

## BRIEF REPORT

# Pulling to Scale: Motor Planning for Sequences of Repeated Actions by Cotton-Top Tamarins (*Saguinus oedipus*)

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Previous research has demonstrated that nontool-using primates are capable of sophisticated motor planning for a single action. The present study extends this work by asking whether monkeys are capable of planning a sequence of repetitive motor actions to accommodate a task demand. We presented tamarins with a tape measure baited with a food reward at near or far distances and measured their manual intergrasp distances as they reeled in the food. In Condition 1, subjects viewed the reward as they pulled, whereas in Condition 2, they received no visual feedback during pulling. Across both experiments, we found that the intergrasp distance in Near trials was significantly smaller than in Far trials, an effect that was demonstrated even during the first two pulls of each trial. These results suggest that tamarins prospectively scale their intergrasp distances in accordance with the distance to the goal. These findings provide further support for the lengthy evolutionary history of sophisticated motor planning abilities in primates.

*Keywords:* motor planning, prospective scaling, sequence planning, nonhuman primates

One of the hallmarks of human cognition is the ability to plan. Whether it is making an evening dinner reservation, booking a flight months in advance, or setting an economic plan in motion that will impact decades of fiscal policy, humans are notoriously adept at planning for the future. Moreover, our skills for planning are also manifest on a much more local scale, evidenced in motor behaviors. Observing how individuals interact with objects in the environment can generate profound insights into the psychological control of behavior (Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012). Motor actions, such as reaching for and grasping objects, are often guided by the actor's anticipation of upcoming postural and task demands (e.g., Rosenbaum et al., 1990). For example, when turning over an inverted glass to fill it with water, adults typically reach for the glass with a thumb-down posture that affords a more controlled subsequent posture when filling it (e.g., Fischman, 1997). The grip choice selected by the actor at the outset of the sequence reflects planning to accommodate later postural demands. The cognitive abilities necessary for this foresight have been posited to provide a scaffold for the development of more sophisticated cognitive abilities such as

tool use (Johnson-Frey, 2004), long term planning (Keen, 2011; van Swieten et al., 2010), and inhibition (Weiss, Chapman, Wark, & Rosenbaum, 2012). Accordingly, understanding the evolutionary roots of motor planning may yield valuable insights into the development of higher-order cognitive functioning. While numerous studies have described motor planning in humans, far fewer studies have investigated the extent to which other species share these abilities.

For humans, planning of motor behaviors emerges early in infancy and exhibits a protracted developmental trajectory. Early in the first year of life, infants adjust their grip selection when reaching for objects that differ in size (e.g., Newell, Scully, McDonald, & Baillargeon, 1989) and orientation (e.g., Lockman, Ashmead, & Bushnell, 1984). By 10 months of age, they are capable of more sophisticated motor planning, such as adjusting the speed of approach when grasping a ball based on whether the intended subsequent action requires precision (Claxton, Keen, & McCarty, 2003). From ages 3 through 10, children continue to refine and develop their motor planning abilities, though adult-like behavior is still not fully realized even in most 10-year-old children (Thibaut & Toussaint, 2010; Weigelt & Schack, 2010).

Data from nonhuman primates (hereafter *primates*) suggest that the most rudimentary motor planning abilities appear to be shared across species. Neurophysiological and behavioral studies have demonstrated that, like young human infants, primates adapt their grip selection based on the physical affordances of the objects to be grasped (e.g., Gardner, Ro, Debowey, & Ghosh, 1999). Evidence for more sophisticated planning may be inferred from the neural activity associated with reaching behaviors in monkeys. Akin to the aforementioned research with

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10-month-old children, motor neurons in the monkey inferior parietal lobule display differential firing rates depending on the forthcoming action performed on an object (Fogassi et al., 2005).

