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REVIEW

USING THE PRECISION OF THE PRIMATE TO STUDY THE ORIGINS OF MOVEMENT VARIABILITY

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Abstract—The study of motor control has long concerned itself with the origins of movement variability. Indeed, a common goal of many computational models of motor control is to predict the empirically observed patterns of movement variability. Competing models thus attempt to capture how the brain constrains variability that is detrimental and/or generates variability that might be beneficial. As humans, it is our own motor performance that interests us most we accept our variability as an essential part of being human, yet we are often frustrated when we cannot precisely repeat a desired movement. While movement variability is often productively studied in humans, uncovering its neural origins requires animal models. Below we describe recent research in which we were able to determine an important source of movement variability using a non-human primate model: the rhesus macaque. The macaque, much like the human, can produce flexible yet highly precise behavior. For this reason, among others, the macaque was an ideal model for the study of movement variability.

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Key words: motor cortex, movement variability, motor noise, movement planning, motor preparation, motor control.

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INTRODUCTION

A central goal of systems neuroscience is to understand how the brain controls movement. This goal is pursued for two reasons. First, disorders of motor control are common and frequently devastating. Second, motor control is a fundamental and challenging computational problem. Movement seems effortless because our brains have evolved to be incredibly good at it. A few moments spent watching videos of humanoid robots will quickly convince one that the problem of motor control is far from understood or solved. As a field, we therefore wish to link our increasing knowledge of the biology of the motor system with computational theories that tell us how motor control could or should work.

Biological investigations hinge critically on a set of useful animal models, while the development of theory has depended on experimental results from both animal models and in large part from the study of human performance. In studies of both animals and humans, it is common for analyses and theories to consider a central and inescapable feature of movement: its variability (Soechting and Flanders, 1989; McIntyre et al., 1997; Messier and Kalaska, 1999; Todorov and Jordan, 2002; Kawato, 2004; Todorov, 2004; van Beers et al., 2004; Sober and Sabes, 2005; Medina and Lisberger, 2007; Schoppik et al., 2008; Joshua and Lisberger, 2014). Repeated attempts to make the same movement – a free throw, a tennis serve, a dart throw – inevitably produce variable results, often to our frustration. We are sufficiently familiar with such variability that it is easy to forget that its source is a mystery. Consider that a simple mechanical device, once calibrated, could make thousands of sequential free throws in basketball or thousands of successful drives off the golf tee. Such a device would lack any flexibility – move it two feet and it would never succeed again – but it would be very reliable. Why are we not like that? Are muscles unreliable effectors? Are the neurons that drive them noisy? Do we in some way trade flexibility for precision? Certainly movement variability can be benign – reflecting the fact

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Abbreviation: EMG, electromyography.

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that many solutions exist – or beneficial – allowing exploration that improves future performance. Yet even in highly practiced tasks some variability remains. Such variability has the potential to be highly detrimental in high-stakes situations involving fighting, fleeing or hunting.

Theories of motor control place a premium on understanding movement variability for two further reasons. First, the pattern of variability and/or errors that is produced by a system may be informative regarding the computations and representations that lie within that system (Soechting and Flanders, 1989; McIntyre et al., 2000). Second, the computations that should be performed – i.e., the computations that allow the best possible performance – depend on the sources of noise and variability (Wolpert et al., 1995; Harris and Wolpert, 1998; Hamilton and Wolpert, 2002; Todorov and Jordan, 2002; Osu et al., 2004; Scott, 2004; Todorov, 2004; Haruno and Wolpert, 2005; Makin et al., 2013). For example, one's theories would be pulled one way if one discovered that variable dart throwing results from an inability to perfectly judge distance using vision. One's theories would be pulled another way if one discovered that variable dart throwing results from unreliable transmitter release at the neuromuscular junction. Computational theories of motor control are thus intertwined with measurements and hypotheses regarding the sources of behavioral variability.

