Adaptive shape processing in primary visual cortex

Justin N. J. McManus^a, Wu Li^b, and Charles D. Gilbert^{a,1}

^aLaboratory of Neurobiology, The Rockefeller University, New York, NY 10065; and ^bState Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing 100875 China

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The ability to derive meaning from complex sensory input requires the integration of information over space and time, as well as cognitive mechanisms to shape that integration. We studied these processes in the primary visual cortex (V1), where neurons are thought to integrate visual inputs along contours defined by an association field (AF). We recorded extracellularly from single cells in macaque V1 to map the AF, by using an optimization algorithm to find the contours that maximally activated individual cells. We combined the algorithm with a delayed-match-to-sample task, to test how the optimal contours might be molded by the monkey's expectation for particular cue shapes. We found that V1 neurons were selective for complex shapes, a property previously ascribed to higher cortical areas. Furthermore, the shape selectivity was reprogrammed by perceptual task: Over the whole network, the optimal modes of geometric selectivity shifted between distinct subsets of the AF, alternately representing different stimulus features known to predominate in natural scenes. Our results suggest a general model of cortical function, whereby horizontal connections provide a broad domain of potential associations, and top-down inputs dynamically gate these linkages to task switch the function of a network.

The cortical processing of sensory information is shaped by the spatial and cognitive context surrounding the sensory stimulus. In visual perception, the very appearance of local image regions is determined not by the regions themselves, but by their relationship to the surrounding visual scene (1). In visual cortical areas with small to intermediate receptive fields (RFs), these contextual influences are manifested by the interaction between stimuli falling within the classical RF (cRF) and stimuli in the extraclassical RF surround (2–5). Likewise, the behavioral context in which a scene is viewed shapes both the observer's perception and the underlying neural responses (6, 7). It is well established that space-, feature-, and object-based attention modulate the gain of neural responses (8–15), and recent evidence suggests even more profound cognitive influences on sensory processing (2, 9, 16–18).

In the primary visual cortex (V1), contextual interactions between the cRF and the surround imbue neurons with integrative properties that likely underlie a range of important visual functions, including contour integration (2, 14, 19), image segmentation (4), perceptual fill-in (20), and perceptual learning (16). It has been proposed that much of this computational sophistication in V1 derives from the plexus of horizontal axon collaterals that run parallel to the cortical surface and that these collaterals integrate visual information over an association field (AF) of spatial interactions (21). The AF (22) is a theoretical construct that forms the basis for current neural network models of V1 (20, 23); according to the theory, V1 neurons with cocircular RFs (RFs that respond optimally to segments of common linear or circular arcs) share the strongest horizontal connections in the network (Fig. S1). This connectivity pattern would implement a basic building block of image segmentation and object recognition, by computationally linking the segments of contours and object boundaries, and it would form the basis of fundamental perceptual qualities, like the Gestalt rules of perceptual grouping. Still, the actual ge-

ometry of the lateral contextual interactions, the very feature thought to endow V1 with its integrative functions, has never been fully characterized. Moreover, previous results have shown that contextual interactions in V1 are subject to dynamic cognitive control (2, 9, 16), raising the possibility that an AF in V1 might undergo concomitant behavioral modulations.

Here, we map the AF in V1 and survey its plasticity under different behavioral states. We trained three monkeys (monkeys A, B, and C) to detect the presence of a cued contour flashed within a field of random line segments (Fig. 1). By recording the activity of single neurons during the task, we could algorithmically construct contours that maximally activated the recorded neuron under different task conditions (see *SI Discussion* for caveats). We observed dynamic patterns of visuospatial integration that match the theorized AF, conferring V1 neurons with adaptive shape selectivity and a potential role in object recognition (24, 25).

