**Not Noise: Correlated Variability Channels Task-relevant Information in Sensory Neurons**

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**Data and Code Availability:** The code used to perform the analyses and generate the figures in this study has been deposited in a public GitHub repository <https://github.com/ramanujansrinath/corrvar>. The electrophysiological data analyzed here are from various datasets, all of which are deposited and freely available at the following locations.

Figure 1: Open Science Framework at <https://doi.org/10.17605/OSF.IO/RN7TU> and <https://github.com/hcc11/GeneralDecoder>

Figure 2: GitHub repository at https://github.com/Beibaibaby/modulation

Figures 3-5: GitHub repository at <https://github.com/ramanujansrinath/flexigain>.

Figure 6: GitHub repository at <https://github.com/ramanujansrinath/corrvar>.

Further information and requests for data or custom MATLAB code should be directed to and will be fulfilled by the corresponding author, Ramanujan Srinath ([ramsrinath@uchicago.edu](mailto:ramsrinath@uchicago.edu)).

# Abstract

Improvements in perceptual performance (such as those associated with stimulus contrast, attention, learning, task-switching, or arousal/motivation) are typically accompanied by decreases in the shared trial-to-trial variability of responses from pairs of sensory neurons to repeated presentations of the same stimulus. This widespread observation appears paradoxical in light of recent findings suggesting that stimulus properties can, in principle, be decoded from neural populations uncorrupted by correlated variability. Correlated variability largely fluctuates along one or a small number of axes in neural population space (or the ‘correlated variability axis’), meaning that it could easily be ignored. To resolve this apparent conflict, we hypothesize that **the correlated variability axis reflects the sensory information communicated out of, rather than encoded in, a population of sensory neurons**. This framework predicts that the behaviorally relevant information is encoded in a way that aligns with, rather than avoids, the correlated variability axis. Our model suggests that this scenario does not harm information coding because in a biologically plausible circuit, the dimensions that contain the most variability also contain the most signal, as might be reflected in projection neurons that communicate with decision areas. We found converging correlative and causal support for our hypothesis in multiple brain areas and tasks. First, monkeys performed better in a change detection task when the representations of the original and changed stimuli happened to align with the correlated variability axis. Second, in a curvature estimation task, the correlated variability axis was aligned with the axis that best encoded curvature in a general way, across shapes that varied in task-irrelevant features. Third, during time periods when monkeys planned a saccade to express this judgment, the correlated variability axis was better aligned with the representation of the saccade plan than other features. Fourth, in a two-alternative forced choice task where monkeys alternated reporting stimulus curvature or color, information about curvature aligned better with the correlated variability axis when it was task-relevant. Finally, we found causal support: the impact of microstimulation on behavior was predictable by the extent to which stimulation-evoked changes in population activity were aligned with correlated variability. These results directly contrast the predominant hypothesis that relevant representations would be aligned to avoid corruption by response variability. Instead, they suggest that the task variables aligned with correlated variability preferentially reflect the information used to guide behavior.

# Introduction

Correlated neural variability is both tightly linked to behavior and, in principle, irrelevant to information coding. Many studies have shown that good performance on perceptual tasks, associated with factors such as attention, learning, arousal/motivation, or the contrast of a visual stimulus, is consistently accompanied by low shared trial-to-trial response fluctuation in sensory neurons1–15. Shared variability is often quantified as the mean spike count correlation (also called noise correlations or rSC) between the trial-to-trial fluctuations in the responses of pairs of neurons to repeated presentations of the same stimulus1. Shared variability has become central to experimental and theoretical investigations of information coding, in part because it is modulated by virtually every process known to enhance perception1,9,16, linked to behavior on a trial-by-trial basis17–20, and sensitive to pharmacological and circuit-level manipulations5,21,22.

These observations initially fueled a widely held hypothesis: that shared variability acts as noise, degrading the fidelity of population codes and impairing the ability of downstream areas to make accurate perceptual decisions23. From this perspective, cognitive processes like attention or arousal improve perception by reducing noise (ref XX ??). However, this interpretation is increasingly difficult to reconcile with theoretical and empirical evidence. Because correlated variability tends to lie within a low-dimensional subspace of neural activity (defined as the space in which the response of each neuron represents one dimension; 16,23–27), an optimal decoder can, in principle, ignore it entirely16,23–27. Consistent with this, we showed recently that attention dramatically reduces correlated variability in visual cortex without substantially altering the amount of sensory information that can be linearly decoded from the population28. Moreover, the same axis that captures the most shared variability also explains nearly all of the task-related choice signals in visual area V429.

These observations present a paradox: if correlated variability does not fundamentally constrain the information available in a sensory population, why is it so reliably related to behavior?

Here, we propose a resolution to this contradiction. Rather than interpreting shared variability as an obstacle to neural coding, we suggest that it reflects the dimensions of neural population activity that guide behavior. Specifically, we hypothesize that behaviorally relevant information is preferentially aligned with the axis of shared variability, defined as the axis in the neural population along which responses fluctuate most across trials. Biologically, correlated variability may reflect the activity of projection neurons that communicate with decision-making areas. In this view, the correlated variability axis reveals the subset of encoded information that is communicated to downstream areas for decision-making, rather than reflecting noise that harms performance.

