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The interface between morphology and action planning: a comparison of two species of New World monkeys

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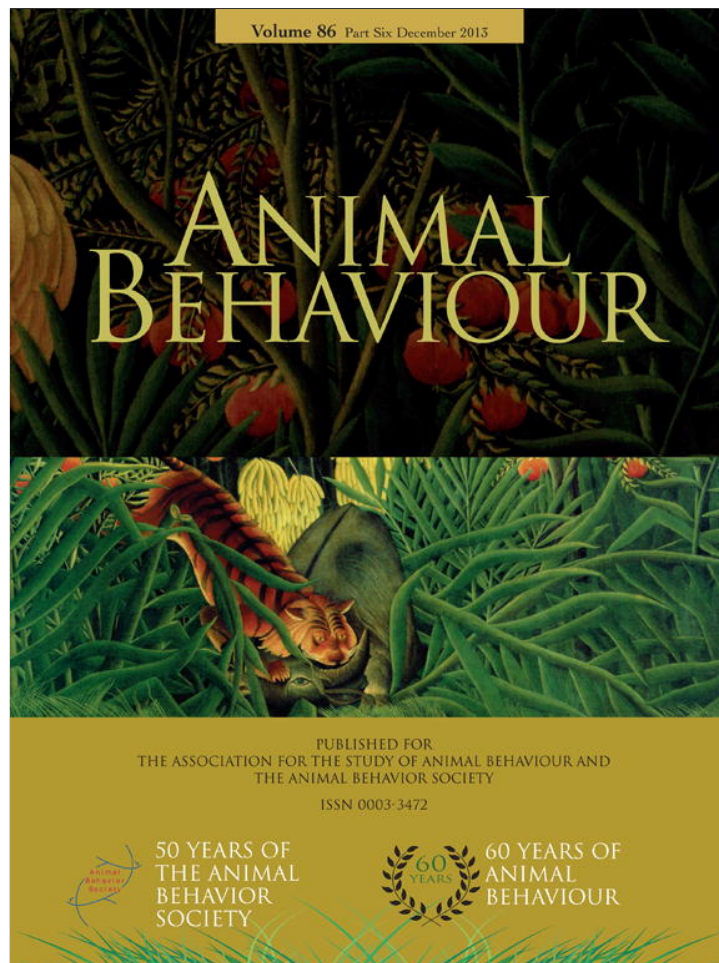
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The interface between morphology and action planning: a comparison of two species of New World monkeys



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Recent research with several species of nonhuman primates suggests sophisticated motor-planning abilities observed in human adults may be ubiquitous among primates. However, there is considerable variability in the extent to which these abilities are expressed across primate species. In the present experiment, we explore whether the variability in the expression of anticipatory motor-planning abilities may be attributed to cognitive differences (such as tool use abilities) or whether they may be due to the consequences of morphological differences (such as being able to deploy a precision grasp). We compared two species of New World monkeys that differ in their tool use abilities and manual dexterity: squirrel monkeys, *Saimiri sciureus* (less dexterous with little evidence for tool use) and tufted capuchins, *Sapajus apella* (more dexterous and known tool users). The monkeys were presented with baited cups in an untrained food extraction task. Consistent with the morphological constraint hypothesis, squirrel monkeys frequently showed second-order motor planning by inverting their grasp when picking up an inverted cup, while capuchins frequently deployed canonical upright grasping postures. Findings suggest that the lack of ability for precision grasping may elicit more consistent second-order motor planning, as the squirrel monkeys (and other species that have shown a high rate of second-order planning) have fewer means of compensating for inefficient initial postures. Thus, the interface between morphology and motor planning likely represents an important factor for understanding both the ontogenetic and phylogenetic origins of sophisticated motor-planning abilities.

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How individuals interact with objects in their environment can yield valuable insights into the psychological control of behaviour (Rosenbaum et al. 2012). In nonhuman primates (hereafter primates), much of the research in this domain has focused exclusively on tool use, an ability that is restricted to a handful of species (see Tomasello & Call 1997). However, seemingly mundane motor actions, such as reaching for and picking up an object, are often guided by an anticipation of upcoming postural and task demands (e.g. Rosenbaum et al. 1990). The paradigmatic example of this is the observation that when a person turns over an upside down glass to fill it with water, he or she typically reaches for the glass with a thumb-down grip that affords a more controlled subsequent posture when filling it (e.g. Rosenbaum et al. 1990). This grip choice at the beginning of the motor sequence reflects planning to accommodate the later postural demands entailed by filling the glass, arguably the element requiring the most precision. The

cognitive abilities required to achieve this type of anticipatory planning have been postulated to act as a scaffold for the emergence of more sophisticated cognitive abilities such as tool use (Johnson-Frey 2004) and longer-term planning (van Swieten et al. 2010; Keen 2011). Thus, understanding the ontogenetic and phylogenetic roots of motor planning may yield insights regarding the foundation of higher-order cognitive functioning.

