

A Central Source of Movement Variability

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Summary

Movements are universally, sometimes frustratingly, variable. When such variability causes error, we typically assume that something went wrong *during* the movement. The same assumption is made by recent and influential models of motor control. These posit that the principal limit on repeatable performance is neuromuscular noise that corrupts movement as it occurs. An alternative hypothesis is that movement variability arises before movements begin, during motor preparation. We examined this possibility directly by recording the preparatory activity of single cortical neurons during a highly practiced reach task. Small variations in preparatory neural activity were predictive of small variations in the upcoming reach. Effect magnitudes were such that at least half of the observed movement variability likely had its source during motor preparation. Thus, even for a highly practiced task, the ability to repeatedly plan the same movement limits our ability to repeatedly execute the same movement.

Introduction

In 1990, Larry Bird of America's Boston Celtics basketball team made 71 consecutive free throws, or foul shots, across almost two month's worth of games. While this is a remarkable feat, one cannot help but wonder: why did he miss the 72nd? Why could he not simply do what he had done the last 71 times? As humans, we take for granted that our behavior is variable, and that repeated attempts will have variable results, but what is the source of this variability? When we err, we often assume that something went wrong *during* the movement. But might variability also arise during motor preparation, well before the first muscle contracts? Answering such questions is critical to the study of motor control. Not only is variability a part of the behavior that must be explained, but hypotheses regarding motor-control strategies are fundamentally linked to hypotheses regarding the noise those strategies combat. Furthermore, different hypotheses can make similar predictions regarding mean behavior, such that deciding between candidate models requires examining movement variability (Kawato, 2004; Todorov, 2004; Todorov and Jordan, 2002). For these reasons, a body of recent work has suggested possible noise sources and has proposed control strategies that

could limit their harm (Harris and Wolpert, 1998; Haruno and Wolpert, 2005; Todorov, 2002; Todorov and Jordan, 2002; van Beers et al., 2004).

Due to their elegance and explanatory power, these models have been very influential. Though they differ in some important ways, all assume that movement variability is generated “online,” during movement. Typically, it is assumed that the relevant noise stems from the periphery, especially at the neuromuscular junction. Recent studies (Hamilton et al., 2004; Jones et al., 2002; Osu et al., 2004; Sosnoff et al., 2005) have sought to characterize online neuromuscular noise precisely because it is proposed to be the key factor limiting performance. Yet there is little direct evidence that online noise is the main source of variability or the principal limit on accuracy. Indeed, some recent observations support the opposite conclusion. Osu et al. (2004) found that electromyographic (EMG) variability was higher, yet movements *less* variable, when cocontraction was increased. van Beers et al. (2004) found that variability in reach velocity was *not* accounted for by standard online noise models. This led them to propose more elaborate forms of online noise, but a more straightforward explanation is that considerable variability arises during motor preparation. Variability in motor preparation (and/or related sensorimotor transformations) has been previously considered important (Gordon et al., 1994), particularly when a target must be remembered (McIntyre et al., 1997; Messier and Kalaska, 1999; Soechting and Flanders, 1989). On the other hand, it has been recently argued that preparatory variability makes a negligible contribution to straightforward tasks using visible targets (van Beers et al., 2004).

The current study seeks to address this question: for a straightforward and well-practiced task, does motor preparation make a sizeable contribution to the observed behavioral variability? Comparisons of behavior with model predictions must contend with interpretational difficulties. Thus, we chose to address the issue directly by recording from neurons in dorsal premotor cortex (PMd) and primary motor cortex (M1) as monkeys performed a delayed-reach task. We compared trial-by-trial fluctuations in delay-period “preparatory” activity (well before reach onset) with trial-by-trial fluctuations in the subsequent reach velocity. We chose this comparison because (1) velocity variability is a ubiquitous feature of reaching, and (2) most delay-active neurons in PMd/M1 are strongly modulated by instructed-speed (Churchland et al., 2006a; Cisek, 2006). That modulation suggests that preparatory activity might also relate to the *natural* fluctuations in velocity. Of course, this is not guaranteed: trial-by-trial preparatory variability might be minimal, and contribute only a small proportion of the eventual behavioral variability. But we did in fact find that velocity variability was predicted by variability in the preceding delay-period activity. The sign and steepness of the relationship scaled, on average, with the sign and intensity of the tuning for instructed-speed. From the strength of this scaling, we estimate that at least half the observed movement variability had its

