placement	Type
1	Front	Deep in	Normal
2	Front	Deep in	Normal
3	Right	Partly out	Normal
4	Right	Deep in	Critical
5	Right	Partly out	Normal
6	Right	Center	Critical
7	Right	Deep in	Critical
8	Left	Partly out	Normal
9	Left	Deep in	Critical
10	Left	Partly out	Normal
11	Left	Center	Critical
12	Left	Deep in	Critical
13	Left	Deep in	Critical
14	Right	Deep in	Critical
15	Top	Center	Critical
16	Top	Deep in	Critical
17	Top	Center	Critical
18	Top	Deep in	Critical
19	Top	Center	Critical
20	Top	Deep in	Critical
21	Left	Deep in	Critical
22	Right	Deep in	Critical
23	Top	Deep in	Critical
24	Front	Deep in	Normal

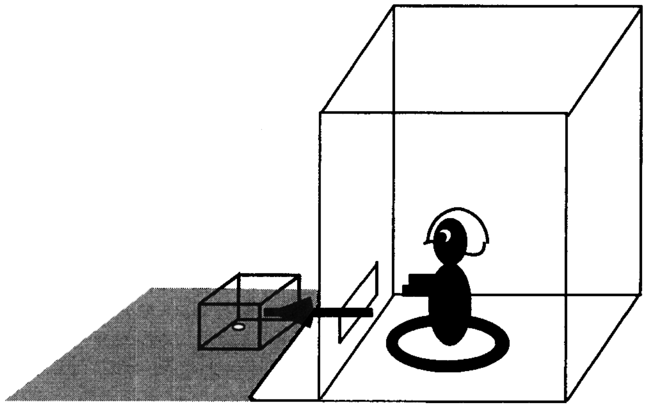


Figure 1. Diagram of the testing setup. Subjects sat inside the vortex box on a platform. Subjects could reach through slit in the center of the front panel.

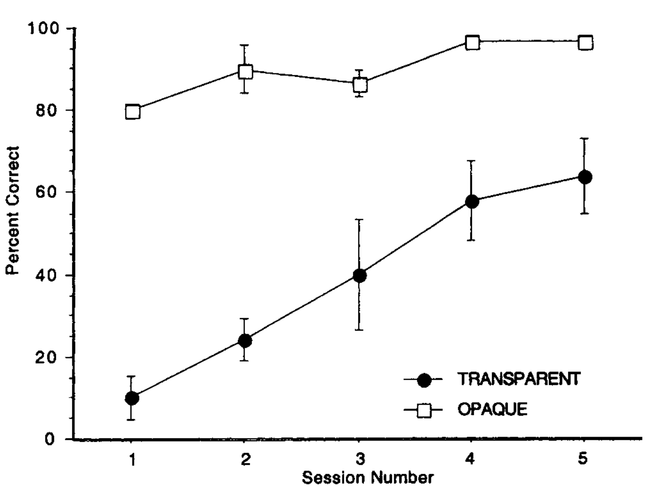
A smaller version (7.2 × 7.2 × 4.8 cm) of the Diamond et al. (1989) reaching box was used. The box was made of transparent Plexiglas and was solid on all sides except two. The box was held in place by a wooden stand positioned in front of the test box opening. One of the open sides of the box was always placed facedown, attached to the stand. As the stand was moved, subjects could be presented with an opening that faced to the front (facing the subject), left (toward the subject's left), right (toward the subject's right), or top (on top of the box).

Procedure. Subjects were each given five 24-trial sessions modeled after those of Diamond et al. (1989). During each trial, a subject was seated inside the test box, with the front panel opening concealed by the opaque occluder and the Plexiglas screen. At the beginning of each trial, the experimenter placed a food pellet into the box. The occluder was then taken away to reveal the box with the pellet inside. The Plexiglas screen was then removed, allowing the subject to retrieve the pellet. To exactly replicate the procedure of Diamond et al. (1989), we varied two factors from trial to trial (Table 1): the placement of the opening of the box (front, left, right, or top) and placement of the pellet inside the box (partly out, in the center, or deep inside). However, for the purposes of our analysis, we divided all trials into two types: *normal* trials, those in which the opening was placed in the front or top of the box and in which the pellet was not placed fully inside the box, and *critical* trials, more difficult trials in which the opening was on the side of the box and the pellet placed fully within the box. During the first two training sessions, subjects were given only 5 s to retrieve the pellet. This time limit was increased to 15 s on Sessions 3 to 5 because subjects had more trouble than expected during the first two sessions. The median number of days between sessions was 5.