In humans, the onset of motor planning is apparent during the early stages of infancy and then develops gradually throughout childhood. Very young infants are capable of adjusting their grip selection when reaching for objects of different sizes and orientations (e.g. Lockman et al. 1984; Newell et al. 1989). By around 10 months of age, infants are capable of more sophisticated motor planning, such as adjusting the speed of approach to grasping an object depending on precision requirements of the task (Claxton et al. 2003). From age 3 years onward, children continue to refine their motor-planning abilities. Remarkably, however, differences between children and adults in motor-planning behaviour persist even later in childhood. In particular, children appear delayed with respect to the capacity to alter their object manipulation not just on the basis of immediate task demands, but on the next task to be

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performed. This ability, termed second-order motor planning (Rosenbaum et al. 2012), is evident in the inverted glass example described above. In turning over the glass, a person initially adopts an awkward object grasp because it ensures a more comfortable posture following rotation. Surprisingly, the ability to engage in this type of second-order motor planning is not consistently demonstrated by children until after their 10th birthday (Adalbjornsson et al. 2008; Thibaut & Toussaint 2010; Weigelt & Schack 2010; Jongbloed-Pereboom et al. 2013; K. Wunsch, D. Weiss, T. Schack & M. Weigelt, unpublished data; reviewed in Rosenbaum et al. 2012).

In contrast to the abundant research conducted with humans on motor planning, far fewer studies have investigated similar effects in primates. Initial studies of motor planning in monkeys suggest that the most rudimentary abilities appear to be conserved across species. For example, both neurophysiological and behavioural measures have provided evidence that, like young human infants, primates are capable of adapting their grip selection based on the physical affordances of the objects to be grasped (e.g. Gardner et al. 1999). More recently, several studies have begun to explore whether primates show second-order anticipatory motor-planning abilities similar to those observed in human adults. In an initial study, Weiss et al. (2007) presented cottontop tamarins, *Saguinus oedipus*, a non-tool-using species of New World monkey, with a food reward placed inside of a cup suspended in either an upright or inverted orientation. When the cup was in the upright orientation, all of the monkeys took hold of it with a canonical thumb-up grasping posture to extract the food. However, when the cup was inverted, the tamarins behaved like human adults do, adopting an inverted thumb-down grasping posture. Thus, without any explicit training, the monkeys demonstrated significant motor-planning skills by inhibiting their natural grasping tendencies and adopting an unusual grasping posture to accommodate a subsequent task demand. This finding was later replicated with several species of lemurs, the most evolutionarily distant living primate relatives of humans and also non-tool-users (Chapman et al. 2010). Together, these findings suggest humankind's second-order motor-planning abilities may have lengthy evolutionary roots, evidenced even in non-tool-using species.

The ubiquity of motor planning abilities in primates has been further attested in Old World monkeys and great apes. Nelson et al. (2011) studied rhesus monkeys, *Macaca mulatta*, using a spoon-reaching task that was adapted from a study conducted with human infants (McCarty et al. 1999). The monkeys were presented with a spoon containing food resting on a stand that encouraged subjects to grasp the handle to initiate transport. Three out of seven monkeys alternated their reaching hand to bring the bowl of the spoon to their mouth efficiently (similar to the performance of 19-month-old human infants; McCarty et al. 1999). Another three monkeys changed their posture to accommodate an efficient grasp with the preferred hand on each trial. These strategies suggest that rhesus monkeys are capable of some degree of anticipatory motor planning. Chimpanzees, *Pan troglodytes*, the only great ape to be tested thus far, have also demonstrated second-order motor planning in the context of a tool use task (Frey & Povinelli 2012). In summary, there is converging evidence from several experiments employing different methodologies that sophisticated motor-planning abilities are shared among primates and were likely characteristic of the ancestral primate species.

Despite the growing evidence for anticipatory motor-planning abilities in primates, there is considerable variability in performance across species. While cottontop tamarins and lemurs were fairly uniform in showing second-order motor planning in the context of the cup task (all tamarins tested showed the effect, and 10 out of 14 lemurs tested in a less well-controlled environment showed the effect), rhesus monkeys did not consistently

demonstrate this effect when presented with an analogous cup task (only two out of nine subjects tested; E. L. Nelson, personal communication). Furthermore, very few chimpanzees studied by Frey & Povinelli (2012) adopted grasping postures that anticipated future task demands in the context of the initial self-directed task reported by the authors (bringing a tool baited with food on one side to their mouth). As noted above, human children up to 10 years of age are also variable in how they select their grasping postures in similar tasks (e.g. dowel transport; Rosenbaum et al. 1990), using a wide variety of strategies that do not seem to conform to the principle of second-order motor planning (e.g. Adalbjornsson et al. 2008).

From a cognitive perspective, this pattern of results is somewhat surprising. The species that more uniformly demonstrate second-order planning are thought to be non-tool-using species (Jolly 1964; Santos et al. 2005), whereas the species that are less consistent all share a capacity for tool use to varying degrees (e.g. Ottoni & Izar 2008; Sanz & Morgan 2010; Macellini et al. 2012). Despite the fact that sophisticated motor-planning abilities are not a sufficient condition for the emergence of tool use (Weiss et al. 2007; Chapman et al. 2010; Frey & Povinelli 2012), a priori one might expect that tool-using species would consistently demonstrate sophisticated motor-planning abilities when interacting with objects. From a morphological perspective, it is similarly counter-intuitive that the species characterized by limited manual dexterity appear to demonstrate second-order motor-planning abilities more consistently. Lemurs, and prosimians more generally, are unable to independently flex or extend individual digits, as they lack the capacity for hand-internal positioning (MacNeilage 1991). Thus, like tamarins, lemurs are restricted to using a whole hand 'power grip' (Napier 1960; MacNeilage 1991). By contrast, primate species (including human children) that are more variable in expressing motor-planning abilities are all capable of precision grips in which objects can be grasped between the finger (or fingers) and thumb (Napier 1960; Costello & Fragaszy 1988; Spinozzi et al. 2004).