We tested whether this hypothesis represents a general principle by analyzing how correlated variability relates to representations of relevant and irrelevant stimulus features, motor plans, and decisions across multiple datasets. In a change detection task, monkeys performed better on stimuli whose representations happened to be aligned with the correlated variability axis. In a curvature estimation task, the axis of correlated variability was aligned with the representation of curvature across heterogeneous shapes, irrespective of irrelevant features. During saccade planning, correlated variability more closely tracked motor plans than sensory inputs. In a task where animals alternated discriminating curvature and color, the alignment of curvature information with the correlated variability axis increased when that feature was task-relevant. Finally, we found causal support for this framework: the behavioral impact of microstimulation was predicted by how closely evoked population responses aligned with the axis of correlated variability. Together, these findings challenge the idea that neural representations avoid subspaces of neural population space corrupted by correlated variability and instead suggest that behaviorally relevant signals are communicated along these subspaces.

By reframing the role of shared variability, our findings provide a new perspective on decades of experimental results, suggesting that correlated variability may serve as a window into the neural computations that drive perception and decision-making.

# Results

While improvements in perceptual performance often coincide with changes in correlated trial-to-trial variability in sensory neurons, theoretical work suggests that such variability may not limit the information that can be. This is because correlated variability, especially in sensory areas, typically occupies a low-dimensional subspace, fluctuating primarily along a single “correlated variability axis”. We investigated our central hypothesis by analyzing the relationship between task-relevant information coding in visual cortex, correlated variability, and behavior. In each data set, we defined the axis of correlated variability as the first principal component (PC1) of neural population activity during a baseline period where rhesus monkeys (Macaca mulatta) fixated a gray screen at the start of each trial, capturing the dimension that explains the most shared variability in spontaneous activity.

**Performance in an orientation change detection task is related to the alignment between the orientation representation and the axis of correlated variability in area V4**

We began by testing our hypothesis in a well-established orientation change detection task2,9,12,20,28–30 (Figure 1A). Different aspects of these data have been published previously21,29. In this task, monkeys fixated a central dot while two Gabor stimuli of the same orientation were flashed repeatedly. At a random and unsignalled time, one stimulus changed orientation, and the monkey was rewarded for making a saccade to its location. In this task variation, the starting orientations of the gratings varied between 0° and 180° across trials, while the magnitude of the orientation change was fixed. This design held task difficulty constant. Our analysis focused on trials in which the change occurred at a cued location that overlapped with the population receptive fields of the recorded V4 neurons. As in all data sets, we defined the axis of correlated variability using the first principal component of baseline activity (Figure 1B, gray dots and bottom axes).

According to our hypothesis, behavioral performance should be better for orientation changes that are most aligned with the axis of correlated variability (Figure 1B, orange arrow) compared to orientation changes that are least aligned (Figure 1B, green arrow). Consistent with this prediction, monkeys were significantly better at detecting the orientation change most aligned with the axis of correlated variability compared to the least aligned orientation change (Figure 1C). This unexpected result in a well-studied task led us to explore our hypothesis further using a theoretical model and four additional datasets encompassing a wide range of stimuli and behavioral demands.

**A circuit model demonstrates that stimulus information can be read out optimally when aligned with the axis of correlated variability**

To explore the computational consequences of aligning stimulus representations with the correlated variability, we constructed a recurrently connected network model (Figure 2A) composed of excitatory and inhibitory units with defined feed-forward (WF), recurrent (WR), and linear read-out (WO) synaptic weights. In our model, noise begins as private, independent fluctuations in each neuron and becomes correlated only through the recurrent weights **W**R. We adopt this formulation because, across all datasets, the axis of correlated variability measured during repeated presentations of the same stimulus is nearly parallel to the axis obtained during baseline gray-screen periods (Supplementary Fig. S X), pointing to recurrent connectivity as the dominant source of these correlations. Previous theoretical and experimental work suggests that learning can tune recurrent connectivity (WR​) such that the network’s slowest dynamical mode aligns with the dimension of network input with greatest signal-to-noise ratio ​ 10,31.In our model, this tuning effectively rotates the stimulus-evoked activity onto the axis of correlated variability (Figure 2B). Consistent with this mechanism, across our five datasets the stimulus-conditioned mean response projects strongly onto the first principal component of baseline activity (median alignment < xxx°; Supplementary Figure SX), indicating that stimulus-evoked activity and the axis of correlated variability are generally co-linear in real data. After learning, fluctuations along the axis of correlated variability decay much more slowly (Figure 2C, black curve) than fluctuations along orthogonal axes, such as the second principal component (Figure 2C, light gray curve). This rotation inevitably boosts variance along the coding axis—because the network’s slowest dynamical mode now lies there—but it boosts the mean separation by an even larger factor: the signal scales as whereas the variance scales only as where is the largest eigenvalue of the recurrent operator GWR​(G is the gain vector). Consequently, for any optimal *single-axis* linear decoder the Fisher information increases, so tuning **WR** to co-align the noise and stimulus axes is advantageous despite the extra shared variability.

We next explored how the alignment between stimulus and readout axes impacts decoding. In our model, we assume that downstream areas can access only a single dimension of the population activity and that the corresponding read-out weights (**W**O) remain fixed throughout the task—consistent with evidence that cortical circuits exploit privileged axes embedded in hard-wired projections. The linear readout axis (Figure 2D, orange arrow) forms an angle θ with the stimulus representation (blue arrow). As this angle increases, the normalized signal variance falls more rapidly than the noise variance (Figure 2E). Consequently, the Fisher discriminability, a measure of decoding performance, peaks when the readout and noise axes are aligned (Figure 2F). These results demonstrate that when stimulus information is aligned with the axis of correlated variability (a biologically relevant scenario, because noise is related to signal in essentially every study that measured both1,10,32–38), the optimal readout strategy is along the axis of correlated variability.