Results

On the first session of the training, all 5 subjects performed poorly and demonstrated repetitive reaching into the solid face of the box (mean critical = 10% correct; mean total = 37% correct). Two individuals (JL, SC) failed to retrieve the pellet on any of the critical trials. All subjects showed the repetitive direct reaches characteristic of young human infants. A significant learning curve (Figure 2) was observed, with subjects performing significantly better on critical trials of Session 5 than on Session 1, paired *t* test: $t(4) = 7.22$; $p < .002$. All 5 subjects demonstrated this pattern of increased performance.

A) Critical Trials



B) Total Trials

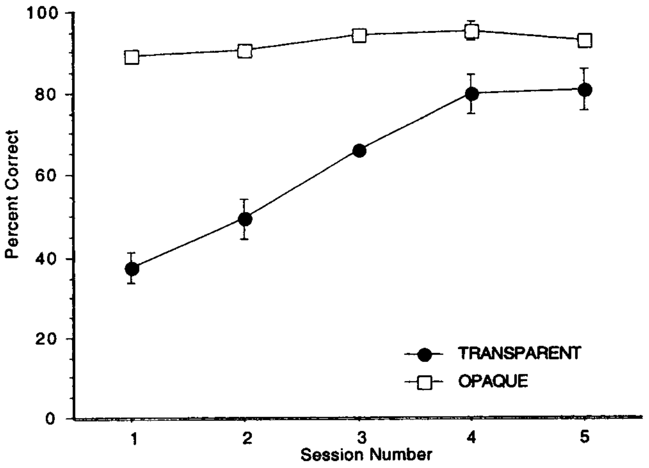


Figure 2. (A) Mean performance (±SE) on critical trials for subjects in the transparent and opaque groups. (B) Mean performance (±SE) across all trials for subjects in the transparent and opaque groups.

Discussion

The poor initial performance of subjects in the transparent group suggested that adult tamarins may exhibit problems of inhibition similar to those found in human infants, infant macaques, and adult macaques and marmosets with lesions to the prefrontal cortex. The persistence of direct reaching into the front wall suggested that the subjects had difficulty inhibiting the prepotent response to reach for the pellet. This interpretation may, however, have been premature. It is possible, for example, that instead of the visual salience of the pellet, the demands of the deferred reaching task caused difficulties for the tamarins. To distinguish between these two alternatives, we decided to use another group of monkeys, the opaque group, to be run on a slightly different setup. Instead of training on a transparent box, the opaque group would be first trained on an opaque box and then later tested on a transparent box. This group would be used to explore the possibility that the transparent group's poor performance was a result of the fact that the subjects could see the pellet through the front Plexiglas wall and consequently were forced to inhibit the tendency to reach straight ahead for it. If this interpretation was correct, then members of the opaque group, which could not see the pellet inside the box, should do significantly better on the task than the transparent group. Furthermore, if seeing the pellet was the problem for the transparent group, then members of the opaque group should perform worse on their first day of transparent training than on their original session with the opaque box. Alternatively, if success required access to an alternative motor routine, then subjects that had succeeded with the opaque box should also quickly succeed when later tested with the transparent box.

Experiment 2

Method

Subjects. One male and 3 females (SP, UB, PC, EM) with no prior experience on this or related tasks participated in the opaque training; because of motivational problems, subject EM was dropped from the experiment after the first session.

Materials. Three different testing boxes were used with the opaque group: an opaque white box (7.2 × 7.2 × 4.8 cm), a transparent box covered with a red grid pattern (7.2 × 7.2 × 4.8 cm), and the original Plexiglas box.