Results

Contour Detection Task and Stimulus Generation. We recorded single neurons in the superficial layers of V1, from trained monkeys performing a contour detection task. Each experiment comprised hundreds of trials of the detection task, whereby a monkey determined the location of a cued contour in a delayed-match-to-sample paradigm (Fig. 1 and *SI Materials and Methods, Task Design*). During the delay period over the course of these trials, we recorded a neuron's responses to geometric stimuli, while the monkey was expecting the cued shape. Before every experiment, we selected a seven-bar contour (a closed circle, a sinusoid, or a straight line; Fig. 1*A*, 2) to serve as the cue in all of the ensuing trials. At the outset of each trial, the cue was presented next to the fixation point, with the central contour segment parallel to the neuron's preferred orientation (Fig. 1*A*, 1). A delay period followed the cue (Fig. 1*B*, 1), during which a stimulus contour, consisting of a number of geometrically aligned contour segments, was presented in the center of two identical fields of randomly oriented bars. The two fields were displayed in opposite quadrants of the computer monitor, with one positioned directly over the RF of the recorded neuron. In each trial, the embedded contour stimulus (Fig. 1*B*, 2) was chosen from a set of shapes created by a contour optimization algorithm (*SI Materials and Methods, Automated Stimulus Generation*). The neural responses to these embedded contours, each repeated over multiple trials, were used by the algorithm to progressively construct the neuron's preferred stimulus over the course of the experiment. At the end of each trial, a seven-bar contour was briefly flashed in each field, just before the fields were extinguished (Fig. 1*C*). The monkey's

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¹To whom correspondence should be addressed. E-mail: gilbert@rockefeller.edu.

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A fundamentally different mode of geometric selectivity was obtained from a neuron recorded while cuing the monkey to detect the circular target (Fig. 3). In its three-bar tuning surface, the cell expressed two broad regions of robust activation, corresponding to different sets of circular contours. This structure was mirrored in the neuron's five-bar surface, which exhibited two peaks along the cocircularity line. Both peaks comprised stimuli whose outermost contour bars were cocircular to the bar in the RF. Close to one

Fig. 2. Shape selectivity for a single neuron recorded during the line detection task. (*Top, Middle, and Bottom*) Responses of the cell (from monkey A) to the three-, five-, and seven-bar stimuli that were generated by the optimization routine. The neuron was recorded during the delay period (Fig. 1) after the monkey had been cued to detect the linear target; the cell displayed a corresponding preference for linear geometries that was apparent for three- and five-bar stimuli.

Fig. 3. Circular optima under the circle detection task. The three-bar (*Top*) and five-bar (*Bottom*) tuning surfaces of one neuron were recorded while monkey B was engaged in the circle detection task. The cell expressed clear selectivity for distinct subsets of circular geometries. The contours at the *Bottom* are the five-bar versions of the target and distracter contours; their colors indicate the corresponding neural responses to these stimuli.

peak, all of the contour bars in each stimulus [e.g., (45° , -65°); (45° , -73°)] were approximately tangent to a single circle; but close to the other peak, the outermost contour bars lay along a broader, open circular arc than the innermost three bars [e.g., (90° , -42°); (90° , -49°)]. The horizontal panel (Fig. 3, *Bottom*) demonstrates that the cell strongly preferred the contours generated by the optimization routine, compared with the distracter- and target-like stimuli. Three characteristic features of our data are evidenced here. First, neuronal response optima were seen as one or more islands of activation—regions of the stimulus space representing contours with a particular spatial scale, radius of curvature, and orientation. Second, neurons were often selective for a contour of a particular orientation and only weakly responsive to the same contour rotated by 180° . Third, most cells were not maximally activated by any of the target or distracter contours the animals were trained to detect; rather, they preferred similar but not necessarily identical stimuli (Figs. S3 and S4).