Our model predicts that aligning behavior with the axis of correlated variability is optimal when the relevant signal is aligned with noise. The model therefore predicts that task-relevant information should be preferentially aligned with the axis of correlated variability. We therefore tested this prediction in a number of situations in which we could compare the alignment of the axis of correlated variability with the representations of task-relevant information and task-irrelevant information.

**Alignment of curvature representation with the axis of correlated variability in V4 predicts behavioral performance in a curvature estimation task**

We next tested the prediction that in a situation where monkeys had to generalize across stimuli that vary in many irrelevant features, the axis of correlated variability would align with the axis that best performs that generalization. We therefore trained monkeys to perform a continuous curvature estimation task (Figure 3A) in which they reported the curvature of any random 3D shape while ignoring other irrelevant features like color, orientation, and thickness profile39. After the stimulus was presented, the monkeys made a saccade to a location on a target arc corresponding to their curvature estimate (0 for straight, 1 for maximally curved). They were rewarded in inverse proportion to their estimation error.

Both monkeys (Figure 3B, green and blue lines) produced consistent curvature estimation, and their performance was comparable to that of humans performing an online version of the same task (Figure 3B, pink line). The stimuli were presented within the joint receptive fields of recorded V4 neurons, which are selective for curvature (Figure 3D-E). The population representation of curvature was dependent on irrelevant shape properties (Figure 3F-G)39, meaning that the best axis for judging the curvature of any one stimulus was different than the best for generalizing across stimuli.

Our central hypothesis predicts that behavioral performance should be better for shapes whose curvature representation is more aligned with the axis of correlated variability (Figure 3C). To test this, we compared the behavioral performance across pairs of shapes tested within the same experimental session (Figure 3H). Consistent with our prediction, performance was consistently better for the shape whose curvature representation was better aligned with the axis of correlated variability.

**The axis of correlated variability aligns with planning-related signals in V4 during flexible sensorimotor mapping**

Many previous studies have identified pre-motor or, more generally, behavioral planning-related signals even in primarily sensory areas, such as V440–46. These signals could be related to motor efference, drawing attention to context-related signals, or surround modulation and normalization relevant for the task47–53. When a behavioral plan is made, downstream areas need to know that plan even more than the sensory signal that guided it. A strong test of our hypothesis that correlated variability aligns with the information that guides behavior is that it should align more with those planning-related signals than sensory signals. However, in most tasks, including all of those we have discussed so far, the sensory information is not dissociable from motor planning. We therefore designed a variant of our curvature estimation task in which we dissociated sensory from motor by varying the length and angular position of the target arc across trials (Figure 4A). This manipulation required the monkeys to flexibly remap curvature estimates to several different saccade directions (Figure 4B).

We previously showed that V4 population responses reformat during the motor planning period (after arc onset), such that both stimulus curvature and the planned saccade are encoded in V4. Because the planned saccade direction is what most directly guides the upcoming action, we hypothesized that the axis of correlated variability would be aligned more strongly with the saccade than the curvature representation (Figure 4C).

Indeed, both curvature and saccade direction could be decoded from V4 population activity. However, consistent with our hypothesis, when those responses were projected onto the axis of correlated variability, decoding performance for curvature fell more sharply than for saccade prediction (Figure 4D), suggesting that the correlated variability axis was better aligned with the saccade-related than the curvature axis.

This finding is further emphasized by comparing responses to different shapes (Figure 4E). We compared the prediction of our decoder using either the curvature or saccade direction axes with projections onto the correlated variability axis. The difference in curvature prediction accuracy between the dedicated curvature axis and the axis of correlated variability (y-axis) was substantially larger than the difference in saccade prediction accuracy between the dedicated saccade axis and the axis of correlated variability (x-axis). This result indicates that saccade-related representations were more consistently aligned with the axis of correlated variability than curvature representations.

**The axis of correlated variability aligns with the behaviorally relevant visual feature**

In the previous experiment, the monkey needed to ignore irrelevant visual features and base decisions on a single, task-relevant feature. Since V4 neurons are selective for multiple visual features and the results above suggest that the axis of correlated variability aligns with behaviorally relevant information (e.g., a motor plan), we next investigated whether this alignment could flexibly shift depending on the sensory feature currently guiding behavior.

To test this, we trained monkeys to perform a two-alternative forced choice task that required decisions based on either curvature or color on randomly interleaved trials (Figure 5A-B). On trials where the two stimuli had the same color, monkeys were rewarded for choosing the more circular (less curved) shape. Conversely, when the two stimuli had the same shape, they were rewarded for making a saccade to the bluer stimulus. Both monkeys successfully made curvature- and color-based choices (Figure 5C), so we divided the data from each session according to the behaviorally relevant feature for each trial. This design allowed us to probe whether the axis of correlated variability in V4 would align more strongly with the representation of curvature on trials in which curvature, rather than color, guided choices (Figure 5D).

