

## BRIEF COMMUNICATIONS

# Hysteresis Effects in a Motor Task With Cotton-Top Tamarins (*Saguinus oedipus*)

Daniel J. Weiss and Jason Wark  
The Pennsylvania State University

The way human adults grasp an object is influenced by their recent history of motor actions. Previously executed grasps are often more likely to reoccur on subsequent grasps. This type of hysteresis effect has been incorporated into cognitive models of motor planning, suggesting that when planning movements, individuals tend to reuse recently used plans rather than generating new plans from scratch. To the best of our knowledge, the phylogenetic roots of this phenomenon have not been investigated. Here, the authors asked whether 6 cotton-top tamarin monkeys (*Saguinus oedipus*) would demonstrate a hysteresis effect on a reaching task. The authors tested the monkeys by placing marshmallow pieces within grasping distance of a hole through which the monkeys could reach. On subsequent trials, the marshmallow position changed such that it progressed in an arc in either a clockwise or counterclockwise direction. The authors asked whether the transition point in right- versus left-handed reaches would differ depending on the direction of the progression. The data supported this hysteresis prediction. The outcome provides additional support for the notion that human motor planning strategies may have a lengthy evolutionary history.

*Keywords:* motor planning, hysteresis, nonhuman primates

Hysteresis can be defined as the influence of prior history on the subsequent state of a system. Much of human perception and behavior is subject to hysteresis effects. For example, the first 50-degree day in Fall may subjectively feel colder than the first 50-degree day in Spring. While the temperature is constant, the prior history dictates whether we respond by bundling up or dressing lightly. More formally, hysteresis effects have been demonstrated for human visual motion perception (e.g., Williams, Phillips, & Sekuler, 1986), auditory perceptual integration (e.g., Deutsch, 1981), speech sound categorization (e.g., Tuller, Case, Ding, & Kelso, 1994), and most relevant to this paper, motor behavior.

A classic illustration of hysteresis in human motor behavior involves rhythmic finger movements. When subjects were asked to oscillate their index fingers horizontally back and forth in parallel (requiring the muscles to move in anti-phase) to the beat of a metronome, as the metronome beat increased to a critical speed, the fingers spontaneously changed to an in-phase pattern of motion (in which the muscles contracted at the same time in both hands,

resulting in a pattern where the distance between the index finger tips no longer remained constant). However, when the frequency of the metronome was lowered below the critical value after a phase transition occurred, the in-phase pattern remained (Kelso, 1981). This finding, along with other similar behavioral data, provided the empirical platform for the Haken-Kelso-Bunz model of self-organization (see Haken, Kelso, & Bunz, 1985), a dynamical systems approach to describing coordinated behavior.

While hysteresis effects may be formally captured by a dynamical systems analysis, they also figure prominently in cognitive models of motor planning. For example, Cohen and Rosenbaum (2004) found that after subjects moved an object from one place to another, they were more likely to grasp the object in the same way when returning the object to the initial location. Subsequent research has suggested that subjects recalled the location at which they initially grasped the object, rather than the posture they adopted for the initial grasp (Weigelt, Cohen, & Rosenbaum, 2007). These findings lend support to a posture-based motion planning theory, a cognitive model that accounts for how movements are planned (see Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001). According to this model, goal postures are selected through a two-stage process. The first stage involves selecting a stored posture for the task at hand and the second stage “tweaks” this selected posture (see Rosenbaum, Cohen, Meulenbroek, & Vaughan, 2006). Thus, according to this model, hysteresis effects in planned motor actions are a form of instance retrieval (the recollection of stored postures) and emerge because it is easier to recall a previously used goal posture (and in some cases, a remembered location) than to generate a new motor plan. From this

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Daniel J. Weiss and Jason Wark, Department of Psychology, The Pennsylvania State University.

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Correspondence concerning this article should be addressed to Daniel J. Weiss, 643 Moore Building, University Park, PA 16802. E-mail: djw21@psu.edu

perspective, hysteresis in motor planning can be viewed as a useful cognitive heuristic.

