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How and why neural and motor variation are related

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Movements are variable. Recent findings in smooth pursuit eye movements provide an explanation for motor variation in terms of the organization of the brain's sensory-motor pathways. Variation in sensory estimation is propagated through sensory-motor circuits and ultimately causes motor variation. The sensory origin of motor variation creates trial-by-trial correlations among the responses of neurons at each level of the sensory motor circuit, and between neural and behavioral responses. We suggest that motor variation is a compromise between multiple competing constraints. The brain strives for motor behavior that is 'good enough' in the face of constraints that tend to promote variation.

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Introduction

Movements are variable. Why? It is tempting to answer that movement varies because neural spike trains are noisy. But it also is possible that the source of motor variation is principled. Variation may arise through a compromise among several competing constraints, because of a limitation on neural processing imposed by the architecture of neural circuits, as a means to optimize some other goals of motor activity — or all of the above.

Spike trains of neurons are stochastic in the sense that spike timing is quite variable. Repetition of the same stimulus leads to approximately equal values of the mean and variance of spike count [1]. It is tempting to think of the stochastic variation in spike counts as 'noise'. The premise of our paper is that some of the variation is 'signal'. There are correlations in spiking across neurons even at peripheral sensory levels; the

existence of convergence and divergence in neural circuits allows those correlations to be propagated through a circuit and to control variation in motor output. Thus, we describe the trial-by-trial fluctuation in neural responses (and behavior) as 'variation' instead of 'noise' as a reminder that the variation may be 'signal'.

Behavioral analysis

The relevance of variation to the neural mechanisms of movement came into clear view when Harris and Wolpert [2*] explained plausible control strategies designed to minimize the variance of the endpoint of the movement. They proposed that the control signals of motoneurons are noisy, and that the noise is proportional to the amplitude of the signal the motoneurons send to muscles. Their theory provided a plausible explanation for the trajectories of saccadic eye movements and reaching arm movements. It also explained why the brain chooses stereotyped movement trajectories when an infinite number of trajectories are possible [3]. Their theory implies, but does not require, that motor variation originate in the final motor pathways.

Smooth pursuit eye movements have provided an excellent behavior for a deeper understanding of signal, noise, and variation in neural sensory-motor processing. Smooth pursuit occurs when a human or non-human primate tracks a small target that is moving smoothly at relatively slow speeds [4,5]. We can track a car as it moves across the horizon, but not a baseball as it races from pitcher to catcher.

On the basis of an analysis of pursuit eye movements, Osborne *et al.* [6**] proposed that sensory processing leads to errors in estimating the parameters of target motion, and that the motor system follows the erroneous estimates loyally, giving rise to trial-by-trial variation in the initiation of pursuit. They observed that the first 100 ms of a pursuit eye movement is quite variable, and showed that >90% of the variation could be accounted for in terms of mis-estimates of the parameters of the sensory stimulus: target speed, target direction, and time of onset of target motion. For example, suppose that a target moves at 20°/s in the up and right direction (1:30 on the clock, or 45° in polar coordinates). To track the target correctly, the brain must estimate the speed and direction of target motion. Osborne *et al.* [6**] suggested that those estimates vary from trial-to-trial, with estimates for speed ranging from about 17 to 23°/s and for direction from about 42 to 48°.

A second component of motor variation emerges late in the sensory-motor pathway. The visually driven initiation

of pursuit is followed by a later ‘steady-state’ response that is driven by corollary discharge of motor commands [7] as well as by visual motion signals [8]. A theoretically based analysis of recordings from the cerebellum and brainstem demonstrate that much of the variation in the steady-state response arises late in the sensory-motor circuit, accumulates as a function of time, and scales with the magnitude of the eye movement [9,10], as predicted by Harris and Wolpert [2*].

Thus, a single framework has emerged that covers arm movements, saccadic eye movements, and smooth pursuit. At least for pursuit [6**] and saccades [11], variation in estimates of sensory parameters drives much of the variation in the first 100 ms of the movement. For longer-duration movements, motor circuitry creates variation as the movement evolves. In pursuit eye movements, the motor component of variation fits the framework of ‘signal-dependent noise’ [2*,10]. The situation with saccades may provide a way to understand the relationship between sensory versus motor sources of noise. Sensory noise could create errors in specification of saccade amplitude [11], while signal-dependent motor noise may dictate a control strategy that leads to their smooth and stereotyped trajectories [2*].

Neural correlates of movement variation

One of the most frequent observations in recordings of neural activity is that spike trains are highly variable, even across repetitions of the same sensory stimulus [12] or of nominally identical movements [13]. Trial-by-trial variation in neural responses appears both in the spike counts across large or small analysis windows and in the intervals between successive spikes [1,14]. The existence of trial-by-trial variation in neural and motor responses raises the question of whether the two are related. A priori, we might guess that the trial-by-trial variation in the spiking patterns of an individual neuron is truly independent noise. If this were true, then the large numbers of neurons at each level of a mammalian sensory-motor system should allow the noise to be averaged away [15], and trial-by-trial variation in neural spike trains should not be related to motor variation.

Recordings from neurons during pursuit contradict the common wisdom that trial-by-trial neural variation is simply noise that can be eliminated easily. The evidence that neural variation is partly a signal comes from analysis of trial-by-trial ‘neuron–behavior’ correlations between the spike trains of individual neurons and the kinematic parameters of eye movement behavior. For pursuit, neuron–behavior correlations appear in area MT [16*,17], the smooth eye movement region of the frontal eye fields [18], the cerebellar floccular complex [9], and several types of neurons in the brainstem [10].

Neuron–behavior correlations imply that some of the variation in the firing of one neuron is being transmitted all the way to the final output. This could occur if the neuron has a powerful influence on the output, or more probably because the trial-by-trial variation in the firing of the neuron under study is a proxy for correlated variation in many neurons that together control the output. Thus, trial-by-trial variation in neural responses can be more than just single-neuron noise — it can be a signal that propagates through the system.

There are clear parallels between our data on pursuit eye movements and others’ data on perceptual judgments. The trial-by-trial variation in the activity of single cortical sensory neurons predicts, albeit weakly, perceptual behavior [19,20]. Thus, a general principle is that one spike train in one neuron at any of multiple levels of a sensory-motor circuit predicts something about the variation in an impending movement.

Shared variation in neural populations: a cause of motor variation

For multiple repetitions of the same sensory stimulus, the variation of neural responses in the sensory cortex has two components [21*]. The same appears to be true at multiple levels of the sensory-motor circuit for pursuit eye movements [10,22*].

The first component is independent variability that is largely private to individual neurons and causes fluctuations in the timing of action potentials. Independent variability can be reduced by averaging across the members of a neural population at downstream sites, where multiple neurons converge onto single post-synaptic targets.

The second component is shared and appears on multiple or even most neurons in a given population. The shared component of variation could arise from top-down influences such as attention or other state-dependent variation [21*], or from correlated variation that is present in sensory representations [23,24]. In the visual system, correlated variation in the responses of motion selective neurons could arise even in the retina [25]. The correlated, shared component of variation is difficult or even impossible to remove by averaging. As a result, it propagates along sensory-motor circuits and ultimately causes trial-by-trial variation in motor behavior.

In smooth pursuit eye movements, the shared component of variation is expressed as trial-by-trial ‘noise’ correlations in the number of spikes discharged by pairs of neurons in extrastriate area MT [23,24]. The magnitude of the correlation varies for different pairs of neurons, and is generally larger if the pairs share preferred stimulus features such as receptive field location, preferred direction, and preferred speed. This particular ‘structure’ in

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