Procedure. The opaque group was given three sessions of 24 trials each following the same order of trials as in Experiment 1. During the first session, the opaque group was tested with the white opaque box. In the second session, subjects were tested with the red-grid box; we assumed that the grid marks would help to demarcate the borders of the box while still allowing the subject to see the pellet. On their third session, subjects were tested with the original Plexiglas box used with the transparent group. The median number of days between sessions was 3.5.

Results

The opaque group performed differently from the transparent group. Individuals demonstrated significantly higher accuracy on their first session of the task, unpaired *t* test, opaque versus transparent, critical (80% correct vs. 10%): $t(6) = 9.49, p < .0001$; Mann-Whitney, $Z = 2.24, p = .03$; total (87% vs. 37%): $t(6) = 10.06$, $p < .0001$; Mann-Whitney, $Z = 2.24$, $p = .03$ (see Figure 2). In addition, subjects also performed well on their second session with the red-grid box (mean percentage correct: critical = 90%; total = 91%). This high performance continued into Session 3, with the transparent box (mean percentage correct: critical = 87%; total = 94%) and did not differ statistically from performance on the first session, with the opaque box paired *t* test: Opaque Session 1 versus Transparent Session 3, critical (80% vs. 87%): $t(2) = 2.0, p > .18$; paired sign test, $p = .50$; total (89% vs. 95%): $t(2) = 2.0, p > .18$; paired sign test, $p = .50$. On its first session with the transparent box, the opaque group performed significantly better than the transparent group on its third session, unpaired *t* test, opaque versus transparent, critical (87% vs. 40%): $t(6) = 2.59, p < .04$; Mann-Whitney, $Z = 1.64, p > .10$; total (95% vs. 66%): $t(6) = 19.71$, $p < .0001$; Mann-Whitney, $Z = 2.24$, $p = .03$. In addition, the opaque group performed better on its first session with the transparent box than the transparent group did on its last day of training (Session 5), although this difference was not statistically significant, unpaired *t* test: opaque versus transparent, critical (87% vs. 66%): $t(6) = 1.80, p > .12$; Mann-Whitney, $Z = 1.50, p = .14$; total (95% vs. 81%): $t(6) = 2.0$, $p > .09$; Mann-Whitney, $Z = 1.64, p = .10$.

Discussion

The opaque group performed reliably better on its first session with the opaque box than the transparent group did during its first session on the Plexiglas box. This finding suggests that the transparent group's initial failure was most likely mediated by the transparency of the box rather than the deferred reaching task per se. It seems that in the transparent condition, the visual salience of the pellet inside the Plexiglas box made direct reaching a difficult response to inhibit, causing the subjects to perform poorly on the task.

It is important to note, however, that subjects originally trained with the opaque box performed far better than those trained for consecutive sessions with the transparent box. Whereas human infants are slightly facilitated from exposure to an opaque box (Diamond, 1990), tamarin subjects originally trained with the opaque box were substantially facilitated when later tested with the transparent box. The fact that adult tamarins learned the task better when trained on the opaque box suggests that something more than merely a problem with inhibition may have been at the root of the transparent group's early failures. If tamarins completely lacked the neurocognitive capacity to inhibit reaching for a pellet that lies straight ahead, then training on an opaque box should not particularly have helped them to overcome this inability when later tested with a transparent box.

An alternative explanation for these results is that because of a slight tendency to reach straight for the reward, the transparent group had difficulty coming up with a good solution to the task. Perhaps when originally trained with the opaque box, the opaque group was able to learn an effective strategy for solving the task (i.e., look and reach around the box for an opening). They were then able to apply this strategy in future sessions regardless of whether the box was transparent. The transparent group, on the other hand, was unable to learn this effective strategy because of the salience of the pellet, which prevented them from learning that reaching around to the side is often the best solution.