Given that hysteresis effects figure prominently in multiple levels of analysis of motor behavior, it is natural to investigate the developmental trajectory of this phenomenon, both in terms of its ontogeny in humans and phylogenetically, where one adopts a comparative approach to explore the possible evolutionary roots of the behavior.

In human infants, there is evidence that hysteresis effects are present as early as 4 weeks of age, at least in the behavioral domain of visual search (Robertson, Guckenheimer, Masnick, & Backer, 2004). By contrast, in object manipulation tasks, the earliest age at which hysteresis effects have been demonstrated so far is in children 4 years of age. In a ball-catching task in which the direction of the ball was systematically manipulated, Rostoft and colleagues (2002) found hysteresis effects for the hand children used to catch the ball. It is unknown whether such motor effects are present at earlier points in development, as one might expect if they follow a similar trajectory as the visual search pattern effects.

While there have been no direct studies of hysteresis effects in reaching by human infants as opposed to young children, perseverative reaching behaviors have been described for very young infants as they search for hidden objects (i.e., Piaget's, 1954, famous A-not-B error). While many explanations have been offered for this phenomenon (see Munakata, 1998), the A-not-B error is certainly consistent with hysteresis. Overall, then, studies of hysteresis in infants and children suggest that these effects are present early in the course of human development, although the precise timeline remains to be determined.

Comparative studies of behavior have confirmed that hysteresis effects are characteristic of many species. One of the landmark studies of quadrupedal locomotion in horses found hysteresis effects in gait transition points in speeding up from a trot to a gallop versus slowing from a gallop to a trot (e.g., Hoyt & Taylor, 1981). Conditioning eyeblink studies with rabbits have also demonstrated hysteresis effects (Baker & Frey, 1979). Moreover, numerous studies have demonstrated hysteresis effects at the level of single unit recordings in primates (e.g., Goldberg, Meredith, & Shall, 1998) and cats (e.g., Shall, Wilson, & Goldberg, 1996).

To the best of our knowledge, however, there have been no studies directly demonstrating hysteresis effects for motor reaching behaviors in nonhuman species. One previous study (Fragaszy, 1986) tested reaching behaviors in squirrel monkeys (*Saimiri sciureus*) and titi monkeys (*Callicebus moloch*). The monkeys were trained to reach for food from a particular opening, and during test trials, the food progressively moved toward a second, untrained opening. While the data were not analyzed from a hysteresis perspective, the general pattern appears to be consistent with a hysteresis account in that animals trained to reach from an opening on the left, tended to use that opening with greater frequency than animals trained to use the opening on the right, who preferred that opening during test trials (Fragaszy, 1986, Figure 4, p. 398). This hysteresis interpretation is somewhat clouded by the intensive training regimen that certainly influenced the observed behaviors. Given the possible cognitive implications involved in the planning and execution of reaching behaviors (see Rosenbaum et al., 2001), a hysteresis demonstration without explicit training could enhance our understanding of the fundamental similarities

and differences across species in the mechanisms underlying motor planning. The present study tests for the presence of hysteresis effects in a motor reaching task in a nonhuman primate species in the absence of directed operant training.

We sought evidence for hysteresis effects in a food grasping task in cotton-top tamarins (*Saguinus oedipus*), a small arboreal New World monkey. Recent research with this species has shown that they are capable of quite sophisticated anticipatory motor planning when interacting with objects (Weiss, Wark, & Rosenbaum, 2007). Specifically, when tamarins were presented with a food reward inside a cup that was suspended in either upright or inverted orientation, their initial grasping posture reflected subsequent task demands (i.e., retrieval of the reward) even in cases where an unusual grasping posture was required. Thus, the tamarins' behavior was consistent with the *end-state comfort effect*, a motor planning effect in which individuals assume initially uncomfortable or unusual postures in the service of accommodating subsequent anticipated postures (Rosenbaum et al., 1990, see Rosenbaum et al., 2006, for review). Because tamarins are not known to be tool-users in the wild (e.g., Hauser, Pearson, & Seelig, 2002; Santos, Rosati, Sproul, Spaulding, & Hauser, 2005), this finding suggests that the emergence of tool-use in humans cannot be explained solely by the evolution of rudimentary anticipatory motor abilities (see Johnson-Frey, 2003, for details on this theoretical account).

