**A diagram of a change detection task

AI-generated content may be incorrect.Figure 1: Behavioral performance in an orientation change detection task is related to the alignment between V4 orientation representations and the axis of correlated variability.**

**A.** Schematic of the orientation change detection task. Two Gabor stimuli with the same initial orientation are flashed repeatedly, and one changes orientation at a random time picked from an exponential distribution. Monkeys are rewarded for making a saccade to the location of the orientation change within 500 ms. (AMY REFS XX) On each trial, the initial orientation was randomly selected between 0° and 180°, while the magnitude of the change was constant across trials. The stimulus most likely to change was cued in blocks (80% valid). We analyzed trials in which the change occurred at the cued location when that location was within the joint receptive fields of the recorded V4 neurons.

**B.** We defined the *axis of correlated variability* as the first principal component of V4 activity during the period where the monkey fixated a gray screen before the first stimulus presentation (gray dots represent these baseline responses). Black dots represent evoked responses to stimuli with different orientations. Our hypothesis predicts that performance is better when the orientation change aligns with the axis of correlated variability (most aligned change; orange arrow) than when it does not (least aligned orientation change; green arrow).

**C.** Validation of the prediction in B. Across sessions, monkeys performed better (had higher hit rate) on the best aligned than on the least aligned orientation change (p<0.05; Wilcoxon signed-rank test). Each dot represents one experimental session (n=20). Marginal histograms show the distribution of hit rates across sessions. The red plus sign and red dashed lines denote man values.

**A diagram of a function

AI-generated content may be incorrect.Figure 2. Alignment of stimulus information with the axis of correlated variability makes correlated variability axis optimal for readout.**

**A.** Recurrently connected network composed of excitatory and inhibitory units with rank-one feed-forward weights (blue), recurrent weights (grey), and linear readout weights (orange). A stimulus enters through . Independent private noise is injected into each neuron and is shaped only by . The network connectivity follows Dale’s law.

**B.** In a generic rank-one network, the stimulus axis (blue arrow) can lie at an arbitrary angle to the first principal component of baseline activity (PC1, grey dots). However, theory and data show that learning tunes the recurrent weights ​so that their slowest dynamical mode aligns with the feed-forward drive conveyed by (Chadwick et al., 2023). After learning-related tuning of *WF*, stimulus-evoked activity rotates onto PC1, making the *noise axis* and *coding axis* one and the same.

**C.** Once this alignment is established, fluctuations along PC1 decay much more slowly than along any orthogonal mode. Power on the slow mode (black curve) persists, whereas power on, for example, PC2 (light grey) vanishes rapidly. Assigning the task-relevant input to the slowest decaying dimension enables the circuit to integrate information over time, providing a normative rationale for the recurrent tuning.

**D.** We examine a linear readout whose axis (orange) forms an angle with the recurrent / noise axis (blue).

**E.** Normalized signal (blue) and noise (gray) variance delivered to the read-out as a function of . Signal variance decreases more steeply than noise variance as the read-out is rotated away from the axis of correlated variability.

**F.** Fisher discriminability peaks at demonstrating that, when the stimulus and noise axes are aligned, the optimal linear decoder is along the noise axis.

A collage of diagrams and graphs

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**Figure 3: Curvature estimation performance is related to the alignment of the curvature representation with the axis of correlated variability in V4.**

**A.** Schematic of the continuous curvature estimation task. Monkeys report the medial axis curvature of a 3D shape while ignoring irrelevant features like color, orientation, or thickness profile (FLEXIGAIN REF XX). Stimuli are presented within the joint receptive fields of the recorded V4 neurons. Monkeys are rewarded for making a saccade to the appropriate location on the target arc (left end for straight stimuli, right end for maximally curved stimuli). Monkeys are rewarded in inverse proportion to their estimation error.

**B.** Behavioral responses of two monkeys (green and blue) plotted as mean reported curvature (normalized from 0 to 1) across various shapes, colors, and orientations. The shaded portion shows the standard deviation. Human participants who indicated the curvature of the same shape stimuli using a slider (pink) performed comparably to the monkeys (r=0.97 between human and monkey choices for matched curvatures).

**C.** Our hypothesis predicts that performance for a shape with a curvature representation that aligns with the axis of correlated variability is better than one that does not.

**D.** Example curvature tuning for three V4 multi-units for one shape. Shaded regions indicate standard error of the mean (SEM).

**E.** Stimulus responses of the units in D plotted relative to each other (black to orange dots are curvature responses to low to high curvatures) and to their respective baseline responses (blue dots).

**F.** Curvature tuning of the first three principal components for three shapes (orange, green, and blue). The shaded region represents the standard error of the mean of the eigenvalues for each component.

**G**. Projections onto the three PCs in F are plotted relative to each other. Conventions as in E.

**H.** Validation of the prediction in C. Each dot represents performance (defined as average error across all trials) for a pair of shapes tested during the same experimental session. Performance was better for the shape that happened to be better aligned to the axis of correlated variability (p<0.001; Wilcoxon signed-rank test). Conventions as in Figure 1C.

**A collage of diagrams and graphs

AI-generated content may be incorrect.Figure 4: The axis of correlated variability aligns with planning-related signals in V4.**

**A.** In a subset of sessions, the length and angular position of the target arc varied across trials.

**B.** Monkeys reconfigure their mapping between curvature judgement and saccade. Mean choice behavior across three arc conditions (the dashed condition is the same across the two panels for comparison) for the two monkeys (colors). Left: across two conditions with shared mapping for lower curvatures (-70°) but different mapping for higher curvatures (+70° vs +30°), saccades diverge for high curvatures. Right: across two conditions with the same arc length (100°) but different angular positions (midpoint at 0° vs -20°), psychometric curves for the two conditions have a vertical offset (32 shapes for monkey 1, 34 shapes for monkey 2).