plane (*SI Materials and Methods, Five-Bar Population Analysis with Sammon's Mapping*). Similar stimuli are mapped to nearby points on the plane, whereas dissimilar stimuli are mapped to distant locations. Fig. 5 demonstrates that V1 neurons can be selective for a diverse range of contours, spanning the whole continuum from lines to circular arcs to undulating contours. The range and complexity of stimulus selectivity seen here reveal a previously undiscovered level of sophistication in V1 shape processing. We additionally color coded the stimuli to indicate the relationship between this stimulus selectivity and perceptual task: the red, green, and blue stimuli elicited strong neural responses under the line, circle, and wave detection tasks, respectively. The clustering of stimuli with the same color

indicates that neurons tended to guide the optimization algorithm toward similar contours under the same task condition. For both monkeys shown here, neurons preferred near-collinear, elongated contours during the line detection task (shown in red). Conversely, neurons steered the optimization toward curved contours during the circle and wave detection tasks (shown in green and blue, respectively). The distribution of preferred stimulus shapes obtained from monkey B (Fig. S5) closely resembles the distribution from monkey C (Fig. 5B), except that contours of the same color do not cluster. Neurons from monkey B also underwent profound changes in their geometric tuning as a function of perceptual task (see next paragraph), but those changes were apparent over the averaged

Fig. 6. Neuronal heat maps are reshaped by task. (A–D) The mean three-bar heat maps averaged over all of the neurons recorded from monkeys A and C during the circle and wave detection tasks (A and C) and during the line detection task (B and D). Because each map is combined from many cells, the set of all stimuli generated by the whole group of cells is depicted over the data. The 32 stimuli from the initial stimulus set are drawn, as are the stimuli overlying the highest regions of the mean response (other stimuli are indicated with gray points). Note the diversity of refinement stimuli created by cells under the circle/wave task, compared with the line task. Arrows on the color scale in C and D show response ($R = 0.40$) to a one-bar geometric “contour” (one bar in the RF, embedded in the random field). Sample sizes: (A) $n = 17$; (B) $n = 36$; (C) $n = 25$; (D) $n = 37$. (E and F) The three-bar heat maps for a single neuron from monkey A under the circle (E) and line (F) tasks.

population response, rather than in the optimum shapes preferred by individual neurons.

To determine how perceptual task might reshape neural tuning surfaces and how those changes might sum up over groups of neurons, we analyzed the population responses to three-bar stimuli. Because the optimization program was always seeded with the same set of three-bar stimuli (*SI Materials and Methods, Automated Stimulus Generation*), the neural responses to this region of the stimulus space can be directly compared across cells and task conditions. We mapped the height of each three-bar tuning surface into the interval [0, 1], to normalize for differences in neuronal firing rates. We then grouped the surfaces that were constructed while the monkeys performed each of the three detection tasks and averaged the data over each group, to obtain three population tuning surfaces. We performed permutation tests between these mean tuning surfaces to determine whether any differences between them were statistically significant (*SI Materials and Methods, Permutation Test*). For all three monkeys, the differences between the average three-bar tuning surfaces under the circle and wave tasks were not statistically significant ($P \geq 0.2$). We therefore pooled the data from those two task conditions and compared the mean of the merged data with the mean surface under the line detection task. The averaged tuning surfaces from monkeys A and C under the line and circle/wave detection tasks are presented in Fig. 6 *A–D*. (The corresponding data for monkey B are shown in Fig. S6.) Over the neuronal populations from all three monkeys, the cumulative response depended as much on the animals' cognitive state as on the actual stimulus geometry. Under the line detection task, the network expressed a narrow selectivity for the linear geometry; under the circle and wave tasks, the network adopted an entirely different mode of selectivity, for circular shapes. The difference between the mean tuning surfaces under the line and circle/wave tasks was statistically significant (monkey A, total number of surfaces, $n = 53$, $P = 4 \times 10^{-5}$; monkey B, $n = 63$, $P = 0.007$; and monkey C, $n = 62$, $P = 0.003$).

