

Movement variability is determined by the timing of the preceding movement

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Motor variability is ubiquitous, and it puts a limit on the precision of our actions. It is widely believed that movement variability is primarily due to the stochastic neural processing underlying movement execution (Churchland et al., *Neuron*, 2006; Chaisanguanthum et al., *J Neurosci*, 2014; Haar et al., *J Neurosci*, 2017). There is even some intriguing evidence that neural variability underlying motor output can be controlled, as in birdsong learning a specific brain region (LMAN) is thought to actively inject exploratory variability into motor output (Tumer and Brainard., *Nature*, 2007). But, in general, we have little understanding of how and the degree to which this variability can be regulated.

Here we identify and characterize a novel mechanism for the control of motor variability, inspired by recent work showing that variability of neural responses are reduced (“quenched”) by the presentation stimuli that can drive the neurons of interest in a diverse set of sensory and motor brain areas – see Fig 1 (Churchland et al., *J Neurosci*, 2006; Churchland et al., *Nat Neurosci*, 2010). In motor areas, the quenching of neural variability occurs during the planning and execution of movement. Here we suggest that this variability reduction enables increases in precision for the planning and execution of movements that occur soon after preceding movements.

Since the duration of variability quenching is not known, we began by examining the precision of reaching movements at a number of different time delays following previous movements - between 0 and 30 seconds. In Experiment 1, participants (n=8) performed 10 cm rightward and leftward point-to-point reaching movements where visual feedback was present only before movement onset (Fig 2a, b). We inserted a pseudorandomly chosen delay ($\Delta t = [0, 2, 4, 7, 10, 15, \text{ or } 30]$ sec) before the target was shown (Fig 2b) in order to control the time between movements (the resulting inter-trial intervals were longer than the assigned delays by about 2.4sec). Based on data from 40 leftward and 40 rightward test trials for each, we computed the movement endpoint variance at each delay. Example data for 0sec and 30sec delays are shown in 2c, and group average data are shown in 2d. The results reveal systematic increases in endpoint variance that asymptote at about 7-10sec both in the longitudinal and in lateral directions (Fig 2d, upper & lower panels), with statistically significant increases in variance following 30sec vs 0sec delays for both the longitudinal (Fig 2d, magenta bars, $p = 0.005$) and in lateral (Fig 2d, orange bars, $p = 0.002$) data. When each participant’s data is normalized by the average variance across the 10, 15, & 30sec delays (Fig 2e), the observed variance increases are well-fit by single exponential functions (longitudinal direction, $R^2=0.86$; lateral direction, $R^2=0.96$), with lateral variance increasing by 105% and longitudinal variance increasing by 50% from 0 to 30sec ($p < 0.001$ and $p < 0.001$, respectively).

In Experiment 2 (n=12), we examined three potential explanations for the observed reduction in variance seen in Experiment 1 by examining the ability of preceding movements in different directions to reduce test movement variance after a time delay. A rapidly decaying proprioceptive sensory memory of the target location could account for Experiment 1 result since the time delays used there altered both the times since previous movement and since visiting the target location, because the preceding movement begins at the target location. But this would predict no variance reduction in the 0° condition in Experiment 2 because the preceding movement does not visit the test target location. Our data, however, are not consistent with this explanation as we find that the 0° condition (Fig 3b) results in a large reduction in variance compared to the 10sec delay-only condition ($p < 0.001$). Analogously, a movement-related increase in alertness or attention could account for Experiment 1 findings but would predict a variance reduction for all movement directions, even when the interceding movement requires a motor activation largely unrelated to the test movement as in the 90° condition. However, our data are not consistent with this possibility, as we find no significant variance reduction in the 90° condition in Experiment 2 (Fig 3b) compared to the 10sec delay-only condition. Instead, Experiment 2 data suggest that previous movement quenches variability for subsequent movement in a direction dependent manner, with little effect on orthogonally-directed (90°) movements, but large variance reductions for same or oppositely-directed (0° or 180°) movements.

Taken together, our results indicate that (1) movement precision can be dramatically improved when movements closely follow preceding movements, (2) this effect is not due to a rapidly-decaying sensory memory from the preceding movement or to general changes in alertness or attention, and (3) the quenching movement variability is significantly larger in the parallel (0°, 180°) than in the perpendicular ($\pm 90^\circ$) axis.