Having established a cross-species similarity with respect to a subset of anticipatory motor behaviors, we decided to investigate perseverative influences on motor behavior. Briefly, the task involved having the monkeys reach through a hole in a Plexiglas door to obtain a marshmallow. The position of the marshmallows relative to the hole changed over trials, advancing in an arc in either a left-to-right (i.e., clockwise) or right-to-left (i.e., counterclockwise) progression. Similar to the developmental study by Rostoft and colleagues (2002), our dependent measure was whether the tamarins chose to deploy a right-handed or left-handed grasp. Our prediction was that if the monkeys were prone to hysteresis effects similar to those reported in previous human studies (Cohen & Rosenbaum, 2004; Rostoft et al., 2002), we would find a shift in the transition point from left to right hand grasps or vice versa depending on whether the successive test positions went from left to right or vice versa.

Because the present method relies on hand choice as its principal measure, it is important to consider the issue of handedness in the subject population being studied. Whereas most people are right-handed, making it possible in human studies to restrict the sample to right-handed individuals (e.g., Rostoft et al., 2002), handedness in nonhumans is difficult to establish. Tamarins are thought to have a slight bias for right-handedness in spontaneous reaching tasks (Diamond & McGrew, 1994; King, 1995), but one study that used a static food-reaching task quite similar to the present study (except that the food was always in a central location) found a bimodal distribution with respect to the preferred hand for retrieving the food (King, 1995). The latter outcome indicates that handedness is, at the very least, not so pronounced that it obviates the possibility of seeing hand switches for reaching, as required to detect hysteresis for hand selection in a reaching task.

## Method

### Subjects

We tested four female and two male cotton-top tamarins (*Saguinus oedipus*). The monkeys were born at the New England Regional Primate Research Center in Southborough, MA, and were brought to Penn State in June 2005. The tamarins were housed in mated pairs in two colony rooms. The tamarins had previous experience with behavioral experiments on motor planning (e.g., Weiss et al., 2007) but no previous experience with the experimental procedures used in this experiment.

The tamarins were maintained at 95% of their free feed weight. They had ad libitum access to water. Use and care of the tamarins conformed to the rules and regulations of the IACUC at the Pennsylvania State University.

### Apparatus

All experiments were conducted with the tamarins situated in a transport box (12" high  $\times$  9.25" wide  $\times$  12" deep) with two walls made of Plexiglas, one wall made of caging, and a front door made of Plexiglas with a hole cut out (1" diameter) so the tamarins could reach through it. The hole allowed the monkeys to reach through up to their shoulder joint. The transport box was located in a soundproof chamber (Acoustic Systems). Trials were recorded with a digital camcorder (Sony DCR HC21) and were burned onto a DVD (Panasonic DMR-ES20).

A small platform (4" h  $\times$  10" w  $\times$  3.5" d) was placed in front of the transport box door so the tamarins could reach through the hole and pick up objects from the surface. The platform sat 1 in. below the center of the hole in the Plexiglas door. A sheet of paper with 11 positions marked on it was placed on the platform in front of the hole. The 11 positions arced around the hole in the door (see Figure 1); they were marked in 15-degree increments (roughly 1/2" separating each position). The distance from position 1 to position 11 was 3.75 in. in a straight line. In order to make the extreme positions easier to reach, they were placed 1/2 in. away from the Plexiglas door (see Figure 1a).

### Procedure

The procedure had three phases: (a) familiarization; (b) a test run in one direction; (c) a test run in the return direction. The main goal of the familiarization period was to ensure that the monkeys could reach for the marshmallows through the hole in the door, which was a concern given that these monkeys are known to have difficulty with transparent objects (Santos, Ericson, & Hauser, 1999). A secondary function of the familiarization trials was to provide some indication of the spontaneous hand preferences of the subjects. During the familiarization trials, a small piece of marshmallow (1/8th of a miniature Kraft® marshmallow) was placed on the center position (Position 6), directly across from the hole in the door. After two consecutive familiarization trials in which the monkeys reached through the hole to grasp the marshmallow (obtaining the marshmallow in at least one of these trials), the monkeys proceeded, no later than 30 s, to the first test run.