Because the construction of five- or seven-bar optimum contours required thousands of trials and hours of recording time, it was not possible to run the optimization algorithm to completion under different task conditions for the same cell. We did, however, generate three-bar tuning surfaces for a subset of cells that were each recorded under two different task conditions. Consistent with the results obtained from averaging the data over the population, we found that the same neurons were able to dynamically change their tuning surfaces according to the cued shape. We recorded from 13 neurons (7 from monkey A and 6 from monkey B) while the animal carried out two separate blocks of several hundred trials each. We switched the cue between the two blocks, and the neural responses under the two task conditions gave rise to two distinct tuning surfaces. Fig. 6 *E* and *F* illustrates the results from one such experiment, in which monkey A was cued to detect first the circle (Fig. 6*E*) and then the line (Fig. 6*F*) while we recorded from the same neuron. Coincident with the change in the cued target, the AF underwent a dramatic shift, from a cocircular to a collinear pattern of facilitation. The direction of this shift in geometric tuning was consistent across the subpopulation of 13 neurons that were recorded under both the line and the circle/wave detection task ($P = 0.013$; permutation test). Fig. S7 plots the average heat map across these 13 cells, obtained under both sets of task conditions. Under the line detection task, the cumulative neural response was dominated by a sharp peak of collinear facilitation. Under the circle and wave tasks, a local maximum near collinearity remained in the population response, but the magnitude of this peak was lower, and the cells' geometric facilitation became distributed along the cocircularity lines. The shift in the three-bar tuning surfaces for the same neurons therefore paralleled the

shift seen between neurons, when different task conditions were used during recordings from different cells.

Time Course of Geometric Selectivity. Finally, we analyzed the temporal dynamics of shape selectivity in V1. An ANOVA analysis (*SI Results, ANOVA Analysis*) revealed that neurons developed an initial mode of geometric selectivity—i.e., neurons began to respond differentially to at least some stimuli—at ~72 ms after stimulus onset (SO). To investigate the timing in more detail, we plotted the evolution of three-bar shape selectivity over the population, as a function of task condition. We pooled the three-bar tuning functions from all three monkeys and separated them according to task condition. Fig. 7 shows the mean heat maps recorded during either the circle or the wave task (Fig. 7, *Left*) and during the line detection task (Fig. 7, *Center*), plotted using various time windows (Fig. 7, *Right*). When the entire duration of each trial is used to construct the mean heat maps (Fig. 7, *Bottom*), the task-dependent differences between the surfaces are highly significant ($P < 4 \times 10^{-5}$; permutation test). To measure the temporal onset of these differences, we moved a sliding 50-ms window across the neural response and plotted the population activity within that window under each task condition. We found distinct patterns of selectivity between the task conditions that began to develop in the window between 70 and 120 ms following SO. The shape of the tuning functions evolved over the next tens of milliseconds, reaching maturity in the time window between 110 and 160 ms. Within this window, differential peaks of collinear and cocircular facilitation were already apparent on the corresponding response surfaces ($P = 0.036$; permutation test). The results suggest that geometric selectivity matures by 110 ms, when neural responses recover from an inhibitory dip in firing probability induced by the random fields (2) (Fig. 7, *Right*). We obtained precisely the same timing results from an analysis of five-bar contours (*SI Results, Five-Bar Timing Analysis* and Fig. S8), indicating that this time course is not unique to three-bar stimuli.

Discussion

V1 has long been recognized as a geometric processor, responsible for parsing the visual scene into its component lines and edges (27). More recent evidence suggests that V1 may also merge these components into perceptually unified wholes (2) via the AF. In the standard model, the pattern of neuronal interconnections in V1 echoes the cocircular statistics of natural images (20, 28): The strongest connections in the network link neurons whose RFs fall along the same linear/circular arcs. Although the AF was originally coined as a psychophysical concept (22), our study directly shows that a network with matching properties exists in V1. Over the population, the strongest contextual interactions we observed fell on, or very near, the cocircularity line (Figs. 6 and 7). However, as an important nuance, the network in V1 never expressed the full range of lateral interactions from the AF at once (which includes all collinear and cocircular interactions). Rather, the neural population expressed subsets of these interactions—peaks of facilitation that shifted their position along the cocircularity line when the perceptual task was changed. Moreover, different cells preferred a diverse range of curved contours, including circles and sinusoids of various shapes, whereas previous results have focused on the responses to straight line geometries. The cortical strategy may be to ensure that the population activity follows a narrow pattern that is appropriate for detecting and encoding smooth contours, while maintaining a richer repertoire of shape selectivity at the level of individual neurons. This diversity of responses may be used to accommodate mechanisms of object recognition and scene segmentation (24, 25).