For each session, we projected V4 responses onto a common axis of correlated variability, computed from the baseline period before the monkeys knew whether the trial would involve curvature or color discrimination (Figure 5E). When monkeys made curvature-based choices, the projection of neural responses onto the axis of correlated variability reflected the stimulus curvature significantly more accurately than when they made color-based choices. This suggests that the axis of correlated variability dynamically aligns with the currently behavior-relevant visual feature.

**Causal evidence: Behavioral effects of microstimulation are strongest when aligned with the axis of correlated variability**

Finally, we causally tested our central hypothesis using electrical microstimulation in the middle temporal area (MT). We chose MT because the effects of microstimulation on the motion judgments have been well-established51,54–58. As in our curvature estimation study, we trained monkeys to perform a continuous estimation task. In this case (Figure 6A), they were rewarded for correctly estimating the motion direction of a random dot kinematogram presented within the joint receptive fields of MT neurons recorded on a multielectrode linear probe. On a randomly selected subset of trials, we paired the visual stimulus with microstimulation on one of two electrodes (*long-stim*). The stimulation electrodes were chosen based on the different direction selectivity of the recorded neurons, determined in separate mapping experiments. We quantified the behavioral effect of stimulation as the change in the slope of the psychometric function relating the chosen direction to the motion direction between long-stim and no stimulation conditions (Figure 6B).

Since we wanted to compare this behavioral impact of stimulation to the impact of microstimulation on population responses, on some stimulation trials, we truncated the microstimulation after 50 ms (*short-stim*) and analyzed responses immediately after stimulation. We chose the stimulation duration for short-stim trials such that there was no measurable impact on behavior (Figure 6C). We calculated the alignment between the axis of correlated variability and the microstimulation-evoked neural population response change for each electrode on short-stim trials.

If behavior is preferentially influenced by activity along the axis of correlated variability, then the stimulation site that evokes responses more aligned with this axis should have a stronger impact on the monkeys’ choices (Figure 6D). As predicted, the stimulation site that pushed neuronal responses in a direction more aligned with the axis of correlated variability (orange dots in Figure 6E) also had a larger impact on behavior on long-stim trials. This provides causal evidence that neural response fluctuations along the axis of correlated variability are strongly related to behavior.

Together, our results show that the axis of correlated variability does not merely reflect noise to be ignored but instead aligns with—and may amplify—the sensory and decision-related signals that guide behavior. This framework reconciles the tight relationship between correlated variability and behavior with the theoretical possibility of decoding information in its presence, pointing to a mechanism by which perception and action can remain flexible, robust, and efficient.

# Discussion

Our results demonstrate that shared, trial-by-trial response fluctuations in visual cortex are not simply noise to be averaged out or ignored. Instead, shared variability reflects the information that guides behavior and dynamically tracks changes in task demands. Using complementary correlative, theoretical, and causal approaches and several visually guided tasks, we demonstrated that:

1. **Change detection is most accurate** when stimulus representations vary along the axis of correlated variability;
2. **When signal and noise are coupled in the same circuit**, decoding along this axis is optimal;
3. **Estimates of visual features improve** when the axis of shared variability aligns with the relevant feature;
4. **The axis flexibly** reflects task demands, from sensory features to action plans;
5. **When perception and action are dissociated**, the axis favors motor intent over sensory evidence;
6. **Causal manipulations are most effective** when aligned with this axis.

Together, these findings support our central hypothesis: the axis of correlated variability reflects the neuronal population activity that is read out to guide behavior. These findings bridge a long-standing gap between theoretical accounts of information-limiting correlations and empirical observations linking them to attention, learning, and behavior. They suggest that variability is not simply tolerated by the brain. Rather than a nuisance, it reflects the substrate of perception and decision-making.

*Why measure correlated variability?*

In recent years, a staggering number of studies have related different aspects of flexible, sensory-guided behavior to a very simple measure of shared variability: the mean correlation between the spike count responses of pairs of neurons to repeated presentations of the same stimulus (termed spike count noise correlations, or rSC). Correlated variability is:

* **Simple to compute** and well-suited to population recordings1;
* **Modulated by nearly every process** that affects perception, including attention, adaptation, learning, task switching, arousal, and stimulus contrast2,8,9,19,30,59–61
* **Linked to behavior** on a trial-by-trial basis20,35;
* **Straightforward to change using causal manipulations**, including pharmacological methods21 and microinfusion of neurotransmitters5;
* **Constrained by circuit architecture**, providing insight into underlying mechanisms62–67.

This ubiquity hints at a deeper role: that correlated variability offers a window into the neural computations that support cognition, as well as a potential means to restore and enhance them.

*Reconciling the links between noise, information coding, and performance on perceptual tasks*

The link between correlated variability and performance on demanding perceptual tasks is pervasive, but enigmatic. Across species, brain areas, and tasks, decreases in correlated variability have been observed alongside good performance on a variety of perceptual tasks. These modulations are typically interpreted as reflecting an improvement in information encoding: reductions in correlated variability are presumed to reflect less noise, which improves readout16,23,26. However, this interpretation is increasingly at odds with theory and data. Theoretical work has demonstrated that optimal decoders can effectively ignore low-dimensional shared variability without compromising performance (ref XX ??). And empirically, we and others have shown that attentional reductions in noise correlations do not improve population-level stimulus encoding14,28,29 (add ‘others’ refs XX ??).

This raises a paradox: if shared variability does not limit information, why does it change with cognition, and why is it so closely linked to behavior?