While behavioral variability may often allow useful exploration, let us for the moment consider variability that is present even when one wishes it weren't, and that limits accuracy and success. Such variability has three proposed physiological sources. First, behavioral variability may result from sensory variability (Sober and Sabes, 2003; Kording and Wolpert, 2004; Osborne et al., 2005; Yang et al., 2012). Second, behavioral variability may result from 'motor noise': imperfect muscles driven by a finite number of noisy neurons (Jones et al., 2002; Hamilton et al., 2004; van Beers et al., 2004). Third, the challenging nature of the underlying computations may result in variable answers (Beck et al., 2012). Put another way, even with the best of information you may not be able to consistently prepare exactly the right 'motor program', simply because the required computations are difficult (Churchland et al., 2006c; Churchland and Shenoy, 2007; van Beers, 2009). All three sources of variability are likely to be present, but it has been unclear which is dominant. Early behavioral studies (e.g., Messier and Kalaska, 1999) assumed that considerable variability was present during motor preparation (also referred to as 'motor programing' or low-level 'movement planning'). Yet computational models frequently omit motor preparation as a source, and focus instead on optimal strategies for combatting sensory and muscle noise. In the experiment reviewed below (Churchland et al., 2006a) we wished to determine whether motor preparation was indeed a substantial source of variability and thus an important limitation on behavioral accuracy.

Our experiment was performed using the rhesus macaque. The macaque possesses a motor system anatomically similar to humans, including direct projections from the motor cortex onto spinal motor neurons (e.g., Rathelot and Strick, 2006; Lemon, 2008). Because our goal is to understand the human motor system, the anatomical similarity of the macaque is presumed to be an advantage: the computational principles at play in the motor cortices are probably similar in the two species. In the present case the use of a primate was critical, because we wished to interface with a large and successful computational literature based on human performance, the majority of which employed reaching tasks. Reaching is something that monkeys also do naturally and skillfully, allowing for a meaningful comparison with human behavior. Of course, the macaque model has some practical shortcomings: in particular the absence of a large toolbox for manipulating circuitry using genetic tools. Despite this, the macaque is a wonderful experimental model that possesses a large set of practical advantages, above and beyond the anatomical similarity to humans. Below we describe how a number of these practical advantages were critical to the experiment reviewed below.

EXPERIMENTAL DESIGN

Our experimental strategy was simple: we would record 'preparatory' neural activity before each movement began, and ask whether variations in preparatory activity predicted variations in the upcoming movement. To pursue this strategy we needed a task with three key features. First, the task had to evoke behavior that was reliable and precise, to insure that we were not simply studying behavioral sloppiness. Second, the task needed to still be sufficiently challenging, such that there was meaningful and quantifiable behavioral variability. Finally, the task needed to allow neural activity to be measured at a time when motor preparation was underway, but before movement had actually begun. To answer our central question, we needed to be able to analyze neural signals related to motor preparation, disentangled from neural signals related to movement execution.

To these ends, we employed an elaboration upon the 'delayed reach task.' The delayed reach task has been employed for nearly forty years (Tanji and Evarts, 1976; Weinrich et al., 1984; Godschalk et al., 1985; Crammond and Kalaska, 1989, 2000; Riehle and Requin, 1989; Kurata, 1993; Snyder et al., 1997; Cisek and Kalaska, 2002; Churchland et al., 2010a; Kaufman et al., 2014) because it allows the measurement of neural events that occur during motor preparation. Fig. 1 illustrates the task and behavior. Monkeys reached to visual targets for juice reward. Each trial began with the appearance of a central spot. The monkey touched and held that spot until a target appeared. Target appearance defined the beginning of a variable (400–800 ms) delay period. At the end of the delay period, a go cue indicated that a reach could now be made to the target. To succeed, the ensuing reach had to land on the target, and had to have a peak speed within an experimenter-imposed window (Fig. 1D). This window depended on target color: green targets required reasonably fast reaches and red targets