The prevailing view of top-down interactions emphasizes their role in gain control or attentional competition (6, 7), but

Fig. 7. Temporal evolution of geometric selectivity. (Left) The three-bar tuning surfaces, in different time windows, averaged from 107 different experiments from all three monkeys. The data in this column were collected during either the circle or the wave task. (Center) The three-bar heat maps, within different time windows, pooled over 72 line detection experiments from each monkey. (Right) The peri-stimulus time histogram (PSTH) obtained from pooling the spikes elicited by all three-bar stimuli from all recorded neurons in each monkey. The region of the PSTH used to construct each pair of response surfaces is highlighted in red. SO, stimulus onset. The tuning surfaces were normalized and averaged as in Fig. 6 A–D. For clarity, only the stimuli in the initial stimulus set are drawn over each surface.

they may also provide an input selection mechanism that enables cortical areas to act as adaptive processors (21). Our data demonstrate that cognitive influences can reprogram an entire network of sensory neurons (*SI Discussion, Role of Expectation*

in Our Experiments). This idea is a major departure from the current paradigm, which holds that top-down influences merely gate the magnitude, rather than the function, of neural responses. Mechanistically, we speculate that the adaptive

processing in V1 involves the top-down gating of horizontal connections (*SI Discussion, Mechanism of Task-Dependent Shape Selectivity in V1*), rather than traditional gain control or a simple reflection of higher sensory processing. Anatomical, physiological, and theoretical work implicate the horizontal connections as the substrate for the geometric contextual interactions (2, 19–21, 23, 29–31). The task dependency of those interactions, shown here, suggests that feedback projections may inhibit some sets of lateral interactions and/or activate others, thereby establishing different network states with different geometric optima. Furthermore, the time course of geometric facilitation is consistent with this mechanism.* traditional attentional effects occur later than the modulations we observed, even in higher cortical areas (15).

Similar cortical mechanisms that impart V1 with its adaptive tuning may imbue other areas with the same flexibility, like the prefrontal cortex with its ability to load and switch between different behavioral programs. Our finding that V1 acts like an adaptive integrator suggests parallels with association cortices, which must also integrate information dynamically as a function of cognitive state.

Materials and Methods

We performed the animal preparation procedures and many aspects of the electrophysiological recordings as previously described (2, 16). We developed

an “optimization” algorithm to adaptively measure neural responses to stimuli composed of discrete contour elements (“contour bars”; Fig. 1). Recordings were taken from macaques while they were in the delay phase of a match-to-sample task, in the midst of their expectation for a cued contour. The optimization algorithm built up the preferred shape for a recorded neuron—under a particular behavioral state—by progressively bringing contour elements into an “optimal” configuration with a fixed bar in the crf. At the start of an experiment, during the delay phase of each trial, the algorithm tested the neural responses to a range of three-bar stimuli, pruning and redefining the stimulus set over hundreds of trials until it converged upon the neuron’s preferred three-bar stimulus. (A three-bar stimulus is a shape composed of three discrete line elements.) The algorithm then searched for optimal extensions of this three-bar stimulus, creating and pruning five-bar stimuli, and later seven-bar shapes, in the search for the neuron’s preferred contour. The optimization program changed the stimulus sets at discrete intervals during an experiment, after hundreds of test trials, but the stimulus presented within the delay portion of any trial was static. We always measured neuronal shape selectivity while monkeys were expecting a single contour from a set of three possible cue shapes (a straight line, a closed circle, or a sinusoidal wave). We assessed the cognitive influence of expectation by comparing the preferred contour shapes generated by populations of neurons while monkeys were expecting each of the cue shapes or by comparing the responses of single neurons before and after changing the expected cue contour. Details of these methods are available in *Results* and in *SI Materials and Methods*. All procedures were in accordance with the National Institutes of Health *Guide for the Care and Use of Laboratory Animals* and with the approval of the Institutional Animal Care and Use Committee at The Rockefeller University.

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