The first test run began with the experimenter baiting either Position 1 or Position 11 (the most extreme positions) with a small marshmallow piece. The monkeys were given an unlimited amount

of time to reach for the marshmallow. If the monkey successfully grasped the marshmallow, the experimenter started the next trial a minimum of 5 s after the onset of the initial reach (and only after the marshmallow piece had been completely consumed). Following the completion of the first trial, the adjacent position was baited (in either a clockwise or counterclockwise direction depending on the starting point). This procedure continued until all 11 positions had been baited. The initial starting position was counterbalanced across individuals, such that some monkeys initially began at Position 1 and ended at Position 11 (clockwise) whereas others began at Position 11 and ended at Position 1 (counterclockwise).

After successfully completing the first test run, the monkeys proceeded to the second test run. This second test run was identical to the first except that the order of presentation was reversed. Thus, if the first test run was in a clockwise progression, the second test run was in a counterclockwise progression (and vice versa). After a 15 s break following the first test run, the experimenter baited the final position that was baited in the first test run. The rest of the second test run then proceeded, as did the first test run, only in the opposite direction for the monkey tested.

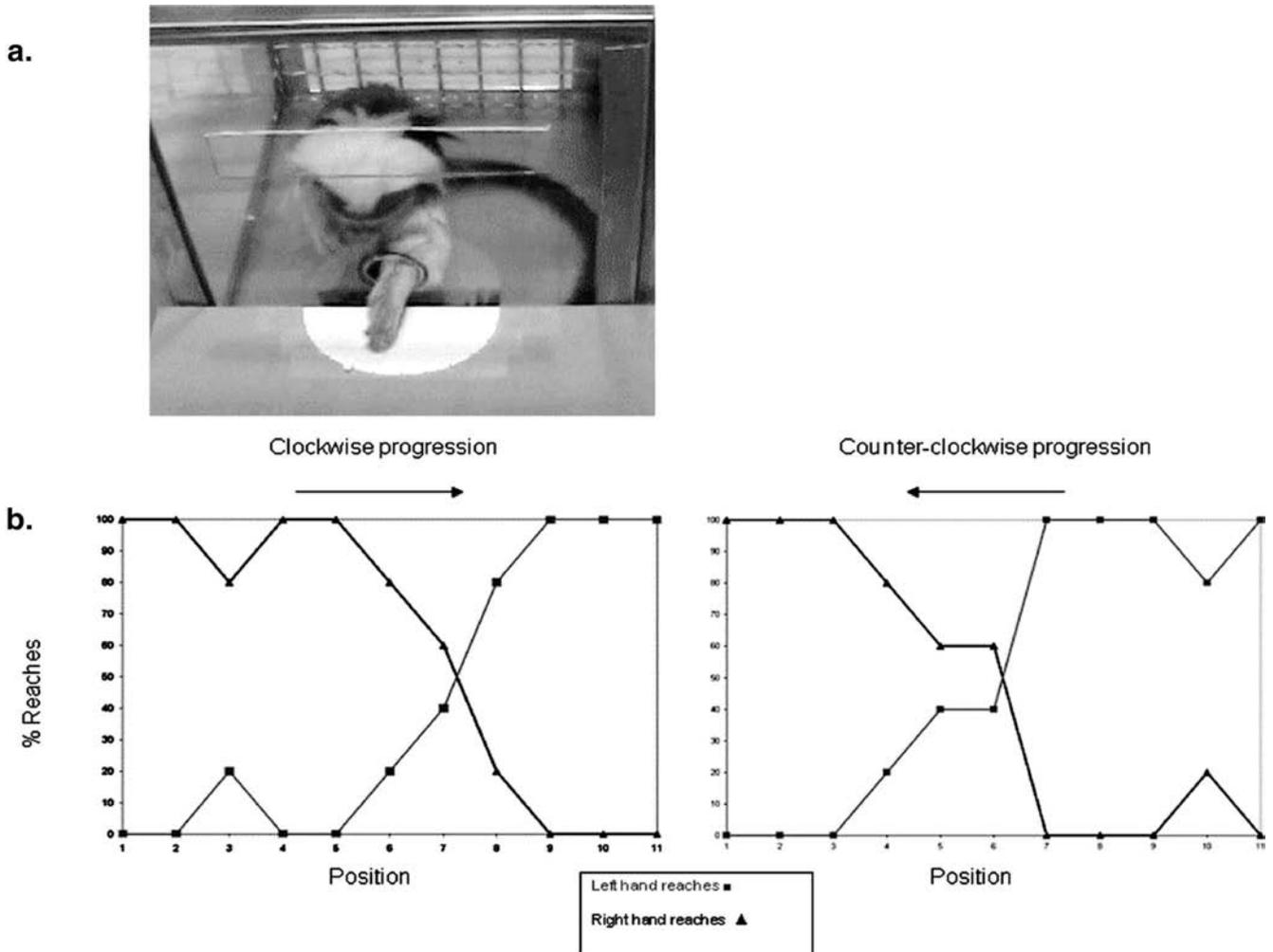
During any trial, if the monkeys knocked the marshmallow off the platform during the course of reaching, the marshmallow was replaced in the position in which it originated. If the monkey knocked the marshmallow off the platform twice in a row, the marshmallow was subsequently placed in the next position.<sup>1</sup> This ensured that there would not be a large discrepancy in the number of overall trials across individuals.