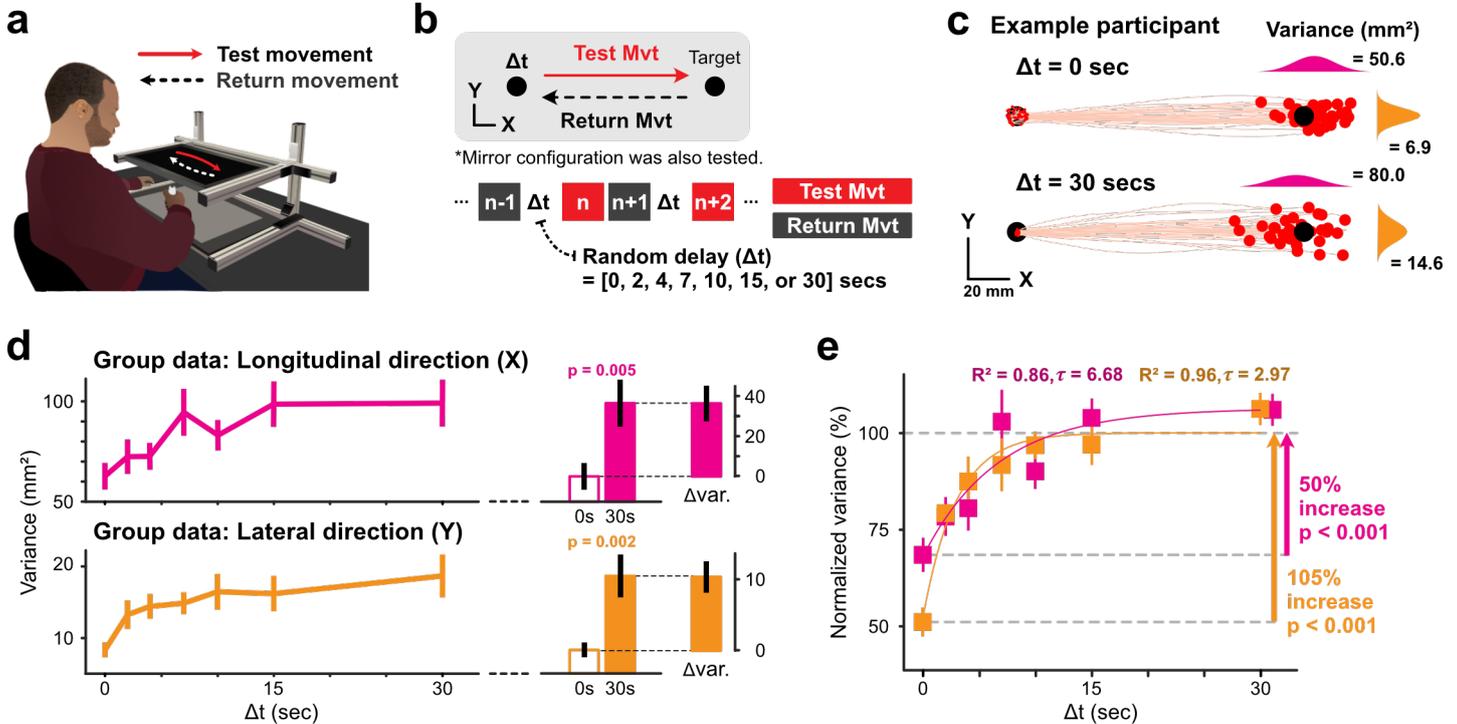
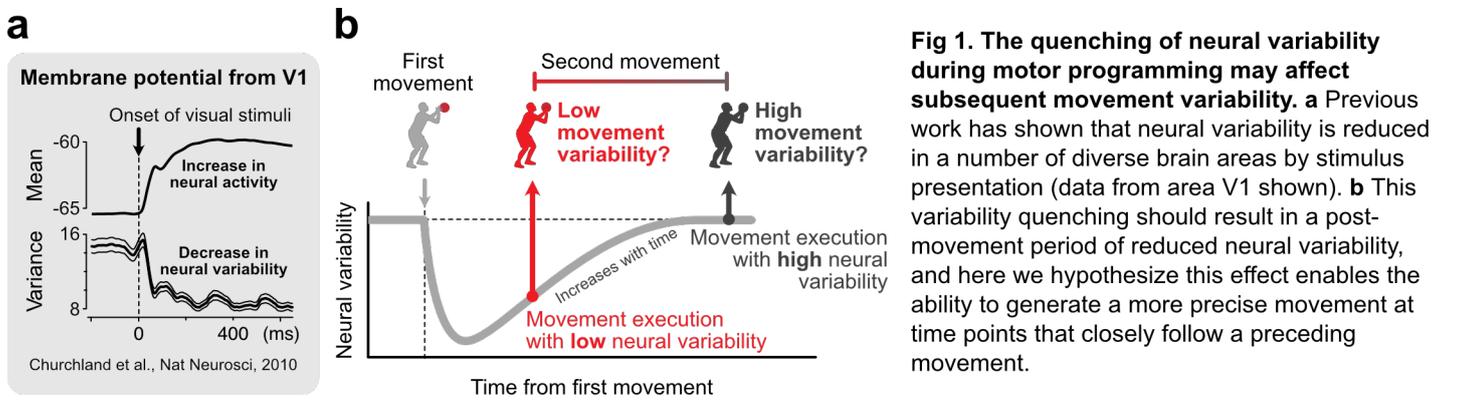


