

Preview

Noise that knows its place

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The variability of neural signals is no longer being disregarded as a nuisance. Here, Terlau et al.¹ show that there is structure even in being noisy: their brain-wide analysis uncovers a sensory-to-association gradient of neural variability—and its adaptive benefits for human behavior.

“Float like a butterfly, sting like a bee.”—Muhammad Ali

These were the words that champion Muhammad Ali used to describe his boxing style as a young athlete brimming with energy and grace. But they might just as well capture how the brain balances flexibility and precision.

A new study¹ out now in *Neuron* shows that the brain’s variability over many trials is not random scatter. The variability that a certain cortical area exhibits follows a hierarchical structure along the cortical axis. In sensory areas—where the “sting” or precision is paramount—variability is reduced to enhance fidelity. In association cortex—where the mind “floats” adaptively—variability increases, reflecting ongoing recurrent dynamics.

In a nutshell, the team around Randolph Helfrich demonstrates that neural variability is a hierarchically structured feature of cortical organization. Using large-scale human intracranial electroencephalogram (EEG) recordings across sensory and association cortices, they show that trial-by-trial variability increases systematically along the cortical sensorimotor-association axis (Figure 1B). The authors show us how neural variability, at different cortical sites and under different tasks, differentially relates to perceptual precision versus cognitive flexibility.

In doing so, this study used not one but two core tasks to dissociate perceptual from cognitive demands: in an attention task, participants focused on visual stimuli without needing to memorize them, which probed perceptual attention. By contrast, the working memory task required participants to actively maintain and compare visual information after a

delay, engaging higher-order cognitive processes. Crucially, both tasks used identical stimuli, enabling the researchers to isolate the neural effects of cognitive load from those of sensory input. This distinction mattered. Terlau, Martini, and Helfrich show that the variability gradient across the cortex surfaces in behavioral outcomes. They found a so-called double dissociation: depending on the task, different levels of neural variability led to better or worse performance. Put simply, more consistency in behavior indicates better performance.² In the attention task, lower variability went hand in hand with more stable, reliable responses. However, in the working memory task, the pattern flipped—more variability supported better performance (Figure 1C).

What do we mean when we speak of “neural variability”? Neural variability is an umbrella term describing potentially many phenomena of neural dispersion. It poses the natural complement to any “point estimate,” or average of neural activity, and, as such, comes in many mathematical flavors.³ Helfrich’s team chose to operationalize neural variability as the median absolute deviation (MAD), computed across many single trials (Figure 1A). MAD is favored for its robustness and is less deterred by outliers than the more common, Euclidean measures of standard deviation and variance are. The authors leveraged this metric to ask how consistent or dispersed neural activation is across repeated presentations of the same stimulus or task condition in widely distributed areas of the human brain (Figure 1B).

An important new insight on the brain-wide mechanics of neural variability became possible because the authors

tested how much different brain areas “talk in loops”: applying weak, site-specific electrical impulses (cortico-cortical evoked potentials [CCEPs]), the authors looked for responses specifically after 100–300 ms, which would reflect feedback and recurrence-driven activity (in contrast to faster, mostly feed-forward responses). They hypothesized that this reciprocity should exert a mediating influence on neural variability, which turned out to be the case. Thus, neural activity in higher cortical areas varies more because these areas entertain more recurrent, echoing connections.

While Terlau, Martini, and Helfrich provide us with an imaginative and compelling demonstration of how neural variability is structured across the cortex and leveraged for behavior, several intriguing questions remain. The role of baseline or ongoing variability—before any task event unfolds—has long been receiving its own share of attention and remains to be more comprehensively understood (for a review, see Waschke et al.³): it likely shapes the terrain on which evoked dynamics operate.^{4,5} Future analyses of Terlau et al.’s data could potentially help us make progress on understanding the relationship between spontaneous, ongoing variability and task- and stimulus-evoked variability in a systemic and brain-wide fashion.

Likewise, the interplay between broadband variability and rhythmic, truly endogenous neural oscillations, such as alpha/beta oscillations (in the 10–30 Hz range), will offer a potential counterpoint and complement to the variability framework, as recent conceptualizations of scale-free (“1 over f”) versus oscillatory neural mechanisms emphasize.⁶ Finally, the