We propose that this latter observation regarding morphological constraints may explain much of the variance in performance observed across experiments involving different primate species. In motor planning, the extended motor system is posited to predict sensory consequences prior to experiencing actual sensory feedback (Wolpert & Ghahramani 2000; Frey & Povinelli 2012). It follows that the costs for adopting a grasp that does not accommodate future postures may be greater for species with limited means of subsequent compensation (due to a lack of dexterity and limited grasping postures). Thus, forgoing second-order motor planning could result in unfavourable consequences with respect to effort or comfort (along the lines of Short & Cauraugh 1999; Frey & Povinelli 2012) relative to species possessing greater manual dexterity. Thus, species capable of exercising precision grips may be able to devise numerous strategies to compensate for adopting a suboptimal initial grasping posture. This assertion is consistent with the variable strategies used by chimpanzees and children in the context of self-directed motor-planning tasks (e.g. Frey & Povinelli 2012; M. G. Fischman, unpublished data).

Consequently, in the present study we sought to collect data on second-order motor planning from additional primate species. We presented a cup task to two primate species that differ in their manual dexterity. Squirrel monkeys, *Saimiri sciureus*, and tufted capuchin monkeys, *Sapajus apella*, are closely related New World monkeys belonging to the family *Cebidae*. In a study comparing prehensile grips in four New World monkey species, Welles (1976) reported that capuchins show greater control in gripping than squirrel monkeys. This report is consistent with a later study that observed capuchins using precision grips while grasping small objects, whereas squirrel monkeys did not (Costello & Fragaszy

1988). Relatedly, perhaps, capuchins are known to routinely use tools in the wild and in captivity (see [Fragaszy et al. 2004](#)), whereas, to the best of our knowledge, there is only scant evidence for tool use in squirrel monkeys (see [Buckmaster et al. 2012](#)). Given the aforementioned studies indicating that sophisticated motor-planning abilities are ubiquitous in primate species ([Weiss et al. 2007](#); [Chapman et al. 2010](#); [Frey & Povinelli 2012](#)), we anticipated that both capuchins and squirrel monkeys would be capable of demonstrating second-order motor planning by inverting their grasping posture when turning over an upside down cup to extract food from within. If it is the case that morphology constrains the expression of motor-planning abilities, then one might expect to observe the species with the more limited grasping abilities (squirrel monkeys) to show second-order motor planning more consistently relative to the species with greater degrees of freedom in grasping postures (capuchins). Conversely, if the cognitive-planning abilities indexed by second-order motor planning are related to those necessary for tool use ([Johnson-Frey 2004](#)), one might expect the capuchins to be more consistent in their use of inverted grasping postures than squirrel monkeys.

METHODS

Subjects and Housing

Six adult squirrel monkeys were tested (two males, four females). Those with known birth dates ranged in age from 14 to 19 years old. Two others were adults estimated to be 14 years old. The monkeys were born in captivity and housed together in a social group at Bucknell University in Lewisburg, Pennsylvania, U.S.A. since 2008. The monkeys were housed in an indoor/outdoor enclosure. Ten capuchin monkeys (three males, seven females) from a social group of 14 animals were also tested at Bucknell University. Nine were adults ranging in age from 4 to 17 years old and one was a 2-year-old juvenile. All monkeys were born in captivity and were either founding members of the colony established in 2000 or born into the group. The capuchin monkeys were housed in a large indoor enclosure. Both enclosures were outfitted with shelves, perches, climbing structures and swings to promote naturalistic movement. Enrichment devices were continually

available. Food and water were available ad libitum. All monkeys except one had participated in prior experiments that involved grasping or manipulation of objects, although none of the previous studies involved exposure to the objects or the apparatus used in this study.

Apparatus

An apparatus for suspending a small plastic cup was modelled after the one used by [Weiss et al. \(2007\)](#). As in the previous study, the apparatus was designed to hold a stemmed cup in either an upright or inverted position at the same height relative to a monkey and encourage subjects to extract the cup only by grabbing the stem. The squirrel monkey apparatus was constructed of wood ($20.3 \times 6.4 \times 1.3$ cm) and had a platform (5.1×5.1 cm) attached to its centre. On the platform, there were two horizontal metal rods (1.3 cm) protruding horizontally (see [Fig. 1a](#)). On the back of the apparatus, there were bolts that could be affixed to wire caging with wing nuts, thereby suspending the apparatus in either orientation. The cup used in the experiment was a transparent plastic champagne glass with the base removed and the handle extended with wood and tape (resulting in a cup that was 7.6 cm tall and 0.6 cm thick with a 5.1 cm diameter mouth; see [Fig. 1b](#)).

