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Trial-by-trial movement variability is predicted by recorded plan activity.

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Variability is endemic to motor performance, but its cause is not well understood. Recent work has proposed that variability is due principally to online noise, most likely arising at the periphery (e.g. Todorov and Jordan 2002, van Beers et al. 2004). The presence of peripheral motor noise is well established (e.g. Jones et al. 2002), and models based on the assumption of such noise (Harris and Wolpert 1998, Todorov and Jordan 2002) elegantly capture many fundamental aspects of behavior. Still, there is little direct evidence that peripheral noise is the primary generator of behavioral variability. To explore the possibility that behavioral variability is due in part to offline sources, we recorded spiking activity from dorsal pre-motor cortex (PMd) using an instructed-delay task. A rhesus macaque was trained to make brisk ($< \sim 250$ ms) reaching movements to radially arranged targets presented on a fronto-parallel screen. The monkey was trained to reach at two different speeds depending on the color of the target. We have previously reported that the delay-period firing rate of many PMd neurons varies with target color/reach speed (Churchland and Shenoy 2003). Behaviorally, distributions of peak reach speed were mostly separate for the two target colors, but there was still considerable variability within the responses to a given target color. For a typical experiment, 120 mm reaches to green and red targets had mean peak speeds of 936 mm/s and 1424 mm/s, with standard deviations of 75 mm/s and 119 mm/s. This provides an opportunity to ask whether, on a trial-by-trial basis, behavioral variability is predicted by delay-period neural variability. Pooling responses for a given target-color, we regressed firing rate against peak reach speed. Of 51 neurons recorded, 24 showed a statistically significant ($p < 0.05$) trial-by-trial relationship between firing rate and speed. Thus, behavioral variability was at least partially determined before the movement began, and cannot have been due solely to online or peripheral noise sources. We attempted to determine what proportion of behavioral variability could be accounted for by the delay-period variability. We compared the slope (spikes/s versus peak speed) of the trial-by-trial regressions with the slope expected given the mean response to each of the two target colors. For some neurons the ratio of these slopes was near one, suggesting that variability in peak speed is due almost entirely to delay-period variability. However, many neurons showed little or no correlation, suggesting the opposite. Simple simulations demonstrate that such results are difficult to interpret without a better understanding of how delay-period activity codes movement. We also attempted to determine whether endpoint variability was related to delay-period variability. However, endpoint variability was so small, relative to the tunings of PMd neurons, that it was statistically impossible to make any statement. In summary, our results demonstrate that variability in peak reach speed is due in part to variability present before the movement begins. They suggest that this contribution is significant, but do little to quantify the relative contributions of online and offline sources of variability.