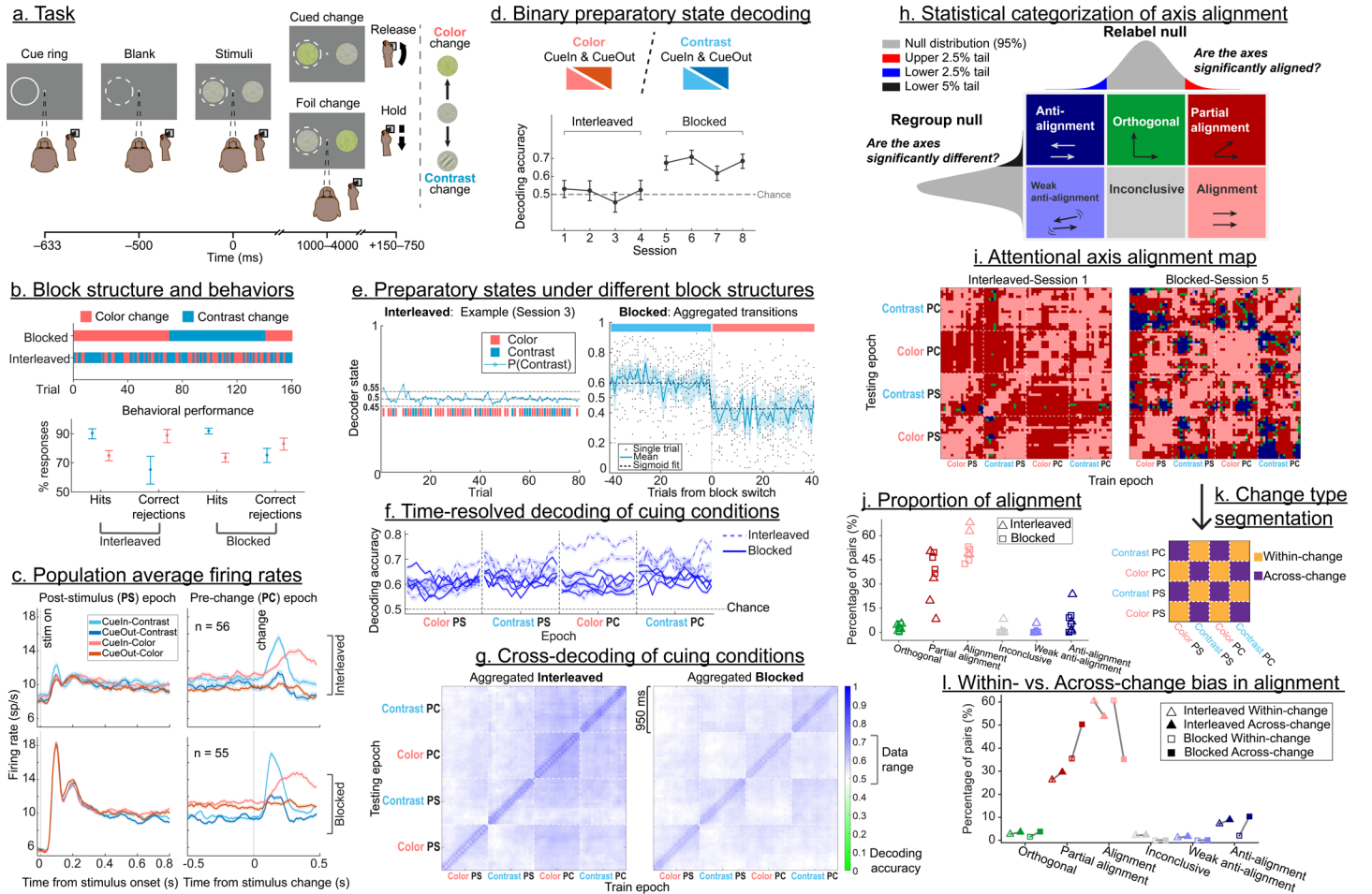# Strategic reshaping of the attentional axis in superior primate colliculus

Summary: Visual attention is used dynamically in natural environments, deployed focally to objects, locations, or features for resolving subtle details and relaxed when viewing clear, unambiguous scenes. However, laboratory work usually uses fixed conditions to isolate attentional effects, creating a paradox: behaviorally, attention is understood to be influenced by multiple internal and stimulus-driven factors, but neuronally, it is often characterized as a simple, low-dimensional gain modulation. To resolve this, we investigated how the geometry of attention in the superior colliculus (SC) adapts as the predictability of task demands varies.

We recorded from SC neuronal populations while monkeys performed a covert attention task with both subtle color changes and supra-threshold contrast changes presented in sessions featuring either an unpredictable (interleaved) or predictable (blocked) structure. Only one type of change happened in each trial, and no information about the type was provided before the change. In predictable sessions, SC neuronal activity preceding the change event revealed change-type-specific preparatory states not observed in unpredictable sessions. At block transitions, preparatory activity switched abruptly to reflect the demands of the new change type. Crucially, geometric analysis showed that switches in preparatory activity were not simple gain modulations. Instead, comparing the attentional axis between the two change types revealed a fundamental geometric reconfiguration: the axis in contrast blocks was sometimes orthogonal or even inverted relative to the axis in color blocks.