### Analysis

The dependent measure was which hand the monkeys used to reach for the marshmallow: right or left. If hysteresis characterizes the monkeys' hand choices, one would expect to find an asymmetry in the pattern of reaching when the marshmallow location progressed in a clockwise pattern (1 to 11) or in a counterclockwise pattern (11 to 1) such that the switch between hands should occur at a position farther to the right for the clockwise pattern and farther to the left for the counterclockwise pattern, with the clockwise progression exhibiting more right-hand reaches and the counterclockwise progression exhibiting more left-hand reaches.

Given the dichotomous nature of the dependent measure, we performed an initial nonparametric analysis focused on the overall difference in the number of reaches across monkeys for direction (clockwise or counterclockwise) versus the other. In keeping with similar experiments reporting hysteresis effects in reaching tasks (e.g., Rostoft et al., 2002), we also aggregated and plotted the reaches of all subjects in both directions to identify the mean transition point (i.e., the location at which the probability of using a given hand crosses the 50% line). The hysteresis prediction was that the transition point would be farther to right for the clockwise progression and farther to the left for the counterclockwise progression.

<sup>1</sup> Note that knocking the marshmallow off the platform tended to occur most frequently in the extreme positions (1 and 11) and never occurred in the hysteresis area for any of the subjects.



*Figure 1.* (a) Grasping the marshmallow in position 8 during experimental procedure. The marks on the paper were darkened in post-processing so they could be more easily detected by the reader. (b) Aggregate graph of right-handed and left-handed reaches in the clockwise and counterclockwise test progressions.

## Results

One experimental session in which the monkey did not complete both test runs was excluded from the final analysis. The same monkey had a second trial excluded due to experimenter error (the wrong location was baited). Likewise, one test run lasted over 20 minutes (over two standard deviations above the mean) and the session was not included in the analysis (as this was taken as an indication of behavioral difficulties). That individual was rerun on a subsequent day.<sup>2</sup>

Five individuals switched hands during test, and four of them demonstrated hysteresis. One monkey always used her right hand, so her data were excluded for the analysis to be carried out, which was concerned with the question of where hand switches occurred. For a monkey that never switched hands, the measure of where the hands switched was undefined. This performance did demonstrate that the monkeys conceivably had the ability to reach all positions with either hand.

The data for the five remaining monkeys are shown in Table 1. Here it is seen that the monkeys that did switch hands used more

right-handed grasps in the clockwise progression than in the counterclockwise progression and used more left-handed grasps in the counterclockwise progression than in the clockwise progression (paired sign test,  $p = .016$ ). Furthermore, the shift from one hand to the other within progressions depended on the progression being tested. The transition point was farther to the right for the clockwise progression than for the counterclockwise progression (see Figure 1b). This outcome is consistent with the hysteresis prediction.