Our findings offer a resolution. We propose that the brain does not suppress correlated variability; it uses it. The axis of correlated variability reflects the aspects of population activity that are flexibly read out. Its alignment with task-relevant information explains its links to behavior, attention, and learning, not because it limits information, but because it **reflects what information is used**.

*Prior work that shaped our hypothesis*

Three lines of prior evidence guided our thinking. First, signal and noise correlations are inextricably intertwined. Neurons with similar tuning tend to have higher noise correlations1,10,16,17,33,35–38, likely due to shared circuit structure10,31,68. Second, we previously showed that in a change detection task, the axis of correlated variability reflects all of the choice-predictive information in V4, even when attention reduces mean correlations. Third, the flexibility of this relationship across stimuli, tasks, and behaviors mirrors the flexible contribution of visual cortex to visually guided behavior. The responses of neurons in areas like V4 and MT, and their correlated variability, are modulated by attention, task switching, reward, and motor planning40,47,48,59,69–71, and yet a stable linear decoder can often predict behavior across those contexts16,23,29,59,72,73. This suggests that the axis of correlated variability adapts to align with task-relevant dimensions while maintaining a consistent role in behavior.

*A biologically plausible implementation*

Traditionally, models of cortical circuits treat signal and noise as separable quantities. In that scenario, low-dimensional noise can be easily averaged out or ignored so that it is irrelevant to behavior23,25. This is contrary to the results presented here, suggesting that, instead, correlated variability is central to the information used to guide behavior.

Our results may simply reflect a biological reality: that signal and noise emerge from the same circuit. The same neurons that encode and transform visual signals have response variability that is bound to be aligned with signal representations10,31,68. The axis that accounts for most shared variability may by necessity be the one that reflects the most signal.

To formalize these ideas, we developed a circuit model that links recurrent network dynamics to the structure of shared variability (Figure 2). In the model, learning shapes the recurrent connectivity so that the network’s slowest dynamical mode, and hence its axis of correlated variability, aligns with the feedforward stimulus representation. This alignment **maximizes information transmission by concentrating both signal and correlated noise onto a single axis, which is the optimal configuration for a one-dimensional decoder**, particularly when the signal and noise covary, as is typical in cortex. The model predicts that decoding performance is optimized when the readout axis aligns with the axis of correlated variability. When signal and noise covary, this alignment enhances integration and decoding, aligning with our experimental findings.

*Causal manipulations for linking neural population representations to behavior in primates*

The primary challenge for using causal manipulations to study the relationship between behavior and correlated variability is the need to measure how manipulations affect neuronal populations. While imaging has been used to measure how electrical stimulation affects neurons in mice74, it is challenging and uncommon to make these measurements using physiology and in monkeys.

The methods we used for measuring the impact of electrical microstimulation on surrounding populations (Figure 6) are broadly applicable for at least three reasons. First, microstimulation remains a uniquely effective causal manipulation for eliciting behavioral changes, especially in primates. Second, microstimulation leverages the functional organization of the cortex: by varying simple parameters, such as current amplitude, one can easily adjust the number and variety of affected neurons. Finally, microstimulation remains essentially the only causal method for assessing the function of small groups of neurons during human neurosurgery or for prosthetics in humans75–79. Understanding the relationship between electrical stimulation, neuronal population activity, and behavior, therefore, has implications both for basic science and translational research.

Here, electrical microstimulation in MT (Figure 6) provided a causal test of our hypothesis. Stimulation perturbed population responses along different axes; behavioral impact depended on whether those perturbations aligned with the axis of correlated variability. This result supports the idea that downstream circuits are most sensitive to changes along this axis.

*Correlated variability as a handle on cognition*

Although correlated variability has primarily been studied from a basic science perspective, our results have translational implications. Correlated variability can be modulated by cognitive states, pharmacological agents, and direct circuit manipulations. If it indeed reflects the information flow from sensory cortex to decision-making circuits, the possibilities for measuring and changing it are endless. Indeed, it is straightforward to modulate correlated variability using existing pharmaceuticals as well as by natural cognitive processes. Our results suggest that correlated variability may provide a powerful biomarker and a potential intervention target for repairing or enhancing perception in health and disease.

In sum, our results reveal that the axis of correlated variability is not just a nuisance byproduct of cortical computation. It is a window into the aspects of neural population activity that flexibly link sensory representations to behavior. By reframing variability as an adaptive feature rather than a limitation, this work offers new insight into the neural basis of perception and points to shared variability as a promising target for understanding and influencing cognition.

# Methods

## Experimental Subject Details

We analyzed data from four different datasets, detailed below:

* Change detection experiment (Figure 1): Subjects were two adult male rhesus monkeys (*Macaca mulatta*, 8 and 10 kg).
* Curvature estimation experiment (Figure 3-4): Subjects were two adult male rhesus monkeys (*Macaca mulatta*, 8 and 9 kg).
* Curvature-color 2AFC experiment (Figure 5): Subjects were two adult male rhesus monkeys (*Macaca mulatta*, 11 and 10 kg).
* Dot direction estimation experiment (Figure 6): Subjects were two adult male rhesus monkeys (*Macaca mulatta*, 8 and 10 kg).