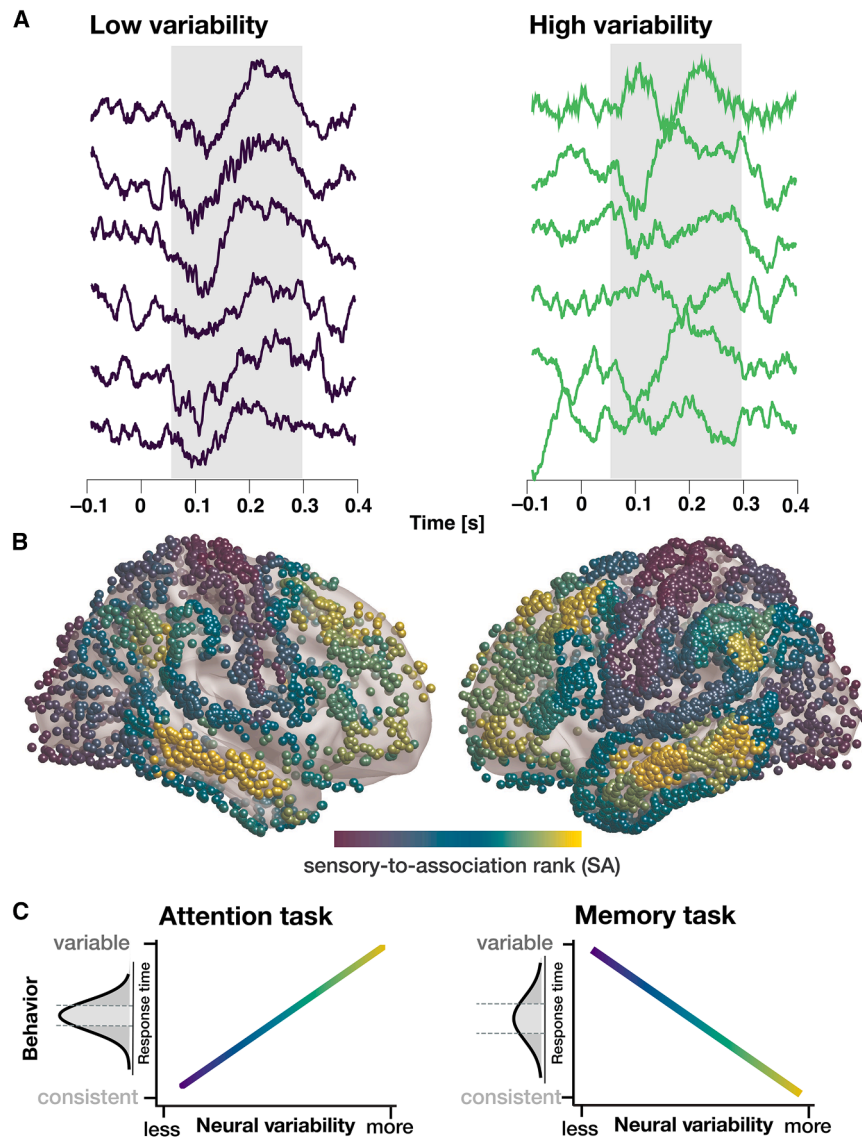


Figure 1. Neural variability depends on cortical area and shapes behavior task dependently (A) Low (left) versus high trial-by-trial variability (right), illustrated on respective sets of five trials. (B) Electroencephalography (ECoG) coverage ($n = 74$) during electrical stimulation with electrodes colored by their sensorimotor-association (SA) rank, adapted with permission from Terlau et al.¹ (C) Behavioral performance depends on neural variability in a task-specific manner. In the attention task, lower variability leads to more consistent (and thus better) performance, whereas in the memory task, higher variability is associated with better performance. Variable behavior is characterized by trials with extreme reaction times (RTs), whereas consistent behavior reflects trials near the mean RT. Average RTs were higher in the memory task than in the attention task.

observed cortical gradient of variability invites comparison with previously established hierarchies of intrinsic timescales⁷—an avenue that could link structured variability more directly to a “temporal architecture” of the human cortex.

Not least, these new findings fit neatly into the broader notion of excitation-inhi-

bition (E:I) balance orchestrating cortical dynamics. Low neural variability is commensurate with a tightly inhibition-regulated regime (i.e., fast but short-lived responses).⁸ Terlau, Martini, and Helfrich show that in sensory areas, this reduced variability actually boosts performance: a nice match with the classic view that a slightly inhibition-tilted system encodes

sensory input more precisely.⁹ In contrast, more excitation leads to a state in which the activity sloshes along recurrent loops that, as shown by Chaudhuri et al.,⁸ create longer intrinsic timescales in higher cortical areas. The new data by Terlau et al. extend this framework by demonstrating that such recurrent dynamics generate more complex patterns of structured variability. In other words, the variability gradient they describe may be the direct consequence of hierarchical differences in recurrent strength, emerging from varying E:I balance across the cortex.

What do these new results teach us? First, the more sensory, and thus low, in cortical hierarchy a brain area is, the more it will exhibit “quenching,” a stimulus-evoked reduction of across-trials neural variability,¹⁰ once a stimulus has arrived. While this quenching supports perceptual precision, the higher-hierarchy, association-cortical areas exhibit increased variability instead—especially during memory maintenance, where quenching predicts better performance (Figure 1C).

Second, this functional gradient in variability is reproducible across tasks and reflects underlying network architecture, with higher variability being a proxy for more recurrent cortico-cortical connectivity.

Why should neuroscientists care? In sum, neural variability is by no means any longer neuroscientists’ large “trash can” of unwanted deviation from an average: the brain varies its response dynamics in site- and task-specific ways and uses variability adaptively along the cortical hierarchy to balance stable perception and flexible cognition. Like Muhammad Ali in motion, the brain attains both fluidity and focus through neural variability in the right time at the right place.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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