

Role of movement preparation in movement generation

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Recent models of motor control have concentrated on the role of *online* mechanisms in generating movement^{1,2}. However, activity in motor and premotor cortex can be present *well before* movement onset: a classic example is the preparatory activity seen when a delay period separates an instruction from a go cue. Does such preparatory activity contribute to subsequent movement generation? We propose the following model. We assume that ballistic movements are largely determined by the state of preparatory activity at the time the movement is triggered. The goal of the nervous system is thus to *optimize* preparatory activity prior to triggering the movement.

Neural network theory suggests that optimization problems can be solved by recurrent networks that settle, over time, to attractor states that represent solutions³⁻⁵. Little physiological evidence for such processes has yet been found, but preparatory activity provides a likely opportunity. It appears to be in need of optimization, and its sustained nature suggests the influence of recurrent circuits, the presence of which is known anatomically. Furthermore, the idea that some time-consuming process underlies motor preparation is well supported by behavioral studies⁶⁻⁸, and it is generally suspected that preparatory activity is related to this process^{7,9,10}. Thus, we propose that prior to movement generation, preparatory activity becomes optimized as it settles to an attractor state, the location of which depends on the sensory, cognitive, and motivational inputs to the motor system (Fig 1).

If we accept these assumptions, then there likely exists not a single attractor, but a subspace of optimal states that are roughly equivalent from the standpoint of the movement goal (e.g. they may produce reaches to the same target, but with slightly different speeds or trajectories). On different trials, activity may settle to different parts of this subspace, a likely source of the copious movement variability exhibited by biological organisms². To test this idea, we recorded neural activity from 111 neurons in the dorsal premotor cortex (PMd) of two monkeys trained on a delayed reach task. We examined trial-by-trial variability in preparatory activity and in peak reach speed (Fig 2.). We found that these two quantities often showed statistically significant correlations, demonstrating that behavioral variability was partially determined before movement onset. The proportion of behavioral variability accounted for was difficult to estimate, but was at least 30%, and probably more^{11,12}.

These data support the idea that preparatory activity plays a causal role in movement generation. They also suggest that optimization proceeds differently on different trials, with preparatory activity settling along different paths to slightly different final states. Is there any way to more directly observe this putative process? We reasoned that preparatory activity might become more consistent, *across trials*, as activity settles to the attractor solution. If so, then measuring across-trial firing rate variability would provide a signature of settling. To do so, we used a ‘normalized variance’ metric, similar to the Fano factor, applied to 98 recordings from PMd of two monkeys. We found that the normalized variance fell from ~1.4 to ~0.9 following target onset, with a timecourse > 100 ms (Fig 3.). This time-course paralleled that of motor preparation, measured behaviorally, and was faster for trials with shorter reaction times¹³ (Fig 4.). These data argue that the normalized variance method provides a signature of the settling of preparatory activity to an attractor state, and that this process is closely related to motor preparation.

The above findings also suggest that the brain waits to trigger movement until after preparatory activity has been optimized. If so, then disruption of preparatory activity, via microstimulation, ought to cause an increase in reaction time (RT). This was indeed the case. When applied following the go cue (0-60 ms), microstimulation of PMd increased RT by a mean of 27 ms (Fig 5, 30 sites, $p < 0.0001$)¹⁴. In contrast, microstimulation of M1 during this time had little effect ($\Delta RT = 1$ ms, $p = 0.76$, 12 sites). As predicted, microstimulation of PMd just prior to the go cue increased RT, but only if the preceding delay period was long enough (>50 ms) for motor preparation to have been at least partially complete.

Taken together, our results argue that, for ballistic movements, successful movement generation is dependent on successful movement preparation. Movement preparation appears to involve the settling of activity to an attractor state that is (if all goes well) optimally suited to produce the desired movement. Of course, our results do not exclude a role for online feedback control. Indeed, part of the purpose of motor preparation may be to set the parameters of online controllers.