To differentiate between these two explanations, we thought it important to assess exactly how much training with the opaque box was sufficient to enable subjects to succeed with the Plexiglas box. If the tamarins were in fact learning an appropriate solution to the task, then they may have required a substantial amount of training with the opaque box. We therefore decided to run another group of subjects, the minimal opaque training group. This group would be given limited exposure to the opaque box before being tested with the transparent box. If success on the transparent box was the result of a learned strategy, then monkeys provided with limited training on the opaque box might not perform as well on the transfer trials as subjects receiving additional training.

Experiment 3

Method

Subjects. Two males and 2 females (DD, ES, ID, MR) with no prior experience on this or related tasks participated in the minimal opaque training.

Materials. Two different testing boxes were used with the minimal opaque training group: the opaque white box used with the opaque group and the original Plexiglas box.

Procedure. The minimal opaque training group was given one session consisting of 28 trials. During the first four trials of this session, subjects were tested with the white opaque box. These four trials were used to give subjects limited exposure to the opaque box. In the following 24 trials, subjects were tested with the Plexiglas box in the same order as was used in Experiment 1.

Results

Subjects performed more accurately on the initial four trials with the opaque box than on the subsequent trials with the Plexiglas box, although this trend failed to reach the level of statistical significance, opaque trials versus transparent trials, critical (75% correct vs. 35%): paired *t* test, $t(3) = 2.25, p < .11$; total (88% vs. 72%): $t(3) = 1.94, p < .15$. All 4 subjects performed more accurately with the opaque box than the transparent box. Subjects in the minimal opaque training group performed significantly better on the trials with the Plexiglas box than subjects in the original transparent group did on their first session, transparent group versus minimal opaque training group, critical (35% vs. 10%): unpaired *t* test, $t(7) = 3.30$, $p < .01$; Mann-Whitney, $Z =$

2.21, $p < .028$, but significantly worse than subjects in the opaque group, opaque group versus minimal opaque training group, critical (87% vs. 35%): unpaired *t* test, $t(5) = 7.90$, $p < .0005$; Mann-Whitney, $Z = 2.12, p < .03$.

Discussion

The minimal opaque training group performed better overall on trials with the opaque box than on trials with the Plexiglas box. Like subjects in the opaque group, however, the minimal opaque training group subjects performed better with the Plexiglas trials after having been trained with the opaque box for only four trials. The difference in performance on the Plexiglas box trials between this group and the opaque group, however, suggests that the amount of training with the opaque box had an important impact on the level of performance with the Plexiglas box. This result also suggests that the transparent group's initial problems with the task were the result of an inability to access an appropriate strategy for solving the task; success required both the inhibition of the straight reaching response and access to an alternative strategy.

We decided to run a final condition to assess whether a more salient food item would cause subjects who had learned to solve the task to return to their initial prepotent responses. In earlier experiments (see Hauser, in press; Hauser et al., 1999), when more salient food items were used as rewards, subjects demonstrated difficulty in performing tasks that they had previously performed quite well. We therefore reasoned that adding a motivational challenge in this paradigm might negatively affect subjects' performance. We reasoned that if failures on this task were the result of problems with inhibition, then raising a subject's interest in the food reward should make reaching straight for the reward more difficult to inhibit and thus should increase the frequency of repetitive reaching responses and cause performance to drop.

We therefore started all subjects on a second phase, designed to provide them with additional training and consequently mastery of the object retrieval task with a Plexiglas box. After meeting performance criteria, subjects were moved to the final salient-stimulus condition, in which a highly desired food reward, a marshmallow, was used instead of the pellet.

Experiment 4

Method

Subjects. The same individuals tested in Experiments 1 and 2 (JL, NC, NQ, PC, RM, SC, SP, UB) were run in this experiment. Because Subject EM never completed Experiment 2, she was not included in Experiment 4.

Materials. Subjects were tested with the same apparatus and the original transparent box used in Experiment 1. In addition to the food pellets used in Experiments 1 and 2, small fruit marshmallows were used as the reward in this condition. The median number of days between Experiments 1 and 2 and Experiment 4 was 5.