In recent years, our laboratory has begun to explore whether nonhuman primates exhibit the type of anticipatory motor planning abilities observed in human adults. In an initial study, we presented cotton-top tamarins (*Saguinus oedipus*) with a food reward placed inside of a cup that was presented in either an upright or inverted orientation (Weiss, Wark, & Rosenbaum, 2007). The monkeys demonstrated remarkable motor planning skills by inhibiting their natural grasping tendencies and adopting unusual grasping postures to accommodate subsequent task demands. This finding was subsequently replicated with several species of lemurs, the most evolutionarily distant living primate relatives of humans (Chapman, Weiss, & Rosenbaum, 2010). Together, these findings suggest that primates, like human adults, are capable of altering object manipulation behaviors to accommodate a forthcoming task. Consistent with this assertion, recent evidence also suggests that rhesus monkeys and chimpanzees engage in similar motor planning (Nelson, Berthier, Metevier, & Novak, 2010; Frey & Povinelli, 2012). Thus, converging evidence across several studies using different methods with a variety of species suggest that sophisticated motor planning abilities are ubiquitous in primates and likely were characteristic of the ancestral primate species.

This conclusion challenges a theory that suggested sophisticated motor planning abilities might represent a sufficient condition for the development of tool-use (Johnson-Frey, 2004). However, as noted in our initial study (Weiss et al., 2007), it is possible that the scope of planning might differ across species. In all of the aforementioned studies, the evidence for motor planning emerged from a single movement, such as how a grasp is deployed or an object is handled. In the present study we sought to extend this line of research and determine whether anticipatory motor planning could be evidenced in a sequence of repeated motor actions. In two experimental conditions, we provided cotton-top tamarins with a string-pulling task (using a tape measure) in which a food reward was baited at different distances from the subject. String-pulling tasks have a rich tradition in primate research (e.g., Köhler, 1925) and a wide variety of species are proficient at reeling in food attached to a string (e.g., Harlow & Settlege, 1934; Heinrich, 1995; Osthaus, Lea, & Slater, 2004). These experiments have typically been conducted in order to assess means-end reasoning. To the best of our knowledge, no one has ever analyzed *how* subjects pull the string in order to study motor planning. We were interested in determining whether the intergrasp distances would vary as a function of the distance to the food item. In Condition 1, the tamarins had complete visual access as they pulled a tape measure baited with food at either a near, intermediate, or far distance from the subject. In Condition 2, the tape measure was baited at a near or far distance and then completely occluded before the subjects had an opportunity to pull on the tape measure. This insured that the results observed in Condition 1 could not have arisen due to visual feedback from observing the food move closer with each pull. We hypothesized that intergrasp distances might vary as a function of the distance to be pulled, indexing anticipatory sequence planning.

## Method

### Subjects

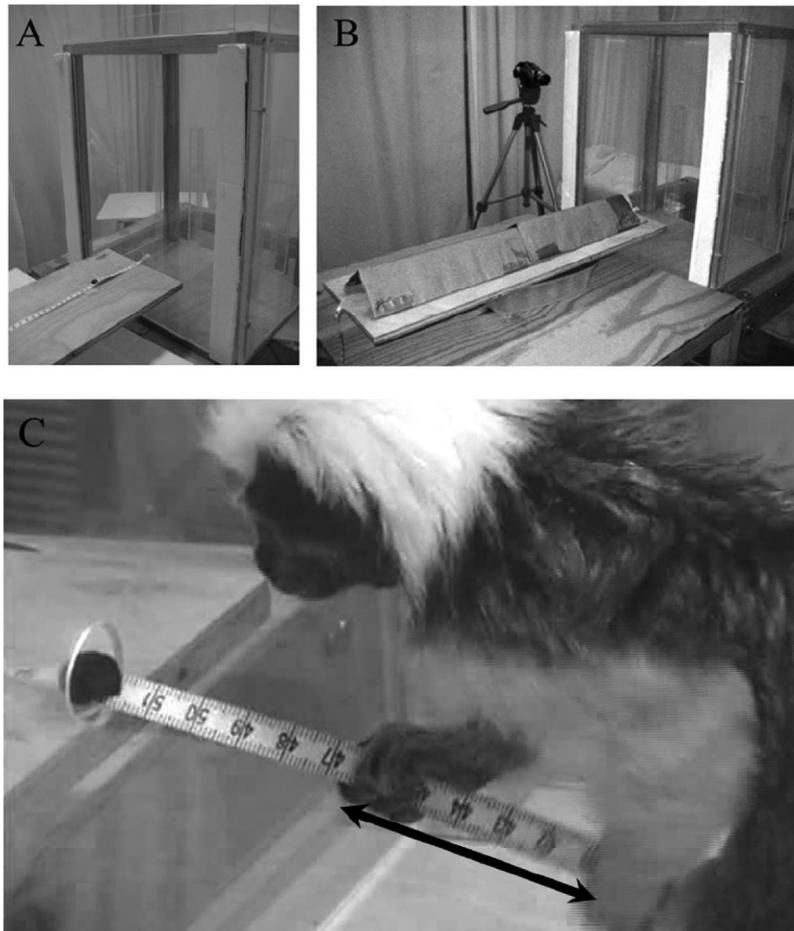
Five female and three male cotton-top tamarins participated in both conditions of this experiment. The tamarins were housed in mated pairs in a colony room. The tamarins had previously participated in behavioral experiments investigating motor planning, though with very different methods (e.g., Weiss & Wark, 2009; Weiss et al., 2007). Thus, they were familiar with the experimental chamber, but were otherwise experimentally naive. Use and care of the tamarins conformed to the regulations of the IACUC at the Pennsylvania State University.