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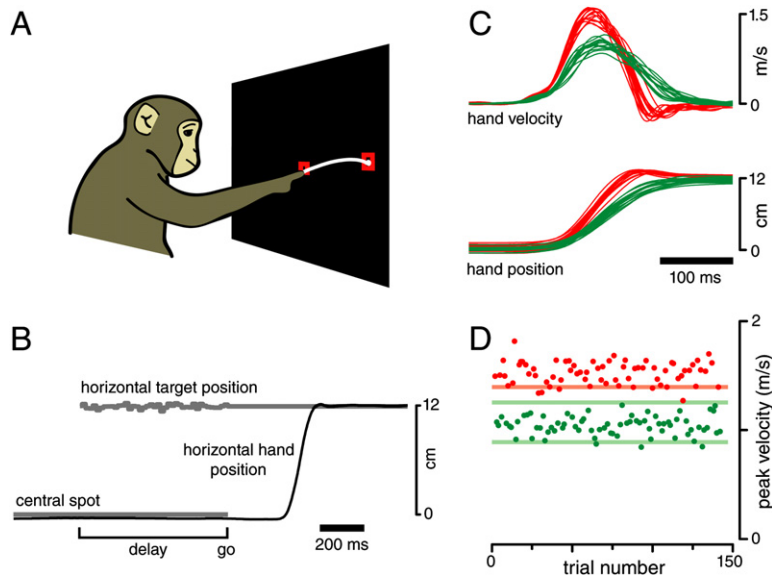


Figure 1. Illustration of the Basic Task

(A) Movements began and ended with the hand touching the display. The hand was a few mm from the screen while in flight. The white trace shows the reach trajectory for one trial.

(B) Timeline of the task and behavior for the same trial. The target jittered slightly (2 mm standard deviation) upon first appearing, and continued to do so throughout the delay period. The cessation of jitter provided the go cue, at which time the central spot was also extinguished. The plot ends at the time the reward was delivered.

(C) Horizontal hand velocity and position for instructed-slow (green) and -fast (red) reaches (0° , 12 cm distant target). During this session, the monkey performed ~ 70 trials for each instructed-speed at this target location. Data in this panel are plotted for every 5th trial, with one trace per trial.

(D) Peak hand velocity is plotted as a function of trial number for every reach to that target location.

source in movement preparation rather than in online noise. Thus, variability in motor preparation is a major source of movement variability, even for a well-practiced and straightforward task.

Results

Behavior and Example Responses

Two rhesus monkeys performed a delayed-reach task (Figure 1A). Figure 1B illustrates the flow of a single trial: a delay period separates target appearance from the go cue, after which a reach is made. Monkeys were trained to reach at different speeds (“instructed-fast” or “instructed-slow”) depending on target color (red or green, respectively). Figure 1C plots hand velocity and position for reaches to a rightwards target (12 cm distance, ~ 15 reaches/instructed-speed). As desired, peak velocities were higher for red targets, and lower (though still fairly rapid) for green targets. Figure 1D plots the peak velocity for all reaches to that target location for that day. Lines give the criteria for success. Performance was generally excellent, particularly as the two instructed-speeds were randomly interleaved (humans typically require training to achieve similar performance). Nevertheless, there was still measurable variability in peak velocity *within* each category. Such variability is a normal, presumably endemic feature of reaching. It has been explicitly noted previously (e.g., Messier and Kalaska, 1999; van Beers et al., 2004) and is also reflected in the universally observed variability of movement duration (e.g., Crammond and Kalaska, 2000; Hoehnerman and Wise, 1991). Similar levels of velocity variability are seen in motivated human subjects. The central question of this study is whether this velocity variability can be predicted by preparatory neural activity recorded during the delay period, well before movement initiation.

We recorded, from PMd and M1, the responses of 136 neurons with tuned delay-period activity. We concentrate exclusively on the response during the delay period, which is known to relate to target direction and distance (Godschalk et al., 1985; Kurata, 1989; Messier

and Kalaska, 2000; Riehle and Requin, 1989; Tanji and Evarts, 1976; Weinrich and Wise, 1982; Weinrich et al., 1984). Delay-period activity also depends upon the instructed-speed (Churchland et al., 2006a). Figure 2A shows example responses from an “instructed-fast preferring” neuron, tested at five target distances in its preferred direction. This neuron responds during the delay period and ceases to respond around movement onset. Delay-period activity is higher for instructed-fast reaches than for instructed-slow reaches (red versus green traces, respectively). The central question is whether, for trials of a given instructed-speed, higher peak velocities are preceded by higher delay-period firing rates. To illustrate the exploration of this issue, Figure 2B plots the occurrence of action potentials for 22 instructed-fast trials, all employing the 6 cm distant target. Reach velocity (black traces) is plotted on top of the mean reach velocity across all trials (gray traces). For presentation, trials are ordered from the fastest to the slowest. If velocity variability results entirely from online noise (e.g., in the muscles) then it should not correlate with the spike rate during the preceding delay-period. However, if velocity variability is partly due to preparatory variability, then such a correlation should exist. By visual inspection alone, it is difficult to determine whether a correlation exists. The natural variability in peak velocity is small and the spiking of the neuron is, like that of most cortical neurons, irregular even within a trial. We discuss below how these features impact our analyses and how statistical power can be improved by the appropriate pooling of data.

Measuring Trial-by-Trial Relationships

Figure 3A illustrates the range of possible effects. Each dot corresponds to one hypothetical trial and plots the delay-period neural response versus peak velocity for instructed-slow (green) and -fast (red) trials. If the neural response can be measured exactly, and if it precisely indicates the “planned” reach speed, then expectations are clear (top panels). Presuming movement variability is not due to preparatory variability (left panel), there should be no preparatory variability, and thus no

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