The capuchin apparatus was identical in almost all respects except that it was scaled to accommodate their larger body and hand size. The apparatus was $30.5 \times 12.7 \times 1.3$ cm with a 12.7×8.9 cm central platform. The metal horizontal bars were 5.1 cm long and 5.1 cm apart, protruding 6.4 cm from the apparatus. The top or bottom of the apparatus could be affixed to a metal shelf in the enclosure to provide both upright and inverted orientations for the cup. The transparent plastic cup used with the capuchins was 12.7 cm tall with a mouth that was 8.9 cm in diameter. The stem was 7.6 cm long and 1.3 cm thick (see [Fig. 1c](#)).

Procedure

Subjects were separated from their group for testing by moving them into a small transport box or a subcompartment of their enclosure dedicated for testing. Depending on the phase of testing (see below), animals were presented with the cup resting on a

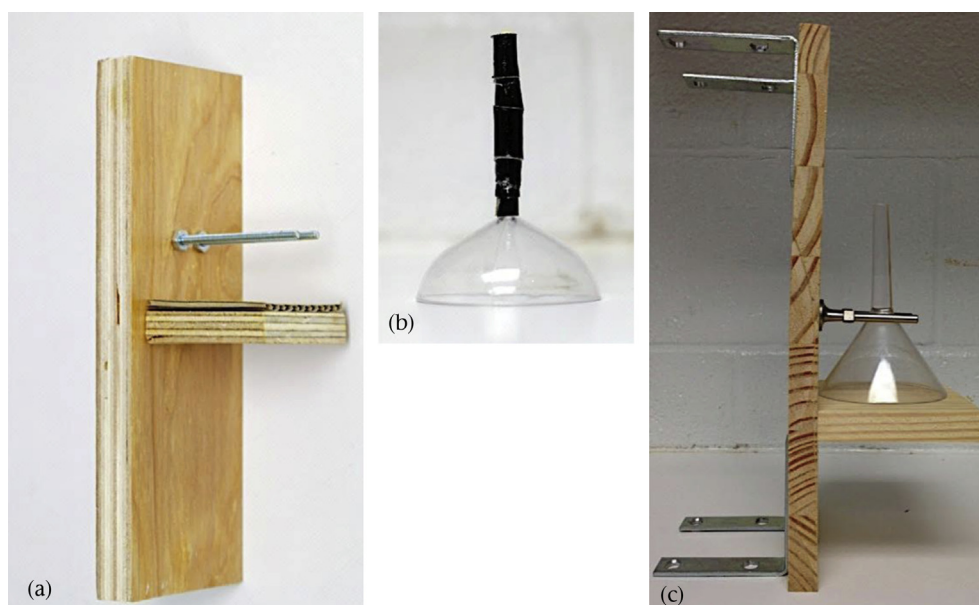


Figure 1. Squirrel monkey (a) apparatus and (b) cup. Capuchin (c) apparatus and cup.

horizontal surface or placed within the apparatus described above. Squirrel monkey cups were baited with half of a miniature marshmallow. Preliminary testing showed that, unlike the squirrel monkeys, the capuchins used their hands to extract a miniature marshmallow out of the cup without turning the cup upright. Therefore, capuchin cups were instead baited with a small amount of marshmallow fluff. This required the capuchins to rotate the cup to an upright position and use their mouth to extract the food reward from the cup, which was more analogous to the actions of the squirrel monkeys with the miniature marshmallows.

Familiarization

Since the monkeys had no experience acquiring food rewards from a transparent container, we familiarized them with the cups prior to testing (similar to Weiss et al. 2007). Each animal received four stages of familiarization in which they could grasp the cup in any manner they chose and remove the food affixed to the inside of the bowl. At the start of each familiarization trial, the experimenter waited until the subject was attending and then baited the cup. In the first stage of familiarization, the experimenter held the baited cup by the stem with the opening facing the subject. If the monkey grasped the cup, the experimenter let go and allowed the monkey to extract the food. In the second stage of familiarization, the experimenter placed the cup on its side on a horizontal surface inside the enclosure with the opening of the cup facing the subject. In the third step of familiarization, the cup was placed on its side facing 90° away from the monkey. In the fourth step of familiarization, the cup was placed on its side with the bowl facing 180° away from the monkey. If the marshmallow was extracted successfully, the animal was immediately advanced to the next step in familiarization. After all steps of familiarization were completed, subjects progressed to testing. If a monkey failed to respond at any time during familiarization or testing, the trial was terminated and that subject resumed at the same point in the sequence on the next testing day.

Testing

All monkeys underwent three test phases. The first test phase included two trials in which the cup was placed in an inverted orientation on a flat surface within the monkey's enclosure. The second test phase included two trials in which the cup was suspended in the upright position in the apparatus described above. In the third test phase, the apparatus was rotated 180° and monkeys received two trials with the cup supported in the inverted orientation by the platform of the apparatus. Experimenters noted the orientation of the monkey's hand (thumb-up or thumb-down) while grasping the stem in either the upright or inverted position. All trials were digitally filmed for offline analysis.

Supplemental trials

If a monkey did not show second-order motor planning in the first set of test trials, we provided 12 supplemental trials across 3 testing days to see whether they would begin to demonstrate the effect with increased exposure to the task. Monkeys received two upright and two inverted trials per day in a randomized order. We used a cup with the same dimensions as before, but tapered the tip of the stem such that it would fit into a hole in the shelving within the monkey's enclosure. This allowed the cup to stand upright on the testing surface without the use of the apparatus.