### Materials

The monkeys were tested in isolation in an experimental procedure room. At the start of a trial, tamarins were located in a transport box (30.5 cm × 23.5 cm × 30.5 cm) constructed of Plexiglas and wire mesh caging with a metal front door that could be removed to provide visual access to the test chamber. The experimental chamber (25 cm × 40.75 cm × 30.5 cm) was constructed of four Plexiglas walls and a Plexiglas ceiling, supported by a wooden frame. The metal door of the transport box was aligned with a Plexiglas door of equivalent size (32.5 cm × 21.5 cm) on the back wall of the testing chamber. The door could be lifted and lowered to allow subjects access the testing chamber. On the front wall of the testing chamber there was a small central hole (2.75 cm diameter) 12 cm above the floor that provided access to a long wooden table (60.5 cm × 18.75 cm; see Figure 1a).

A flexible, plastic tape measure (150 cm × 1 cm) labeled with centimeter measurements was stretched out flat, extending 65 cm from the inside of the chamber to the edge of the table, with the remainder draped over the far end of the table out of view of the subject. The initial 3 cm of the tape measure was threaded into the testing chamber through the hole in the Plexiglas wall. A set of sealed metal disks served as a weight for the tape measure (10.2 cm diameter; 49.56 g) and was located between the 60.5 and 65 cm mark at the far end of the wooden table relative to the subject in every trial. This ensured that the force required to pull the tape measure was always equivalent. A Plexiglas disk (3.7 cm diameter) was affixed to the tape measure with transparent tape. High-quality food items (raisins in Condition 1; marshmallows in Condition 2) were placed on the disk which was larger than the hole, and thus, acted as a stopper for the tape measure. When subjects pulled the disk to the hole, the food item became easily accessible.

The apparatus used in Condition 2 was identical to the one used in Condition 1, except for the addition of a brown paper tunnel that covered the tape measure (see Figure 1b). The tunnel prevented subjects from viewing the movement of the food while pulling the tape measure. The tunnel was triangular in shape, measuring 54 cm long with openings at each end (5.5 cm × 7 cm). The front opening of the tunnel was covered with a gray cotton curtain to preclude subjects from viewing the tape measure. All trials were recorded with two digital camcorders simultaneously, placed on either side of the testing apparatus (see Figure 1b).



*Figure 1.* The apparatus used in Condition 1 (Panel A) and Condition 2 (Panel B). In Panel C, a tamarin grasps the tape measure with both hands during pulling behavior. The arrow depicts the dependent variable of interest, the distance between grasps.

## Procedure

In Condition 1, each test session consisted of six trials: two with the raisin placed at a near distance (13 cm), two at an intermediate distance (26 cm), and two at a far distance (52 cm). The order of trials in a given session was pseudorandomized such that no session contained two consecutive trials of the same type. The initial trial type of each session was counterbalanced within and across subjects. Subjects participated in two test sessions for Condition 1 and four test sessions for Condition 2.