**C.** Our hypothesis predicts that if V4 responses are modulated such that they reflect the planned saccade (FLEXIGAIN REF XX), then the saccade decoding axis should be better aligned with the axis of correlated variability than the curvature decoding axis.

**D.** Validation of the prediction in C. The saccade decoding axis is better aligned with the axis of correlated variability than the curvature axis. While both curvature (green) and planned saccade (orange) can be readily decoded from V4 responses, those projected onto the axis of correlated variability are more predictive of saccade (orange dashed) than curvature (green dashed) (mean curvature prediction falls by 0.39 p<0.001 t-test, mean saccade direction prediction falls by 0.12 p<0.001 t-test; n=117 shapes.)

**E.** The difference in curvature prediction accuracy between the curvature axis and the axis of correlated variability (y-axis) is much larger than the difference in the saccade prediction accuracy between the saccade axis and the axis of correlated variability (x-axis) (p<0.0001 Wilcoxon signed-rank test; n=117 shapes). Conventions as in Figure 1C.

**A collage of diagrams and graphs

AI-generated content may be incorrect.Figure 5: The axis of correlated variability aligns with the visual feature that is relevant for behavior.**

**A.** Schematic of a two-alternative forced choice task in which monkeys make either curvature-based or color-based choices (FLEXIGAIN REF). If the two stimuli have the same color, the monkeys are rewarded if they make a saccade to the more circular shape. If the two stimuli have the same shape, the monkeys are rewarded if they make a saccade to the bluer stimulus. One of the stimuli is presented in the joint receptive fields of V4 neurons.

**B.** Pairs of stimuli are selected from either the same row (curvature trials) or the same column (color trials).

**C.** Both monkeys reliably make choices based on color and curvature on interleaved trials (30 sessions for monkey 1, 27 sessions for monkey 2; 268 and 96 color-based trials and 246 and 96 shape-based trials on average for each monkey, respectively).

**D.** Our hypothesis predicts that the axis in V4 representing the currently relevant feature will be more aligned with the axis of correlated variability.

**E.** Validation of the prediction in C. When the monkey makes curvature-based choices, the projection of V4 responses onto the axis of correlated variability predicts the curvature of the stimulus more accurately than when the monkey makes color-based choices (p<0.005; Wilcoxon signed-rank test). Each dot represents a single session and corresponds to the correlation between stimulus curvature and projection onto the axis of correlated variability, averaged across trials when the monkey makes curvature-based choices (x-axis) versus color-based choices (y-axis).

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**Figure 6: Causal test of our central hypothesis: the behavioral impact of electrical microstimulation is largest when it is aligned with the axis of correlated variability.**

**A.** Schematic of our motion direction estimation task in which monkeys estimate the direction of a random dot kinematogram displayed in the joint receptive fields of MT neurons recorded using linear probes (DOUG REF XX). The trial structure is illustrated on the right. After assessing the direction selectivity of recording sites in an independent mapping experiment, we chose two electrodes for electrical microstimulation. After the monkey fixated a central spot and the target ring appeared, the visual stimulus was presented. Monkeys were rewarded for accurately estimating the direction of motion by making a saccade to a corresponding point on the target ring. On some randomly interleaved trials, either a long period of microstimulation (long-stim; for the full duration of the visual stimulus) or short microstimulation train (50 ms) was applied on one of two selected electrodes. We analyze the impact of microstimulation on MT responses during the marked analysis period (gray shaded region; 50 to 150 ms after the last stimulation pulse). We compared the monkey’s behavior on no-stim and long-stim trials. We selected the short-stim parameters to minimize the behavioral impact of stimulation while maximizing the neural impact. This design followed the logic in (REF XX; from Moore and Armstrong, 2003ish).

**B.** Example direction estimation behavior in no-stim and long-stim trials for one session. The two stimulation electrodes had preferred directions of 20° and 300°, respectively, and stimulation biased the monkey’s choices toward those directions. We quantified the behavioral effect as the difference in the slope of the linear fits in the no-stim and long-stim conditions (slopes are indicated in the labels at the bottom right).

**C.** Example z-scored response histogram across all dot stimuli for the recording sites along the probe for no stimulation (left) and short-stim trials (right). The short 50 ms stimulation pulse train was delivered on the third site (indicated by the red box). We evaluated the effect of the stimulation by using a 100 ms response window after the end of stimulation to calculate a response vector for each of the two stimulation sites in every experimental session.

**D.** Our hypothesis predicts that choices will be most affected by electrical microstimulation when stimulation moves neural activity along the axis of correlated variability.

**E.** Validation of the prediction in D. For each session (two connected dots), we identified the stimulation electrode that moved MT population activity in a direction that was more aligned with the axis of correlated variability. For each electrode, we calculated the vector of population activity defined by the firing rate of each neuron on short-stim trials. We then calculated the projection of this vector onto the axis of correlated variability (x-axis; orange dots represent the electrode with the larger projection, so, by definition, orange dots are to the right of their respective green dots representing the other stimulation electrode). The impact of microstimulation on choices (difference in slope between long-stim and no-stim trials) is larger for better-aligned stimulation vectors (a majority of orange dots are above their respective green dots). Mean behavioral effect for more vs less aligned short-stim vector = 0.39 vs 0.26 as depicted by the open circles on the right (error bars indicate SEM).