In order to quantify the transition point, we adopted a technique used in Rostoft et al., 2002. We defined a hysteresis area for subjects by comparing the transitions used in the clockwise versus counterclockwise test runs. The mean transition point was defined

<sup>2</sup> In the subsequent test run for that individual (LS), the marshmallow was not replaced if it was knocked off the platform in order to speed the trial and minimize inattentiveness. The marshmallow was knocked off a total of 6 out of 24 times, but never in the position directly preceding a hand switch (i.e., in both test runs, the trials in which the monkey switched hands followed a successful trial).

Table 1  
Reaching Data Reported by Individual

Monkey name	Fam 1	Fam 2	Test direction	1	2	3	4	5	6	7	8	9	10	11
Homer	R	L	Clockwise →	R	R	R	R	R	<b>R</b>	<b>L</b>	L	L	L	L
			Counterclockwise ←	R	R	R	R	R	<b>R</b>	<b>L</b>	L	L	L	L
Jerry	R	R	Clockwise →	R	R	R	R	R	<b>R</b>	<b>R</b>	<b>L</b>	L	L	X
			Counterclockwise ←	R	R	R	R	R	<b>R</b>	<b>L</b>	L	L	L	R
Lisa	R	R	Clockwise →	R	R	R	R	R	<b>R</b>	<b>R</b>	<b>R</b>	<b>L</b>	L	L
			Counterclockwise ←	R	R	R	R	R	<b>R</b>	<b>L</b>	L	L	L	L
Mulva	L	L	Clockwise →	X	R	L	R	<b>R</b>	<b>L</b>	L	L	L	L	X
			Counterclockwise ←	X	R	<b>R</b>	<b>L</b>	L	L	L	L	L	L	L
Susan	L	L	Clockwise →	R	R	R	R	R	R	<b>R</b>	<b>L</b>	L	L	L
			Counterclockwise ←	R	R	R	<b>R</b>	<b>L</b>	L	L	L	L	L	L

Note. Bolded values represent transition points in the progression (i.e., the locations at which subjects appear to switch their preferred grasping hand).

as the position at which the preference for the left versus right hand reaches crosses the 50% line (see Figure 1B; Rostroft et al., 2002). The mean transition point was situated between points 7 and 8 (7.22) in the clockwise progression. The mean transition point was situated between points 6 and 7 (6.18) in the counterclockwise progression. Thus, the hysteresis area extended from 6.18 to 7.22.

It is useful to consider performance on the familiarization trials to better understand the main results, presented above. In the familiarization trials, two of the five monkeys used only the right hand, two used only the left hand, and one used both hands about equally often. The individuals who used the left hand during familiarization were more likely to use the left hand during test, and vice versa (paired sign test  $p = .031$ ). Surprisingly, the one monkey who used the two hands with equal likelihood in the familiarization phase was the one monkey that did not show a hysteresis pattern during the test phase.

### Discussion

The experiment reported here provides the first analyzed evidence we know of for hysteresis effects in a reaching task performed by a nonhuman species. The tamarins exhibited a sizable hysteresis area with respect to right versus left hand reaches when they were presented with marshmallows in a clockwise versus counterclockwise test progression. The position at which the tamarins switched hands to grasp for the marshmallow tended to be farther to the right for trials that used a clockwise test progression and was farther to the left for trials that used a counterclockwise test progression. These results are consistent with the hysteresis prediction. Hysteresis was manifested in four of the five monkeys who switched hands during the test phase of the experiment.

The finding of a hysteresis effect in this task is consistent with the results reported for human children in a similar task. As mentioned above, Rostroft et al. (2002) obtained evidence for hysteresis among children engaged in a ball catching task. The size of the hysteresis area reported in their study, using a ball catching task, mirrored those reported in our study (roughly 1 full position). Our results thus extend the findings of Rostroft et al. (2002) to a different task and species.