At the onset of each trial, the experimenter attached a raisin to the disk (on the tape measure) out of view from the subject. The transport box door was then removed, providing the subject visual access to the food. The Plexiglas door was then lifted allowing the tamarin to enter the testing chamber and access the tape measure. Subjects could pull the tape measure in any manner they chose with the trial lasting until the food was consumed. After each trial, the subject returned to the transport box and the apparatus was reset. All subjects participated in Condition 1 prior to Condition 2 with a minimum of 3 months elapsing between conditions.

In Condition 2, each test session consisted of four trials; two Near (13 cm) and two Far (52 cm).<sup>1</sup> The order of these trial types was pseudorandomized and the initial trial type of each session was counterbalanced within and across individuals. The only difference from Condition 1 was that after the tamarin watched the experimenter bait the tape with food, the experimenter lowered the tunnel over the tape measure on the table. A second experimenter then lifted the Plexiglas door to allow the tamarins access to the chamber.

All trials were coded frame-by-frame (using Adobe Premiere) by an experimenter viewing both video camera recordings. The dependent variable of interest was the distance between hand grasps on the tape measure. This intergrasp distance was defined as the amount of tape between the subject's hands when both hands were gripping the tape simultaneously (see Figure 1c). We recorded the distance from the top part of one hand to the top of the

<sup>1</sup> Since we found no significant differences between the grasping distances observed in the Intermediate and Far trials in Condition 1 (see Results), in Condition 2 we tested only Near and Far distances.

other (this measurement was consistently clearer for coding than using the bottom of one hand to the top of the other). Locations of the hand on the tape were recorded in half-centimeter units as this was the smallest unit of measurement that could reliably be determined. Two coders (one naïve to the experiment) analyzed every trial. Any discrepancy exceeding 0.5 cm was resolved by having two coders review the trial together and reach consensus on the correct measurement. Interrater reliability for grasp location in Condition 1 was calculated at 85.1% and 89.6% for Condition 2. There was a strong positive correlation between the grasp locations for Coder 1 and Coder 2, in both Condition 1,  $r(360) = .998, p < .0001$ , and Condition 2,  $r(315) = .998, p < .0001$ .

In Condition 1, the average number of pulls in Near trials was 2.04 (range: 1–3), in Intermediate trials, 3.81 (range: 2–6) and in Far trials, 7.82 (range: 4–11). In Condition 2, the average number of pulls in Near trials was 2.14 (range: 1–3) and in Far trials, 7.26 (range: 5–13). Trials in which the tamarins obtained the food using a single pull were excluded from analysis because they did not yield intergrasp distances. These trials were not comparable to the types of multi-action sequences evidenced in the other conditions (where single long pulls could not be used to obtain the food). To equate for the removal of single-pull Near trials, we excluded all Intermediate and Far trials in which the intergrasp distance measured or exceeded 12 cm (the distance of a single-pull Near trial).

## Results

### Condition 1

Eight monkeys participated in Condition 1. One female was excluded from analysis due to consistently using her mouth to pull the tape measure. Five of the seven remaining monkeys completed two sessions of six trials. For the other two monkeys, four trials (out of 84 total trials across all subjects) were excluded from analysis due to mouth pulling (three) or refusing to pull (one). Consequently, these two individuals participated in two supplementary test trials. Four subjects completed a total of seven Near trials using a single pull, which were excluded from analysis. Thus, the final tally for the analysis of Condition 1 included 21 Near trials, 28 Intermediate trials, and 28 Far trials. To equate for these exclusions, within Intermediate and Far trials individual grasps greater than 12 cm were also excluded from the analysis. Three subjects produced a total of eight such exclusions (two Intermediate and six Far).

We found that there was a systematic effect of trial type on intergrasp distance; the intergrasp distances in the Near trials were smaller than those in the Intermediate or Far trials (see Figure 2). A within-subjects ANOVA confirmed a significant main effect of trial type,  $F(2, 5) = 11.918, p = .001$ , (Mauchly's  $W = .851, p = .668$ ). Post-hoc paired  $t$ -tests were conducted using Bonferroni adjusted alpha levels of .017 per test to account for family-wise error. Results indicated that the average intergrasp distance was significantly smaller in the Near condition ( $M = 4.8$  cm,  $SD = 1.2$  cm) than the intergrasp distances in both the Intermediate condition ( $M = 6.4$  cm,  $SD = 1.7$  cm),  $t(6) = -3.951, p = .008$ , and in the Far condition ( $M = 6.1$  cm,  $SD = 0.9$  cm),  $t(6) = -4.032, p = .007$ . The pairwise comparison of the Intermediate condition with the Far condition was nonsignificant,  $t(6) = 1.156, p = .292$ .