Before training, all monkeys were surgically fitted with a customized titanium head-post (Crist Instruments Co., Hagerstown, MD). Monkeys were then trained to perform their respective tasks until satisfactory performance was reached. To enable electrophysiological recordings, we chronically implanted monkeys with 96-channel microelectrode arrays (Blackrock Neurotech, Salt Lake City, UT) for recordings in V4 or acute recording chambers over area MT. For the acute recordings, we used 24 or 32-channel linear probes (V- and S-probes; Plexon Inc., Dallas, TX) positioned using grids (Crist Instruments Company Inc., Hagerstown, MD) and advanced using a hydraulic microdrive (Kopf Instruments, Tujunga, CA). All animal procedures for experiments in Figures 1, 3, 4, and 6 were approved by the Institutional Animal Care and Use Committees of the University of Pittsburgh and Carnegie Mellon University, where the electrophysiological and psychophysical data were collected. Animal procedures for experiments in Figure 5 were approved by the Institutional Animal Care and Use Committees of the University of Chicago. Additionally, all data and analyses in this study are reported in accordance with ARRIVE animal use and reporting guidelines.

Curvature estimation experiment (Human version)

We conducted an online psychophysics experiment in which humans reported the curvature of 3D shapes identical to those used in the monkey version shown in Figure 3. These experiments were approved by the Institutional Review Board (IRB) of Carnegie Mellon University. The experiment was conducted on the online psychophysics platform, Gorilla ([www.gorilla.sc](http://www.gorilla.sc)80), and 40 human subjects (ages 19-64; average age 28) were recruited via Prolific ([www.prolific.co](http://www.prolific.sc)) between February 7 and 11, 2022. Participants were randomly assigned to one of two groups that each reported the curvatures of five random shapes and their orientation and curvature variations. Because this study was conducted online, we included additional measures to ensure task compliance. We collected data from three questionnaires, which included compliance, demographics, and feedback, per the IRB protocol. Additionally, we detected their monitor size and scaled images accordingly. We confirmed the image size via a standardized credit card size check protocol.

## Experimental Methods

### Common Experimentation Apparatus

Visual stimuli were displayed on a 24” ViewPixx monitor (1920 × 1080 pixels; 120 Hz refresh rate) or a CRT monitor (1024×768 pixels; 120 Hz refresh rate), both calibrated to linearize intensity, placed 52-60cm away from the monkey. The behavioral experiments (behavioral monitoring, visual display, reward delivery, experimental, and data syncing) were performed using custom MATLAB software and the Psychophysics Toolbox81. A square marker on the screen was flashed at the onset of stimuli, which was captured by a photodiode to synchronize the stimulus display with data acquisition. We monitored eye position using an infrared eye tracker (EyeLink 1000 Plus; SR Research). Spiking activity, local field potentials, eye position, and task events were recorded at 30K samples/s using either CerePlex E headstage and CerePlex amplifier (Blackrock Neurotech, Salt Lake City, UT) or Trellis software and Ripple recording hardware (Ripple, Salt Lake City, UT).

### Common behavioral, electrophysiological recording, and analysis considerations

Filtering and spike thresholding: We band-pass filtered (250-5000 Hz) the raw electrical activity (acquired at 30K samples/s) and detected threshold crossing timestamps on each recording channel with a manually set threshold (2-3x RMS signal value for each channel). These spiking events, the original raw data, and stimulus-locked photodiode activity were all saved at 30 KHz, and the eye tracking signals were saved at 2 KHz. In this study (as in previous studies from which these data originate), we did not distinguish between sorted single-unit and multi-unit activity.

Baseline response: In all datasets, we calculated the baseline response during the trial epoch after stable fixation and before the onset of the visual stimulus. During this time, the monkey was fixating on a central dot displayed on a gray screen. In most experiments, we varied this duration between 150 and 250 ms, drawing randomly for each trial from a uniform distribution to prevent the monkey from learning the precise timing of the task. We calculated the spike rate for each unit during a fixed, minimum duration for each session.

Stimulus response: We calculated the stimulus-evoked spike rate after a latency of 50 ms (to allow for latency of responses in V4 and MT) during the stimulus display epoch for trials with stable fixation. The details of stimulus durations were specific to each experiment and are detailed below.

Neuron inclusion: For all population-level analyses, we only included units if their average stimulus-evoked response was at least 10% higher than during the baseline, gray-screen period.

Trial inclusion: In all datasets, we analyzed only trials in which the monkey completed either correctly or incorrectly. We excluded trials during which the monkey made a premature saccade to break fixation or those where we detected spurious electrical noise artifacts in the neural recordings.

Calculation of the axis of correlated variability: We performed Principal Components Analysis (PCA) on the baseline activity for each session and defined the axis of correlated variability as the first principal component of this activity. In previous studies2,12,30, we have calculated this axis, spike count correlations, or the covariance matrix using repeated presentations of the same stimulus. We repeated this analysis for the curvature estimation dataset for sessions with more than 100 repetitions of the same base shape. We found that the two axes thus calculated were parallel (correlation r = 0.86; p<0.001). Since the baseline response can be measured during every trial, we opted to calculate the axis of correlated variability using this response.