Procedure. Both groups were first given a random-order training phase, in which 18 of the 24 trials within each session were *critical* trials. Trials in this phase were presented in a random order, not the standardized order used in the first two experiments, to ensure that subjects were performing well on the reaching task irrespective of whether they had learned the order of the trials. Subjects were required to achieve a performance level of 80% correct for two consecutive sessions before moving on to the salient-stimulus condition.

In the salient-stimulus condition, subjects were given a random-order session in which a marshmallow was substituted for the pellet in 6 of the 24 trials. In food preference tests, subjects consistently pick marshmallows over pellets (D. Weiss, personal communication, March 1997). Furthermore, marshmallows are larger than pellets and also are less commonly used as rewards during experiments. The marshmallow was used to increase the desirability of the target object and thus potentially increase the difficulty of inhibiting a direct reaching response.

Results

Seven of the 8 subjects reached criteria in the random-order training phase in only two sessions. (The other subject, NC, took three sessions.) There was no significant difference in the number of training sessions required to meet criteria between the transparent and opaque groups, unpaired *t* test, transparent versus opaque (2.2 sessions vs. 2 sessions): $t(6) = .75$, $p > .48$; Mann-Whitney: $Z = .45$, $p = .66$. During the salient-stimulus condition, both groups performed at 100% during the six marshmallow trials. Both groups were at ceiling performance on both the marshmallow ($m = 100\%$) and the normal trials (99%); there was no statistical difference between performance on the marshmallow and regular trial types. The percentage of direct reaches into the front Plexiglas wall was also recorded for the two trial types. Although there was a slight trend for subjects to make more direct reaches during marshmallow trials (mean proportion = .27) than regular trials (mean proportion = .23), this trend failed to reach statistical significance, paired *t* test, $t(7) = .85, p > .42$; paired sign test, $p = .29$. There was no difference in the amount of direct reaching for subjects in different groups, opaque versus transparent, unpaired *t* test, $t(6) = .52, p < .62$; Mann-Whitney: $Z = .75, p = .46$.

Discussion

Both groups performed perfectly on the salient-stimulus phase; their accuracy was at a ceiling level and was thus unaffected by the change in object salience. Similarly, although there was a slight trend for more reaching during marshmallow trials, there was no statistical difference in the frequency of repetitive reaching between marshmallow and regular trials. This result further suggests that the original problem for the transparent group was a difficulty with learning an appropriate solution to the task. Once subjects had acquired an alternative to reaching forward for the pellet, they had no difficulty retrieving salient items from inside of the box.

Thus, tamarins start off with a slight inhibitory problem and then, with sufficient training, overcome their tendency to reach forward, learning an appropriate motor routine. In fact, the training is so effective that it allows subjects to inhibit even stronger prepotent responses (i.e., reaching for a highly preferred food reward). If this account is correct, it suggests that some of the tamarins' problems on other search tasks can be explained in terms of an initial difficulty in inhibiting prepotent actions. Our findings also suggest that tamarins given sufficient experience with alternative motor solutions should learn to overcome the initial difficulties of most search tasks.

This account also makes some predictions for future work with human infants and macaques on this task. Our results suggest that giving human infants more hints about the solution to a task (e.g., providing extensive training with an opaque box, etc.) may allow them to overcome their inhibitory failures earlier. Similarly, even prefrontally lesioned macaque monkeys may show increases in performance when trained with an effective solution to the task.

General Discussion

A more thorough understanding of the structure and differentiation of the tamarin prefrontal cortex should shed light on the patterns of response we have presented. Few studies have investigated the neocortex in tamarins, but such investigations may increase our understanding of both the neural underpinnings of the tamarins' initial inhibitory failures and the overall differences in inhibitory abilities among primates.

In conclusion, these studies demonstrate that although tamarins exhibit some initial problems with the inhibition of prepotent action tendencies in object retrieval tasks, they are able to overcome these response biases with explicit training. Although the nature of subjects' later success on the task is somewhat unclear, our findings suggest that some of tamarins' failures in other explicit search tasks may be the result of similar inhibitory difficulties.

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