These findings offer a resolution to the paradox between multifaceted attentional behavior and its seemingly simple neuronal correlates. The apparently low-dimensional neuronal manifestation of attention may be an artifact of simplified tasks. Dynamic geometric reconfiguration may be a core computational strategy, enabling flexible prioritization of features, objects, and locations to guide behavior in natural environments. Uncovering the universality of these adaptive mechanisms will require experimental paradigms that embrace, rather than constrain, the dynamic nature of cognition.

Additional details:

a. Task

d. Binary preparatory state decoding

h. Statistical categorization of axis alignment

i. Attentional axis alignment map

b. Block structure and behaviors

e. Preparatory states under different block structures

c. Population average firing rates

f. Time-resolved decoding of cuing conditions

g. Cross-decoding of cuing conditions

j. Proportion of alignment

k. Change type segmentation

l. Within- vs. Across-change bias in alignment

Methods: Neuronal and behavioral data were collected from monkeys performing a covert change detection task (**Fig. a**). While maintaining central fixation throughout the trial, monkeys were required to release a joystick in response to changes at a cued location and ignore changes at an uncued foil location by holding the joystick. Two types of changes were possible in each trial: a threshold-level saturation (color) change or a suprathreshold contrast change. Depending on the session, color and contrast trials were either interleaved or grouped by type in blocks (**Fig. b**). The trial structure and components were identical for both change types, differing only in the change event itself. The results presented here are based on 112 neurons from the intermediate SC of one monkey (P), with a second monkey (R) showing quantitatively comparable findings.

To quantify change-type-specific preparatory activity, we trained linear support vector machines (SVMs) on population activity in the 500-ms window before the change to classify color and contrast trials (**Fig. d**). Using a leave-one-out cross-validation scheme, we estimated posterior probabilities from SVM scores to track the trial-by-trial confidence of the change-type classification (**Fig. e**). Separately, we trained a second set of SVMs to decode the cued location (in vs. out of the receptive field) using a sliding-window, cross-temporal approach (150-ms window and 50-ms step; **Fig. f, g**). This analysis was applied to both color and contrast trials across two epochs: post-stimulus (PS; 50–1000 ms) and pre-change (PC; -950–0 ms). To analyze the geometry of the attentional axis, we computed the cosine similarity between SVM weight vectors. Similarity values were statistically categorized by comparing them against two null distributions (**Fig. h**). A **Relabel** null, created by randomly shuffling the cue in/out labels, was used to determine if the axes were significantly more aligned than chance. A **Regroup** null, created by keeping trial labels intact but randomly regrouping the trials from both decoders into two new sets, was used to test if the two axes were significantly different. This null distribution provides the expected similarity under the hypothesis that no true difference exists between the two trial groups being compared. Combining the two tests allowed us to classify the alignment between axes into geometric categories.

Results: Behavioral performance was comparable for both peri-threshold color and supra-threshold contrast changes (**Fig. b**). Beyond the expected differences in change-evoked activity (**Fig. c**), we found that blocking trials by change type induced distinct preparatory neuronal states: change type was readily decodable from pre-change activity in blocked, but not interleaved, sessions (**Fig. d**). Trial-by-trial SVM posterior probabilities confirmed this finding: during interleaved sessions, the decoder state hovered near chance, but during blocked sessions it switched sharply at block transitions (**Fig. e**). This indicates that monkeys were aware of the block structure and adapted their preparatory states accordingly. These distinct states resemble a simple change in attentional gain—as pre-change firing rates show greater modulation for color than contrast (**Fig. c**)—an idea supported by the neural code's generalizability across both time and change type (**Fig. g**). However, despite being generally cross-decodable, geometric analysis revealed rich dynamics of attentional modulation. To directly inspect the attentional axes, we categorized their alignment across time and changes using the two-null method illustrated graphically in **Fig. h**. While Alignment and Partial alignment were the most frequent relationships overall (**Fig. i, j**), a striking pattern emerged when comparing within- vs. across-change types (**Fig. k**). In interleaved sessions, the geometry was stable, showing no systematic difference between within- and across-change comparisons (**Fig. l**, minimal separation between open and filled triangle markers). In contrast, blocking induced a dramatic reconfiguration where the attention axis changed far more across change types than within them. This was marked by a significant decrease in *Alignment* and a corresponding increase in *Partial alignment* (rotation) and *Anti-alignment* when comparing across changes (**Fig. l**, larger separation between open and filled square markers). This demonstrates active reshaping of the SC's neural geometry, rotating the attentional axis to create distinct representations tailored to specific task demands.

Our findings suggest a unifying principle explaining the SC's diverse cognitive roles. The apparent conflict between abstract cognitive encoding and more fixed participation in oculomotor control may be an artificial construct of static tasks. We propose the SC's functional architecture is geometrically plastic. The SC may dynamically reconfigure its coding axes to sculpt task-specific subspaces on the fly. This would be a fundamental mechanism for cognitive flexibility, revealed only by paradigms that emulate the shifting demands of natural behavior—those that we must strive to create in the laboratory.