### Change detection experiment

We analyzed data from a previously published dataset in which monkeys performed a cued attention change-detection task while we recorded neuronal activity from area V49,29. Briefly, we analyzed data from a subset of 20 sessions during which the monkeys performed a variant of the change detection task with multiple starting orientations but a constant change amount. During instructional trials, monkeys fixated a central dot while we flashed a single Gabor at the location where the orientation was likely to occur. During subsequent trials, monkeys maintained central fixation while two peripheral Gabor patches were flashed repeatedly (200 ms on, 200-400 ms off). These Gabors had an orientation drawn from a limited set of either [0°, 45°, 90°, 135°] or [0°, 36°, 72°, 108°, 144]. At a random time, the orientation of the Gabor at the cued location changed, and the monkeys were rewarded for making a saccade to the changed stimulus. The orientation change amount was constant throughout the session at either 45° or 36°, depending on the starting orientation set. Spatial attention was manipulated in blocks of trials, each starting with a set of instructional trials. In this study, we only analyzed 80% of the trials in which the change occurred at the cued location. The stimulus responses were calculated for each flash during the 60-130ms epoch after stimulus onset. Average behavioral performance for each session was calculated as the percentage of hits in detection. Miscellaneous experimental details of session inclusion, mean firing rates, receptive field mapping, etc., can be found in the original publications9,21,29.

### Curvature estimation experiment

We analyzed data from a previously published dataset in which monkeys performed a continuous curvature estimation task while we recorded activity from area V439. Briefly, we analyzed data from a subset of 82 sessions during which monkeys fixated a central dot presented on a gray screen while a randomly generated 3D stimulus was shown in the joint RF of V4 neurons for 550-800ms. For each session, 3-6 stimuli were drawn from a set of 120 base shapes that vary in overall shape (thickness profile, gloss, twist, length, out-of-plane rotation, etc.) or in-plane orientation only or color only. The curvature of the selected shapes was varied, drawn from a uniform distribution across trials in 20 (monkey 1) or 10 (monkey 2) steps. After the stimulus presentation period, a target arc was presented in the upper hemifield. In a majority of sessions, a 140° target arc was presented centrally (82 sessions). In a non-overlapping set of sessions (57 sessions; relevant for analyses in Figure 4), either the angular position (0° or +-20°) or the length of the arc (100° or 140°), or both, were randomized across trials. After the presentation of the arc, the monkeys made a saccade to the arc to indicate their curvature inference. These saccade directions were converted to curvature inference by mapping the possible saccades (-70° to 70° on the 140° centrally presented arc, say) to a scale of 0-1. The reward amount fell linearly along the arc centered on the correct curvature value up to a threshold (+-0.1), after which it fell to 0. We calculated the stimulus-evoked firing rate for each unit during an epoch of 50-550 ms after stimulus onset to allow for V4 response latencies. We calculated the arc-evoked firing rate during an epoch of 0-150 ms after the onset of the arc. Average behavioral performance was calculated for each shape across curvature variations as one minus the average absolute error in curvature judgement. Details about stimulus construction, behavioral timing, reward landscape, and RF mapping can be found in the original manuscript39.

### Curvature-color 2AFC experiment

We analyzed behavioral and neural data from V4 in a two-feature discrimination two-alternative forced-choice (2AFC) experiment. Data from monkey 1 were analyzed and discussed as part of a previous manuscript39. We added additional data from monkey 1 and repeated experiments in monkey 2. Briefly, 25 shape stimuli were created by varying the color between gray and blue (isoluminant) in 5 steps and the ‘curvature’ of the stimuli in 5 steps. The curvature was varied by creating homeomorphs of stimuli between an equilateral triangle and a circle using linear interpolation. After the monkey fixated a central dot for 150-250 ms, two shapes that either shared a common curvature value or a common color were sampled from the grid of 25 stimuli and presented in opposite hemifields (with one stimulus location overlapping the joint RFs of V4 neurons). The stimuli were displayed for 200-250 ms, after which the fixation point was removed, serving as a go cue for the monkey to make a saccade to one of the two stimuli. The monkey was rewarded with a drop of juice for selecting the stimulus that was bluer and more circular. We calculated the stimulus response during a window of 50-200 ms after stimulus onset for each trial. We measured behavioral performance (psychometric) curves by calculating the difference in value of the visual feature (color or curvature) that the monkey can use to guide behavior between the stimulus in the RF and the stimulus in the opposite hemifield. This difference could take eight values between -4 and 4, excluding 0, as we did not present two identical stimuli. Psychometric curves in Figure 5 depict the probability that the monkey chose the stimulus in the RF for each comparison.

### Dot direction estimation experiment

We analyzed data from experiments in which monkeys performed a continuous random dot direction estimation task while we recorded neural activity in the middle temporal area (MT) (Figure 6). Different aspects of this dataset (e.g., behavior, reward relationships under various contexts, etc.) have been analyzed in a previous manuscript82. Briefly, monkeys fixated a central dot on a gray background before a target ring was presented for 200-400 ms. Then, as the monkeys continued to fixate, a dynamic random dot kinematogram was displayed at a location that overlapped the RF of the MT neurons. Monkeys were rewarded for making a saccade to a location on the target ring that corresponded to the direction of the kinematogram, not where the target ring intersects the dot motion vector. Behavioral accuracy was calculated as the slope of the linear relationship between the actual dot direction and the monkey’s saccade direction. Unlike the other datasets in this manuscript, the neural data in this experiment were recorded using linear probes with 24 or 32 channels, rather than microelectrode arrays; however, the data were acquired, pre-processed, and analyzed in the same manner. The probes were inserted such that recorded MT units had highly overlapping RFs but different direction tuning preferences. The RFs and direction tuning preferences were measured using an independent experimental protocol to guide stimulus placement and selection of microstimulation sites.