Ethical Note

Research adhered to the *Guide for the Care and Use of Laboratory Animals* (NRC 2011) and was approved by the Bucknell University IACUC (protocol PGJ-06). Animals participated voluntarily and did

not undergo any stress while they were separated for testing. Outside of the testing situation, the only stress the animals may have experienced was that typical of primates living in hierarchical social groups.

RESULTS

Squirrel Monkeys

All six subjects completed the four familiarization phases as well as the three test phases. The monkeys either used a one-handed grasp on the stem of the cup or a two-handed grasp on the bowl. The one-handed grasps on the stem consisted of either a thumb-up or thumb-down hand orientation, whereas the two-handed grasps on the bowl were always thumb-up. One subject never grasped the stem during any of the test phases (she used a two-handed grasp on the bowl in both upright and inverted trials) and she consistently appeared agitated when given the task. Since our behavioural measure involved grasping by the stem of the cup, we excluded her from the analysis. When the cup was inverted on a flat surface within the enclosure, four of the five remaining subjects used a thumb-down grasp on the first trial. On the second trial, all five monkeys used a thumb-down grasp. In summary, during the first two trials, nine out of 10 times, the monkeys used an inverted grasping posture. By contrast, when the cup was placed in an upright orientation within the apparatus, all monkeys adopted the canonical thumb-up grasping posture with either one or both hands for both trials (Fig. 2).

When the apparatus was turned over and the cup was inverted, all subjects but one managed to remove the cup by grasping the bowl with both hands; therefore, we did not analyse these data. The one monkey that did grasp the cup by its stem adopted a thumb-down grasping posture in both trials of this test phase.

Capuchin Monkeys

In the first test phase, when the cup was inverted on the shelf, all monkeys used a one-handed grasp on the stem in either an upright or inverted orientation. Three of the 10 monkeys adopted a thumb-down grasping posture on the stem in the first trial. In the second trial, again three out of 10 monkeys adopted the thumb-down grasping posture, although only two monkeys used a thumb-down grasp in both trials. Overall, in the first two inverted cup trials, the capuchin monkeys used an inverted grasp on six out of 20 total trials. In the second test phase, when the cup was upright in the apparatus, all 10 monkeys grasped the cup using the canonical thumb-up grasping posture with either one hand on the stem or both hands on the bowl in all trials (Fig. 3). In the third test phase in which the cup was inverted within the apparatus, none of the capuchins inverted their grasp as they removed the cup. Of the 20 trials, 17 were one-handed upright grasps on the stem and three were two-handed grasps on the bowl. Throughout all test phases, if the monkeys did not grasp the cup in the most efficient manner, they would correct that grip with the aid of the other hand at some point prior to acquiring the reward and dropping the cup.

Given that only four out of 10 capuchins ever inverted their grasping posture, we provided the capuchins with three supplemental days of testing consisting of two upright and two inverted trials each day. The capuchins inverted their grasp in 30% of the total trials on their first day of testing (trials 1 and 2). The capuchins inverted their grasps in 20%, 10% and 25% of the total trials on supplemental days 1, 2 and 3, respectively (trials 3–8; Fig. 4). Notably, the only individuals that adopted thumb-down grasping postures during the supplemental testing days were the ones that already did so in the initial trials. Therefore, we saw no evidence of

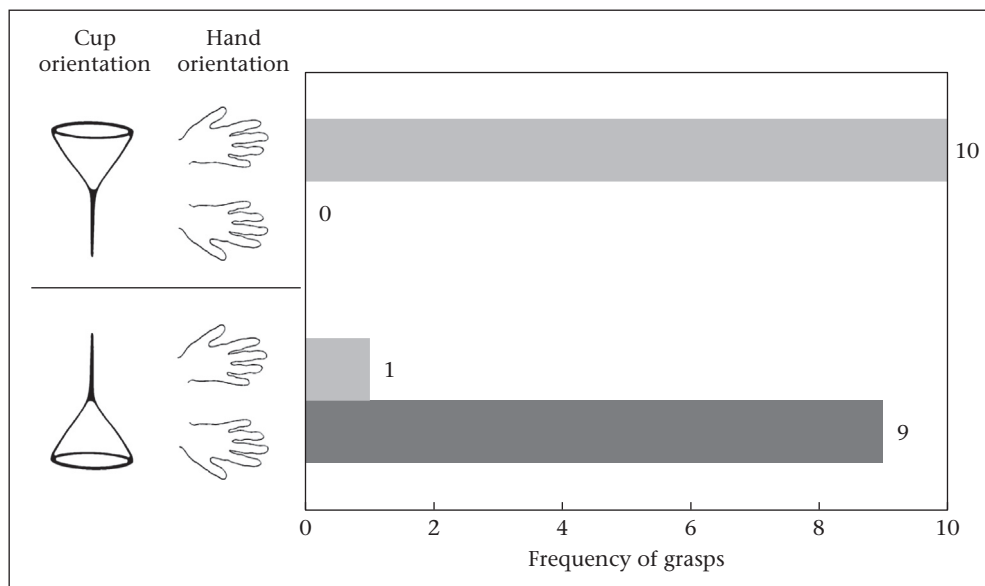


Figure 2. Frequencies of grasping orientations used by squirrel monkeys as a function of whether the cup was in an upright or inverted position. The graph shows the first two trials of each orientation pooled across the five monkeys.

individuals learning to use inverted grips over the course of the experiment.