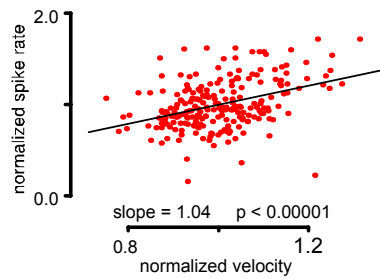
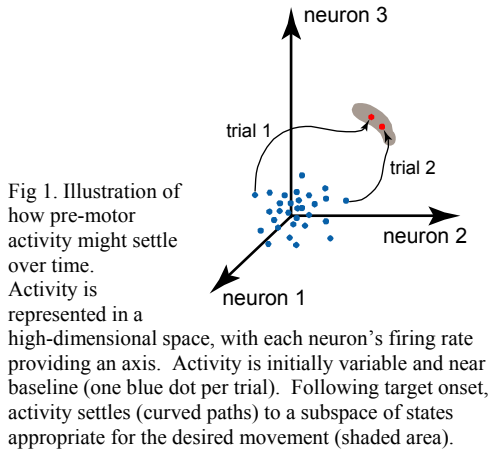


Fig 2. Trial-by-trial relationship between firing rate during the delay period and subsequent peak reach velocity. Data are from one neuron, and are collapsed, after normalization, across target locations.

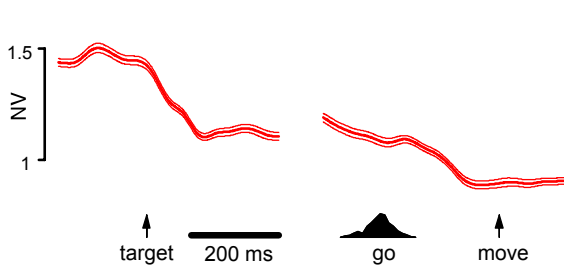


Figure 3. The normalized variance (NV) analysis, applied to data from 47 single and multi-unit isolations, recorded simultaneously using an implanted electrode array. The monkey performed a center-out reaching task. For each isolation and target location, the NV was computed as a function of time using:

$$NV(t) \propto \frac{\sum_{trial=1 \rightarrow n} (r_{trial}(t) - \bar{r}(t))^2}{n \bar{r}(t)}$$

where $r(t)$ is the firing rate at time t , obtained by filtering the original spike-train with a Gaussian. The mean and standard error were then taken across all isolations and locations. These data indicate that firing rates, measured across trials, become more similar with time, consistent with the theory that activity is settling to an attractor state.

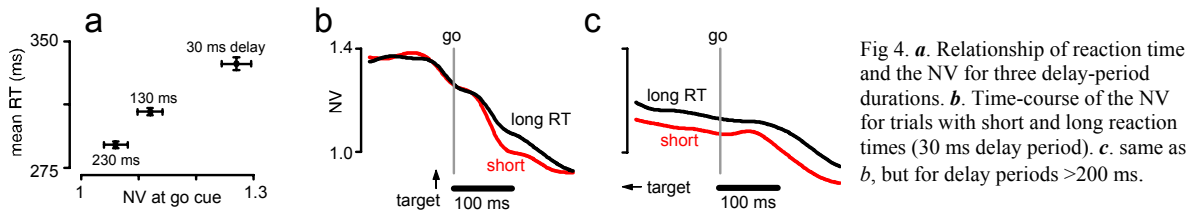


Fig 4. **a.** Relationship of reaction time and the NV for three delay-period durations. **b.** Time-course of the NV for trials with short and long reaction times (30 ms delay period). **c.** same as **b**, but for delay periods >200 ms.

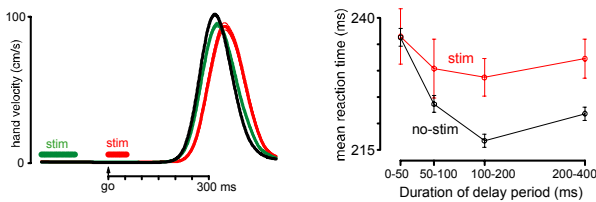


Fig 5. Left panel, hand velocity as a function of time, with and without microstimulation. Right panel, reaction time grows shorter with longer delay periods, but not if preparatory activity is disrupted just before the go cue.

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Support: Helen Hay Whitney, NIH, BWF, NSF, ONR, Sloan, Whitaker