



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

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