Overall, six of the 10 capuchins never adopted a thumb-down grasping posture during the course of the study. Of the remaining four subjects, one monkey inverted her grasp on all eight inverted cup trials, one inverted her grasp four times, one inverted her grasp three times, and one inverted her grasp twice. In summary, the capuchins used a thumb-down grasp in only 21% of the total trials when the cup was inverted on the shelf.

We used a z test for proportions to determine whether the number of individuals showing second-order motor planning throughout all of the experiments was equivalent across species. To keep the comparison equivalent across species, we compared only the second test phase in which the subjects lifted the cup off of the

shelf (only the capuchins removed the inverted cup from the apparatus using the stem, and never with an inverted grasp). As noted earlier, all five squirrel monkeys showed the effect in at least one trial, whereas four out of 10 capuchins showed the effect at least once across all trials. This represented a significant difference between groups ($P = 0.026$).

We appeared to have found a species difference if there were no other underlying differences in our two subject populations that could account for differences in performance. Two possibilities were age, as young monkeys may have performed differently than older monkeys, and the amount of research experience the animals had manipulating or grasping objects. To assess this possibility, we explored the relationship between the grasp used in the inverted cup trials and the age and research experience of the animals

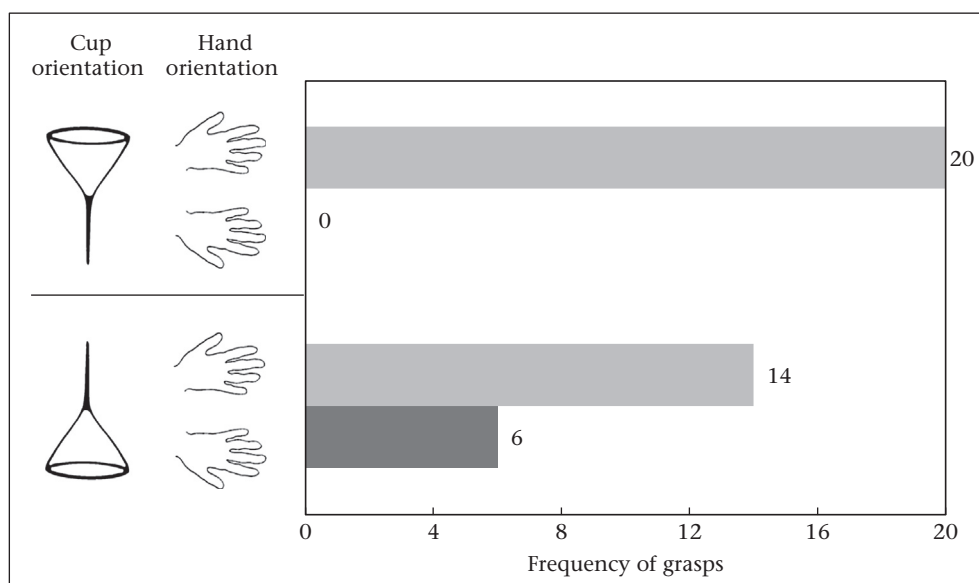


Figure 3. Frequencies of capuchin grasping orientations as a function of whether the cup was upright or inverted. Frequencies indicate the first two trials of each orientation pooled across the 10 monkeys.

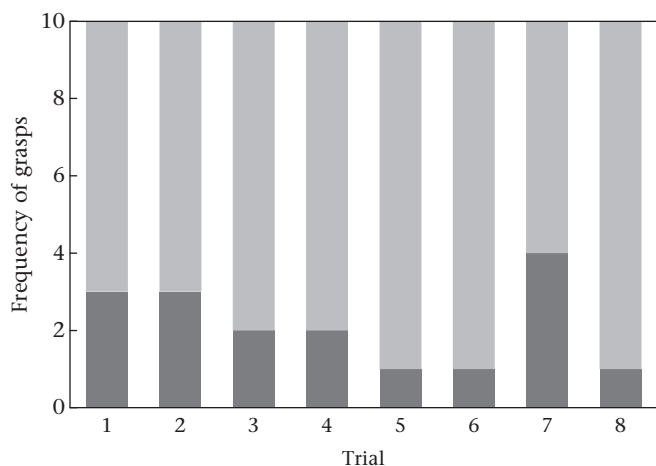


Figure 4. Grasping posture frequencies for the 10 capuchin monkeys for the inverted cup condition across all eight trials. ■: upright grasps; ■: inverted grasps.