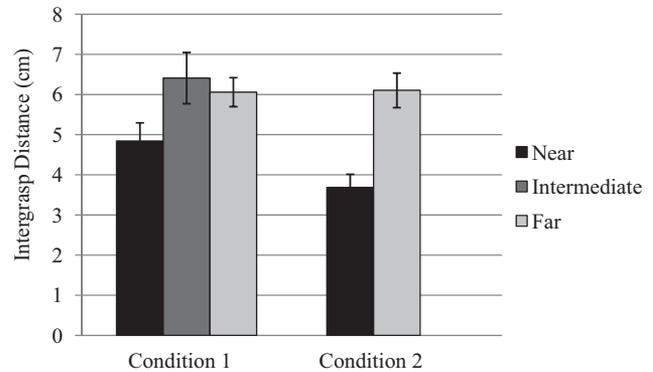


Figure 2. Average intergrasp distances in Near, Intermediate, and Far trials for Condition 1 (left) and in Near and Far trials for Condition 2 (right).

To determine whether the above differences in intergrasp distances by trial type were present at the start of the trials, we examined the first two intergrasp distances of each trial, comparing these in Near, Intermediate, and Far trials. Specifically, we wanted to rule out the possibility that the differences between intergrasp distances emerged over the course of the trials. We found that the intergrasp distances generated in the first two pulls of Near trials were smaller than those in Intermediate trials. Using a within-subjects ANOVA, the main effect of trial type was significant,  $F(2, 5) = 6.813, p = .011$  (Mauchly's  $W = .745, p = .478$ ). Post-hoc  $t$ -tests were conducted using Bonferroni adjusted alpha levels of .017 per test. Results indicated that the average intergrasp distance in the Near condition ( $M = 4.8$  cm,  $SD = 1.2$  cm) was significantly smaller than the intergrasp distance in the Intermediate condition ( $M = 6.3$  cm,  $SD = 1.7$  cm),  $t(6) = -3.293, p = .017$ . The pairwise comparison of the Near and the Far condition ( $M = 5.4$  cm,  $SD = 0.66$  cm) was nonsignificant,  $t(6) = -1.778, p = .126$ . The pairwise comparison of the Intermediate condition with the Far condition was also nonsignificant,  $t(6) = 2.099, p = .081$ . Notwithstanding the lack of statistical power, the means trended in the expected direction of the analysis for all trials.

It is possible that the subjects learned to associate their intergrasp distances with the food distance as a result of their experience with the trials over multiple experimental sessions. In order to rule out this effect of experience, we compared the average intergrasp distances for the very first Near, Intermediate and Far trial for each tamarin. We found that the first trial data conformed to the same pattern: intergrasp distances in the first Near trials were smaller than those in the first Intermediate or Far trials. The within-subjects ANOVA revealed a significant main effect of trial type  $F(2, 5) = 5.253, p = .028$  (Mauchly's  $W = .467, p = .218$ ). Post-hoc  $t$ -tests were conducted using Bonferroni adjusted alpha levels of .017 per test. The average intergrasp distance in the Near ( $M = 2.1$  cm,  $SD = 2.3$  cm) condition was significantly smaller than the than in the Far condition ( $M = 5.5$  cm,  $SD = 1.2$  cm),  $t(5) = -4.539, p = .006$ . The pairwise comparison of the Near condition with the Intermediate condition ( $M = 4.5$  cm,  $SD = 2.4$  cm) was nonsignificant,  $t(5) = -1.703, p = .149$  and neither was the comparison of Intermediate and Far conditions ( $M = 5.5$  cm,  $SD = 1.2$  cm),  $t(5) = -1.032, p = .349$ .

In order to determine whether intergrasp distances were consistent through the course of a trial, we analyzed whether pull number could predict the intergrasp distance of these pulls in Far trials (the only distance that yielded a sufficient number of individual pulls for the analysis). We found that pull number (over the course of a trial) was not a significant predictor of the intergrasp distance. This was confirmed by a linear regression analysis,  $F(1, 144) = .005$ ,  $p = .944$ .