In subsets of trials, one of two pre-selected contacts was microstimulated using a biphasic, 200 Hz pulse train with an amplitude ranging between 20 and 40 µA. During *long-stim* trials, this pulse train temporally overlapped the visual stimulus. We used these trials to measure the behavioral effect of microstimulation on that channel, calculated as the difference between the slope relating the dot direction to the saccade direction. During *short-stim* trials, the pulse train started ~140 ms after stimulus onset and lasted for 50 ms. We quantified the effect of this short microstimulation train by calculating the stimulation-evoked spike rate for each recording site during the epoch 50 ms after the termination of the last pulse and lasting 100 ms. (We tried 50 ms, 100 ms, and 150 ms epoch durations and found qualitatively similar results.) Other details of RF mapping, session selection, and behavioral training and timing can be found in the original manuscript82.

### Curvature estimation experiment (Human version)

Since the curvature estimation task is bounded on both ends, subjects routinely overestimate lower curvatures and underestimate higher curvatures. Additionally, we aimed to eliminate the possibility that idiosyncrasies in learning history contributed to any systematic variation in behavioral performance between the two monkeys. It was not feasible to repeat the curvature estimation experiment with many more monkeys, so we designed an online human psychophysics experiment to be run on a large cohort of people, providing us with a baseline to compare monkey performance to. After a set of compliance- and demographics-related questionnaires, humans performed a slider-based version of the curvature estimation experiment where a horizontal slider was presented with a stimulus image. The initial position of the slider was randomly set across trials, and humans had to use their computer mouse to select a value between 1 and 10 in steps of 0.1. The stimulus images were drawn from the same image set used for the monkeys. We divided our human cohort (n = 40) into two groups. Each group was shown 20 curved variations of 20 shapes (five base shapes at four orientations each). After each trial, the correct curvature was indicated on the slider along with their choice. The maximum time allowed per trial was 4 seconds. We recorded each choice and reaction time. No subject was excluded from analysis.

## Statistical Analysis and Quantification

### Calculation of stimulus axes and comparison with behavior

To quantify the visual information content that is aligned with the axis of correlated variability, we calculate the correlation of the projection of evoked responses on the axis of correlated variability with the stimulus feature. Where appropriate, we also calculate a feature-specific decoder by training a cross-validated linear regression model and compare the decoder performance with the correlation found above. This common analysis across all our datasets forms the scaffolding of the various tests of our central hypothesis. The details of these analyses are experiment-dependent and are detailed below:

Change detection experiments: We first projected the responses for all oriented gratings on the axis of correlated variability. Then, for each starting and change orientation pair, we calculated the performance of a leave-one-out cross-validated linear model for classifying the two orientations. Of all pairs, we selected the most and least aligned pairs and compared the behavioral performance for those pairs (Figure 1C).

Curvature estimation experiments: For each recording session and base shape, we first projected all stimulus-evoked responses onto the axis of correlated variability. We correlated these projections with the curvature feature value. In other words, we compared the performance of a linear curvature decoder trained on the stimulus-evoked responses projected onto the axis of correlated variability. For each pair of shapes in a given session, we defined the most and least aligned shapes as the ones that had the highest and lowest correlations (or decoding performance). We then compared the average behavioral performance (one minus the average absolute behavioral error) for those two shapes (Figure 3H).

Arc manipulation experiments: To test whether behavioral planning-related activity or feature-related activity varies along the axis of correlated variability, we trained two linear decoders on the activity immediately following the onset of the target arc – one to decode the curvature of the visual stimulus (like above) and one to decode the planned saccade. We compared the performance of these decoders with the performance of curvature and saccade decoders trained on the same responses but projected onto the axis of correlated variability (Figure 4D). We did this separately for each shape (although previous results suggest that a shape-general curvature and saccade decoder would also work just as well39). We calculated the difference between the decoder prediction accuracies of the curvature decoders and the saccade decoders. We found a larger drop in curvature decoding performance when projected onto the axis of correlated variability (Figure 4E).

Curvature-color 2AFC experiments: To test whether the information about the visual feature that the monkey uses to guide behavior is the one has the larger projection on the axis of correlated variability, we split each session into two sets of trials – ones in which the monkey uses color to guide choices (trials during which the curvature of the two shapes was the same), and ones in which the monkey uses curvature to guide choices (trials during which the color of the two shapes was the same). We projected the responses of these trials on the axis of correlated variability and correlated them with the respective feature value. We found that when the monkey uses curvature to guide decisions, curvature can be decoded on the axis of correlated variability, but not when the monkey uses color to guide decisions (Figure 5E).

Dot direction estimation experiments: To causally test if stimulating neural activity along the axis of correlated variability would have a greater behavioral effect (versus stimulating orthogonal to it), we quantified the neural and behavioral effects of microstimulation. First, we calculated the projection of the effect of microstimulation on the neural responses (measured as the short stimulation-evoked population response vector; details above) on the axis of correlated variability. We performed this analysis separately for both stimulation sites and identified the site with the larger projection. Then, from the long-stim trials, we calculated the size of the behavioral effect of microstimulation (measured as the difference in the slope of the psychometric curve with and without stimulation; details above). We plotted the size of the behavioral effect against the projection on the noise axis calculated above (Figure 6E).

### Statistical tests

In most cases, we used non-parametric tests (Wilcoxon signed-rank test or the Mann-Whitney U test) to test for the hypothesis that two sets of randomly selected samples come from the same bounded or unbounded distribution. The sample sizes are indicated in the figure panel and/or legend.

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