(Table 1). As a group, the squirrel monkeys tended to be older than the capuchins, so age might have accounted for the difference if older monkeys tended to use a thumb-down grasp. However, the three oldest capuchins never used a thumb-down grasp and those capuchins that did were younger than the squirrel monkeys (Table 1). The capuchin monkeys tended to have more research experience involving grasping and manipulation, partly because they participated in tool use studies (hammer and insertion tools) of which the squirrel monkeys were incapable. Intuitively, one

Table 1
Sex and age of each subject indicating the outcome of the grasping task and experimental experience

Species	Subject	Sex	Age (years)*	Outcome†	Experience‡
Squirrel monkey	Km	F	19	+	B, G, R, T
	Le	M	15	+	B, T
	Dg	M	14	+	B
	Db	F	~14	+	B, I, R, T
	Hn	F	~14	+	B, R, T
Capuchin monkey	Dv	M	17	-	B, E, H, I, M, T
	Mt	M	17	-	B, H, I, M, T
	Nt	F	17	-	B, C, E, H, I, M, T
	De	F	11	+	B, C, E, H, I, M, T
	Nk	F	10	-	B, C, E, H, I, M, T
	Nw	F	9	+	B, C, E, H, I, M, T
	Sc	F	7	+	B, C, E, M
	Sd	F	6	+	B, C, E, M
	Nb	F	4	-	I
	Sm	M	2	-	-

* Birth dates of two squirrel monkeys were unknown, and ages are based on age estimates at the time of their acquisition in 2000.

† A plus sign indicates that the animal used a thumb-down grasp on at least one of the first two inverted cup trials; a minus sign indicates that they did not use a thumb-down grasp in either trial.

‡ Extent to which subjects previously participated in tasks involving manipulation or grasping: **B** (bimanual task): animal receives a tube it can grasp in one hand and remove food from with the other hand; **C** (cup rotation): involves horizontally rotating a cup attached to a swivel to remove a reward from an opening that originally faced away from the animal; **E** (exchange of token): animal grasps a metal object from the experimenter and exchanges it for food; **G** (grasping task): animal reaches around an opening in one side of a box to obtain a reward; **H** (hammer tool): animal grasps a stone and uses it to crack open a walnut; **I** (insertion tool): animal grasps a stick and inserts it into a tube to push out a reward; **M** (moving platform): animal grasps vertical handles on a circular horizontal platform and pushes the handle to rotate the platform and obtain rewards; **R** (rake tool): animal grasps a stick with a rake-like end and pulls on the stick to receive a reward placed inside the rake; **T** (touchscreen): involves a variety of cognitive tests (e.g. reversal learning) requiring the animal to reach through its caging and manipulate a touchscreen.

might predict that more research involving manipulating or grasping would promote more thumb-down grasps perhaps due to extra experience. Indeed, two of the capuchin monkeys that used a thumb-down grasp (De and Nw) did have the maximum amount of research experience (Table 1). However, two others (Nt and Nk) had the same amount of research experience and did not use a thumb-down grasp. Furthermore, the squirrel monkeys generally tended to have less research experience and all of them used a thumb-down grasp. Taken together, differences in age and/or research experience between the species did not appear to be systematically related to use of an inverted grasp.

DISCUSSION

We sought to determine whether capuchin monkeys and squirrel monkeys would show second-order motor planning as has been demonstrated in tamarin monkeys (Weiss et al. 2007), lemurs (Chapman et al. 2010) and chimpanzees (Frey & Povinelli 2012). Furthermore, we were interested in determining whether the rate at which second-order motor planning is expressed varies across species that differ in cognitive abilities and manual dexterity. Consequently, we presented the monkeys with the cup task used in previous experiments (Weiss et al. 2007; Chapman et al. 2010). We found that, as predicted, both species were capable of second-order motor planning, as individuals from each species inverted their grasping posture to turn over a plastic cup and extract food from inside the bowl. This pattern of results provides further evidence that second-order motor planning may be ubiquitous in primates, and perhaps characteristic of the ancestral primate species (Chapman et al. 2010). Interestingly, this effect was evidenced in all squirrel monkeys tested (five), but in only four of 10 capuchin monkeys (some sparingly) tested, despite many opportunities to do so. Furthermore, the overall rate of inverting the grasping posture for the capuchin monkeys was quite low even when provided with additional trials. These findings are consistent with the hypothesis that primates that are incapable of precision grasps and that seem to have fewer degrees of freedom with respect to manual dexterity appear to demonstrate second-order motor-planning abilities more consistently.

As noted above, while the evidence thus far suggests sophisticated motor planning is ubiquitous in primates, there appears to be considerable variability in the rate of expression across different species and across development in humans. Interestingly, with the exception of human adults, individuals who clearly express advanced prospective planning abilities in the context of tool use tend to be more variable in the extent to which they consistently show second-order motor planning in experimental tasks. Our findings with squirrel monkeys and capuchins mirror this pattern. Less than half of the capuchins in our study inverted their grasp, most at very low rates. Capuchins are known to plan prospectively in the context of tool use (Visalberghi et al. 2009; Fragaszy et al. 2010a, b; Liu et al. 2011) and are capable of precision grasping (Costello & Fragaszy 1988). Conversely, the squirrel monkeys behaved more like the tamarin monkeys, in that all of the monkeys tested demonstrated the effect. Like tamarins, squirrel monkeys have limited manual dexterity (Costello & Fragaszy 1988) and, to the best of our knowledge, there is only one account of squirrel monkeys using tools (Buckmaster et al. 2012). This pattern of findings can be better understood by means of a feed-forward internal model of the extended motor system (such as Wolpert et al. 1998; Frey & Povinelli 2012). If the task of the extended motor system is to predict sensory outcomes prior to execution (see Frey & Povinelli 2012), then it stands to reason that such computations may be intimately tied to the morphological constraints of the body. Thus, it is likely that the consequences for movements that

are inconsistent with second-order motor planning differ across species that vary in their degree of manual dexterity. For example, the costs for a chimpanzee to adopt a seemingly awkward final position while transporting food from the end of a dowel to its mouth may be insufficient to elicit modification at the outset of a motor sequence (Frey & Povinelli 2012). Conversely, for a species with more limiting morphological constraints (with respect to grasping or overall flexibility), the costs of assuming analogous postures may be much higher. This could result in more frequent anticipatory modifications to motor sequences to better accommodate the later postural demands.