## Condition 2

Seven monkeys participated in Condition 2. One monkey was excluded from the analysis due to behavioral difficulties (dropping the tape measure between pulls and lifting the curtain to peer into the tunnel). For the remaining six monkeys, eight trials were discarded due to lack of hand-over-hand pulling (four), the video being obstructed by the subject (two), and camera malfunction (two). These trials subsequently were conducted again. Three monkeys used a single pull to reel in the food in Near trials and these trials were excluded from analysis. Thus, the Condition 2 analyses included 35 Near trials and 38 Far trials. To equate for the exclusions in Near Trials, we also excluded a total of seven pulls with intergrasp distances of 12 cm or greater in Far trials (produced by four individuals).

In Condition 2, we found that the intergrasp distance was smaller in Near compared with Far trials, confirming what was found in Condition 1 (see Figure 2). A paired-samples  $t$ -test revealed that the average intergrasp distance in the Near trials ( $M = 3.7$  cm,  $SD = 0.78$  cm) was significantly smaller than the intergrasp distance in the Far trials ( $M = 6.1$  cm,  $SD = 1.1$  cm);  $t(5) = -4.55$ ,  $p = .006$ . To ensure that the effect was present early on, we compared the first two data points in the Near and Far trials. We found that even in the first two data points, the intergrasp distances in the Near trials were smaller than those in Far trials. A paired-samples  $t$ -test revealed that the average intergrasp distance in the Near trials ( $M = 3.7$  cm,  $SD = 0.8$  cm) was significantly smaller than the intergrasp distance in the Far trials ( $M = 5.5$  cm,  $SD = 0.7$  cm);  $t(5) = -4.837$ ,  $p = .005$ . All monkeys exhibited these patterns of behavior.

As in Condition 1, we examined the progression of intergrasp distances over the course of Far trials. A linear regression analysis across all monkeys on far trials revealed that pull number was not a significant predictor of the distance between grasps,  $F(1, 194) = .048$ ,  $p = .827$ .

## Discussion

In humans, it has been established that sequential motor actions tend to be planned prior to their enactment (e.g., Sternberg, Monsell, Knoll, & Wright, 1978). Our goal was to determine whether cotton-top tamarins are capable of anticipatory motor planning for a sequence of actions that accommodate a task demand. In Condition 1, with the food visible throughout the entire trial, the tamarins used smaller intergrasp distances when pulling the tape measure during Near trials than they used for the Intermediate and Far trials. This tendency was robust and consistent across all individuals. The findings from Condition 1 thus suggest that the subjects scaled their intergrasp distances according to the distance to be pulled. In Condition 2, the tape measure was occluded

immediately after subjects watched the food being placed. Even with the absence of visual feedback while pulling, the tamarins scaled their pulling behavior. Together, the pattern of results suggests that subjects planned for the intergrasp distances to be used in pulling actions prior to actually pulling the tape measure.

We considered two alternative explanations that might result in observed scaling of intergrasp distances; namely, that physical forces on the tape measure were different across Near and Far conditions or that the tamarins developed an association between the food distance and the intergrasp distance over the course of the experiments. With regard to physical forces, it is possible that inertia exerted a more significant influence on the average intergrasp distance in Near trials than in Intermediate or Far trials. The force required to pull the tape measure at rest (pulls early in the sequence) may have been larger than the force required to pull the tape measure when it was already in motion (pulls later in the action sequence). If inertial forces differentially impacted performance in Intermediate and Far trials, one would expect initially small intergrasp distances early in the pulling sequence (when inertia was highest), followed by larger intergrasp distances later in the trial (once inertia had been overcome). However, the results of our linear regression analyses do not support this account, as we discovered that the intergrasp distances were consistent over the course of Far trials. Therefore, it seems unlikely that the scaling effect observed in both experimental conditions could stem from physical forces impacting trial types differentially.

Similarly, our findings do not support the gradual development of an association between smaller intergrasp distances and closer food items and larger intergrasp distances and farther food items. Distance scaling was present even in the first trials of Condition 1 suggesting that the tamarins did not develop this association after repeated exposure to the task. Rather, the results suggest that tamarins are capable of anticipatory motor planning for a sequence of repeated motor actions even in a novel task.