Theoretically, the present findings are important when considered in light of cognitive models of motor planning. It is worth noting that our findings do not adjudicate between different models of motor planning. For example, the Rostroft study (2002)

interpreted their results through the lens of a dynamical systems approach. Likewise, results from the A not B task mentioned in the Introduction have also been accounted for using a dynamical systems approach (e.g., Schutte & Spencer, 2002; Thelen, Schöner, Scheier, & Smith, 2001). In a similar vein, our data are also compatible with this theoretical approach. However, we view dynamical systems and cognitive approaches to motor planning as being cast at different levels of analysis. Dynamical systems approaches are abstract mathematical descriptions, whereas cognitive approaches tend to focus on the internal processes and mechanisms underlying motor behavior (see Rosenbaum, in press). Unlike conditioned eyeblink or single unit recording studies (e.g., Baker & Frey, 1979; Shall et al., 1996), behaviors that are unlikely to be influenced by top-down cognitive mechanisms, the data presented here, as well as in our previous work on anticipatory motor planning (Weiss et al., 2007), provide a foundation for a comparative approach to cognitive theories of motor planning. The findings presented here suggest that tamarins, like humans, prefer to reuse previously adopted motor behaviors when it is feasible to do so. As suggested elsewhere (Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007), this method of generating plans is computationally more efficient than generating new plans from scratch for every successive movement.

The results of our study are consistent with the pattern of grasping reported by Fragaszy (1986) with both squirrel and titi monkeys. The conclusion of that study mentions the possibility that some perseverative motor patterns may be shaped by ecological factors such as size of home range, foraging strategies, and diet (as evidenced in Fragaszy & Mason, 1983). Indeed, recent studies of discounting behaviors in tamarins and marmosets have reprised this idea, demonstrating that even closely related species may exhibit different patterns of spatial and temporal discounting that map onto their feeding ecology (Stevens, Hallinan, & Hauser, 2005; Stevens, Rosati, Ross, & Hauser, 2005). However, such cross-species differences have only emerged in the context of “far space” tasks, tasks that require the animals to travel some distance for food. A travel task (i.e., “far space”) study involving titi and squirrel monkeys (Fragaszy, 1980) also reported different patterns of behavior across species that mapped on to ecological factors. One future direction for our research will be to test behavioral perseverance patterns in a “far space” task with tamarins and compare the results to the findings reported here, as well as the previous findings with titi and squirrel monkeys. Tamarins have a similar home

range- and group-size as titi monkeys, but also move rapidly during prey capture and ordinary locomotion similar to squirrel monkeys (see Fragaszy, 1986). Thus, the results of such a study may elucidate which ecological factors play a role in shaping perseverative and planning behaviors.

A curious incidental finding of the present study was that the one monkey who showed no hand preference in the familiarization phase did not demonstrate the hysteresis effect in the test phase. While our familiarization trials provide only a crude measure of handedness, this finding may have an interesting parallel in the human motor planning literature. Children who have weak or undeveloped lateralization, such as children with Developmental Coordination Disorder (DCD) and children with Specific Language Impairment (SLI), show a marked difference from typically developing children in performance on a reaching task similar to ours (Hill & Bishop, 1998). Thus, an interesting avenue for future research will be to explore further the relation between lateralization in nonhuman primates and motor planning, as well as other, abilities (see Vallortigara, Rogers, & Bisazza, 1999 for discussion on the emergence of laterality).

A final observation is that in humans, motor planning skills are thought to support higher-level cognitive functions, such as tool-use (e.g., Wolpert, Ghahramani, & Flanagan, 2001) and imitation (Mataric, 2002). While these cognitive domains may not be entirely exclusive to humans (e.g., Bard, 2007; Povinelli, 2000), the degree of complexity exhibited by humans appears to exceed that demonstrated by any other species. By adopting a comparative approach we can assess the degree to which precursors for these sophisticated human abilities are shared with nonhuman species. The findings reported here, in conjunction with our previous work on anticipatory motor effects (Weiss et al., 2007), suggest a lengthy evolutionary lineage for the cognitive abilities underlying the planning of motor behaviors. A future direction for this research will be to delineate whether there are differences evidenced across species in more complex instances of motor planning, as might be predicted by theories suggesting that human proficiency in tool use arose from enhanced motor planning abilities (e.g., Johnson-Frey, 2003).

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