Interestingly, the apparatus modelled from the previous tamarin study (Weiss et al. 2007) was not effective for the squirrel monkeys and yielded a different pattern of results for the capuchin monkeys. The squirrel monkeys managed to extract the cup by grasping its base and therefore the data could not be analysed (as the dependent measure required subjects to grasp the stem). The capuchins, however, did use the stem but did not invert their hands to extract the cup. In the tamarin study, extracting the cup from the apparatus resulted in greater uniformity in second-order motor planning relative to when subjects picked up the cup from the floor. For the capuchins, the opposite was true, as the only demonstrations of second-order motor planning were observed in the context of the less constrained task. These results further underscore the fact that capuchins appear to show less second-order motor planning in the cup task than other New World monkey species that have been tested.

Our findings suggest several future avenues for research. One issue that has yet to be addressed is the source of individual variation in second-order motor-planning abilities. For example, over half of the capuchins never inverted their grasp to extract food from the cup. It would be natural to wonder whether they behave differently in other contexts involving planning or object manipulations (such as tool use). Likewise, it would be of interest to determine whether the expression of anticipatory motor-planning abilities is correlated with other cognitive abilities such as inhibitory control (which may be necessary to inhibit the canonical grasp and adopt an usual grasping posture) or foresight (see Weiss et al. 2012). Given that there is individual variability in performance across many species, understanding the source of variation may lead to a better appreciation of how motor planning interfaces with other higher-order cognitive abilities such as long-term planning and tool use. It would also be of interest to explore whether capuchins, like the chimpanzees tested by Frey & Povinelli (2012), would show second-order motor planning more consistently when the costs of the task are high. For example, in humans, the precision requirements of the task are important for the expression of end-state comfort (e.g. Rosenbaum et al. 1996). Correspondingly, when the precision requirements for the task are higher, capuchins might show second-order motor planning with greater regularity.

A final consideration is that our results suggest a future direction for research to resolve the surprising developmental finding that human children up to about age 10 years do not appear to engage consistently in second-order motor planning to the same extent as human adults (Adalbjornsson et al. 2008; Thibaut & Toussaint 2010; Weigelt & Schack 2010; Jongbloed-Pereboom et al. 2013; K. Wunsch, D. Weiss, T. Schack & M. Weigelt, unpublished data; reviewed in Rosenbaum et al. 2012). It is possible that, similar to primate species that are capable of precision grasping, human children do not frequently invert their grasping posture when turning over a glass because they can easily compensate later in the motor sequence. This notion is consistent with the reports that the children tend to adopt a variety of other strategies for engaging in this task (e.g. Adalbjornsson et al. 2008; K. Wunsch, D. Weiss, T. Schack & M. Weigelt, unpublished data). Notably, over the course of

development, children become more likely to use second-order motor planning when reaching for objects, although adult-like consistency is not evident even in children up to 10 years of age (e.g. Thibaut & Toussaint 2010; Weigelt & Schack 2010; Jongbloed-Pereboom et al. 2013; K. Wunsch, D. Weiss, T. Schack & M. Weigelt, unpublished data). It is currently unknown why the developmental trajectory for this ability in humans is so protracted. Our findings suggest that it could be related to the physical changes associated with maturation, as younger children may be more flexible than older children and adults. Alternatively, it could reflect changes in cognitive abilities or sensory motor skills, as suggested elsewhere (e.g. Wunsch et al., in press). One experiment that may help adjudicate between these accounts is to impose limitations to the degrees of freedom in grasping (such as by having subjects grasp while wearing a mitten) and determine whether that elicits an increase in second-order motor planning (as might be predicted by the morphological constraint hypothesis). Note also that adult humans tend to engage consistently in second-order motor planning when grasping objects (reviewed in Rosenbaum et al. 2012) despite having sufficient degrees of freedom to compensate for suboptimal initial grasps (in particular, relative to other primate species reviewed here). It is possible that the optimization of motor actions in adults emerges not only due to changes in planning abilities, but rather as a consequence of a constellation of factors, including experience (e.g. weighted integration of multiple biases (WIMB) model; Herbolt & Butz 2012). Consequently, future research with both humans and nonhumans will need to address more precisely the underlying representations for anticipatory motor-planning abilities and the causal factors that lead to their emergence at both the individual and group level.

In summary, our study has provided further evidence that the sophisticated motor-planning abilities observed in humans are ubiquitous in primates and share a lengthy evolutionary history. Given the current debate surrounding the idea that cognition may also be rooted in the perceptual and motor systems (e.g. Adams 2010; Shapiro 2011; Letheby 2012), it is notable that the pattern of results reported here offers a different type of connection between the body and mind. Our findings, in concert with other motor-planning studies, suggest that the expression of motor-planning capabilities may be impacted by the constraints imposed by morphology, as the motor system may compute the consequences for actions in relation to the limits imposed by different biological designs.

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