Fig 2. A recent preceding movement can dramatically improve movement precision. Experiment 1 was designed to investigate whether movement variability grows with the time interval since a previous movement. **a**. Participants ($n=8$) performed rapid 10 cm point-to-point movements without visual feedback (which was only available before movement onset). **b**. We pseudorandomly inserted different time delays ($\Delta t = [0, 2, 4, 7, 10, 15, \text{ or } 30]$ secs) between return and test movements to manipulate the recency of preceding movement. **c**. Endpoints of test movements (red filled circles) from a representative participant were considerably more variable after 30sec delays compared to 0sec delays. **d**. Raw endpoint variance in subject-averaged data systematically increased with the delays both in the longitudinal (X, upper panel) and lateral (Y, bottom panel) directions. **e**. Movement variability normalized by their asymptotic levels within participants (the mean of the variance observed at 10, 15, & 30sec). For both lateral & longitudinal variance, the observed increases were well characterized by single exponential curves. The data for increases in lateral direction variability was, unsurprisingly, cleaner given the much smaller raw variability levels. This data displayed smaller error bars, an R^2 of 96% for the single exponential fit, a time constant of 3sec, and 0-to-30sec variability increase of 105%.

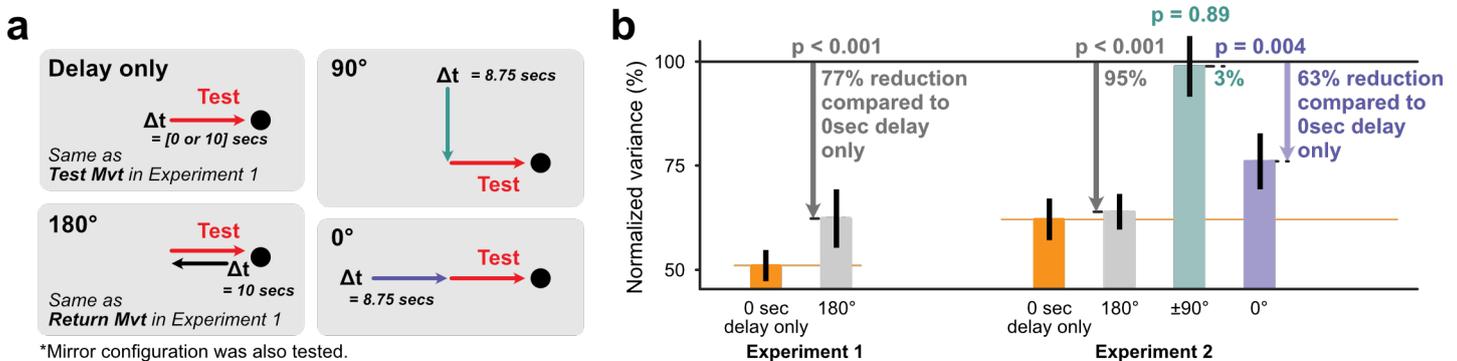


Fig 3. The direction of preceding movement determines the amount of variance reduction. **a**. Trials from five different conditions were randomly interleaved during the course of experiment 2 ($n=12$): 0sec and 10sec delay-only trials identical to those in Experiment 1 (upper left) where delays immediately preceded test movements, and trials with 9 or 10sec delays before 0° , 90° , or 180° movements that then preceded test movements (lower right, upper right, & lower left panels, respectively). The 0sec and 10sec delay-only conditions were used as a references for fully-reduced and un-reduced levels of variance, whereas the 0° , 90° , and 180° conditions tested the ability of movements in different directions to quench the variability accrued during the preceding 9 or 10sec delay. **b**. The results showed differential effects for the preceding movement directions on the quenching of movement variability. No clear variance reduction was observed for preceding movements at 90° , but large statistically significant reductions were observed for preceding movements at 0° and 180° . These findings are not consistent with effects due to rapidly-decaying sensory memory from the preceding movement or to general changes in alertness or attention (see main text).