As noted above, previous research in our laboratory has demonstrated that cotton-top tamarins (Weiss et al., 2007) and lemurs (Chapman et al., 2010) exhibit motor planning in object manipulation tasks. This planning was evidenced through the planning of a single action (e.g., grasping the stem of a cup with the thumb facing downward) in anticipation of a future task demand (extracting food from the cup). As noted, those findings challenged the theory that sophisticated motor planning abilities may be exclusive to proficient tool users (see Johnson-Frey, 2004). The present study extends research on motor planning in primates by demonstrating planning for a sequence of repeated actions. In some ways, the task employed here was simpler than the cup task used in previous studies (Chapman et al., 2010; Weiss et al., 2007), as those required the subjects to forgo (or inhibit) a species-typical posture in order to adopt a novel posture that accommodated the final grasping posture. In the current study, the tamarins engaged in pulling behaviors that appear to be natural for them with no inhibition necessary. Future research will explore whether tamarins are capable of motor planning for a series of varied motor actions that entail inhibition of species-typical behaviors.

A somewhat surprising finding from these experiments is that the tamarins scaled their pulling behavior even when they could not see the food moving toward them as they pulled. This stands in contrast to recent findings with corvids that report a significant decline in performance on the classic string-pulling ex-

periment when visual feedback was restricted (Taylor et al., 2010). This suggests that a perceptual feedback loop may guide the string pulling behavior. Why are the tamarins not subject to the effects of a similar perceptual feedback loop in this experiment? The answer to this question may be related to differences in complexity of the behavioral sequence that must be assembled to solve the task. Corvid string-pulling experiments require the coordination of multiple effectors (beak and foot) and motor sequences that include multiple novel actions (see Werdenich & Huber, 2006). In our experiment, the tamarins could solve the task using a single effector type (hands) and repetitions of a single action (manually pulling the tape measure) that appears to be within the existing behavioral repertoire. That the tamarins' scaling behavior was not contingent on visual feedback suggests the intergrasp distances were planned in advance of pulling the tape measure.

Although it is unlikely that solving the tape measure task requires insight learning (though see Weiss et al., 2012), scaling to the distance of a reward no longer in view does require the ability to act on a mental representation of the object hidden from view and an appreciation of the means-end nature of the task. Consequently, we propose that the minimal cognitive prerequisites for this type of performance include object permanence, an egocentric representation of space, an appreciation of means-end relationships, and the ability to plan sequences of motor actions to accommodate a task demand (here, the distance between the food and the subject). Although object permanence is well established in numerous species (see Santos & Hood, 2009 for review), in order to scale correctly to the distance to the food, the tamarins not only need to maintain a representation of the food object, but must also encode the distance to the object, arguably using an egocentric representation of space indicating the distance to the food from the subject when it was last viewed. Further, as noted above, another requirement of this experimental paradigm is the capacity to solve a means-end task. Previous studies have shown that tamarins can be trained to solve a means-end task in which an object is used to obtain a food reward (e.g., Hauser, 1997) and here we demonstrate that tamarins can solve such tasks in the absence of explicit training. In sum, we propose that tamarins engage in a constellation of cognitive abilities in order to scale the distance between grasps to the distance of the food reward, particularly in the absence of visual feedback.

A final remark concerns why the tamarins chose to scale to the distance of the food. It is possible that this scaling represents an efficient strategy for transporting the food that does incur less cost in terms of effort than other strategies (such as using a canonical grasp-distance regardless of the distance to the food). This is an open question that must be addressed in future work. Recently, researchers have endeavored to develop an experimental paradigm to quantify the perception of cost of reaching and walking actions in human adults (e.g., Rosenbaum, Brach, & Seminov, 2011). This paradigm, or some variant thereof, might profitably be applied to the present work in order to delineate the types of computations and considerations that educe the scaling behavior. Regardless of the underlying motivation for scaling, our work has demonstrated that tamarins are capable of more sophisticated anticipatory motor planning than previously supposed, suggesting that humankind's

impressive planning abilities may indeed have a lengthy evolutionary history.

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