J Neurophysiol 99: 2745–2754, 2008.
First published April 9, 2008; doi:10.1152/jn.90211.2008.

Invited Review

Models and Measurements of Functional Maps in V1

Naoum P. Issa,[1] Ari Rosenberg,[2] and T. Robert Husson[2]
[1]*Department of Neurobiology and* [2]*Committee on Computational Neuroscience, University of Chicago, Chicago, Illinois*

Issa NP, Rosenberg A, Husson TR. Models and measurements of functional maps in V1. *J Neurophysiol* 99: 2745–2754, 2008. First published April 9, 2008; doi:10.1152/jn.90211.2008. The organization of primary visual cortex has been heavily studied for nearly 50 years, and in the last 20 years functional imaging has provided high-resolution maps of its tangential organization. Recently, however, the usefulness of maps like those of orientation and spatial frequency (SF) preference has been called into question because they do not, by themselves, predict how moving images are represented in V1. In this review, we discuss a model for cortical responses (the spatiotemporal filtering model) that specifies the types of cortical maps needed to predict distributed activity within V1. We then review the structure and interrelationships of several of these maps, including those of orientation, SF, and temporal frequency preference. Finally, we discuss tests of the model and the sufficiency of the requisite maps in predicting distributed cortical responses. Although the spatiotemporal filtering model does not account for all responses within V1, it does, with reasonable accuracy, predict population responses to a variety of complex stimuli.

INTRODUCTION

How are scenes encoded in the visual system? We know from single-unit studies that individual neurons are preferentially sensitive to a small set of stimulus features and that neuronal sensitivity to these features varies across the cortical sheet within a visual area (Hubel and Wiesel 1962). Over the last 20 years, optical imaging has allowed the activity of large regions of cortex to be recorded (Blasdel and Salama 1986; Grinvald et al. 1986) and a compelling series of maps detailing the tangential organization of response properties has emerged (including, among many others, Blasdel 1992a,b; Bonhoeffer and Grinvald 1991; Hubener et al. 1997; Kalatsky and Stryker 2003; Weliky et al. 1996). Cortical maps have been most thoroughly studied in the primary visual cortex (V1), in which the relationships among several feature maps, including orientation preference, ocular dominance, and spatial frequency (SF) preference, have been detailed extensively (Hubener et al. 1997; Issa et al. 2000). A theoretical model of neuronal responses has recently been used to join together these functional maps into a coherent framework for predicting the distributed pattern of cortical activity induced by a visual scene (Baker and Issa 2005; Mante and Carandini 2005). In this review, we discuss the classic spatiotemporal filtering model that describes the linear responses of neurons in V1, how this model has been applied to the distributed architecture of V1, and how it accounts for many of the response patterns in V1. This model reflects an important step toward developing a theory of distributed encoding in primary visual cortex and may provide a template for studies of other sensory areas.

Address for reprint requests and other correspondence: N. P. Issa, The University of Chicago, Department of Neurobiology, MC0928, 947 E. 58th Street, Chicago, IL 60637 (E-mail: naoum@uchicago.edu).

MOTIVATION FOR A SPATIOTEMPORAL ENERGY DESCRIPTION OF THE ORGANIZATION OF V1

Early optical mapping studies focused on neuronal tuning parameters whose organization had already been illustrated by single-unit recordings (Blasdel 1992a,b; Blasdel and Salama 1986; Bonhoeffer and Grinvald 1991; Bonhoeffer et al. 1995). Orientation preference and ocular dominance maps were found to be interrelated, tending to run perpendicularly to one another (Crair et al. 1997; Hubener et al. 1997; Obermayer and Blasdel 1993), as Hubel and Wiesel (1962, 1974) first suggested from microelectrode recordings. Subsequent mapping studies addressed additional features that are less well clustered, like direction selectivity (Shmuel and Grinvald 1996; Weliky et al. 1996) and SF preference (Fig. 1) (Everson et al. 1998; Hubener et al. 1997; Issa et al. 2000; Shoham et al. 1997). The different maps of V1 all vary across cat cortex, with wavelengths ranging between around 0.5 and 1 mm, and the combination of these parameters extends the original hypercolumn description of cortical modules (Hubel and Wiesel 1977). Although these studies characterized how various parameters were mapped across the cortex, it was not clear whether the group of maps was sufficient to predict cortical responses to complex images.

The first serious test of whether these maps can predict responses to complex stimuli came in Area 17 of the ferret. Basole et al. (2003) asked whether the spatial properties of texture stimuli alone determine which cortical orientation domains are activated. They found that changing the velocity of an image (either its direction or speed) could have large effects on which cortical orientation domains were activated (summarized in Fig. 2). Because the shifts in cortical activity happened even when the spatial statistics of the image did not change, the findings were unequivocal in demonstrating that the spatial properties of stimuli alone do not determine how cortical domains are activated.

Based on these findings, Basole et al. (2003) suggested that the cortical maps of orientation, spatial frequency, and direction preference did not provide an appropriate description of cortical activity and, instead, proposed an alternative description of cortical organization: rather than having several separable parameters mapped across the cortical surface, they suggested that primary visual cortex would be better characterized by a single map that encodes spatiotemporal energy. As Horton and Adams (2005) point out in a recent review of cortical columns, this was a radical departure from previous models of V1 organization. For functional mapping, its main implication was that maps of individual parameters, like orientation or SF preference, could not be used to understand the area's responses to complex stimuli. Instead, it would be necessary to map responses to stimuli with a variety of spatiotemporal energies.

0022-3077/08 $8.00 Copyright © 2008 The American Physiological Society

Downloaded from jn.physiology.org on June 11, 2008

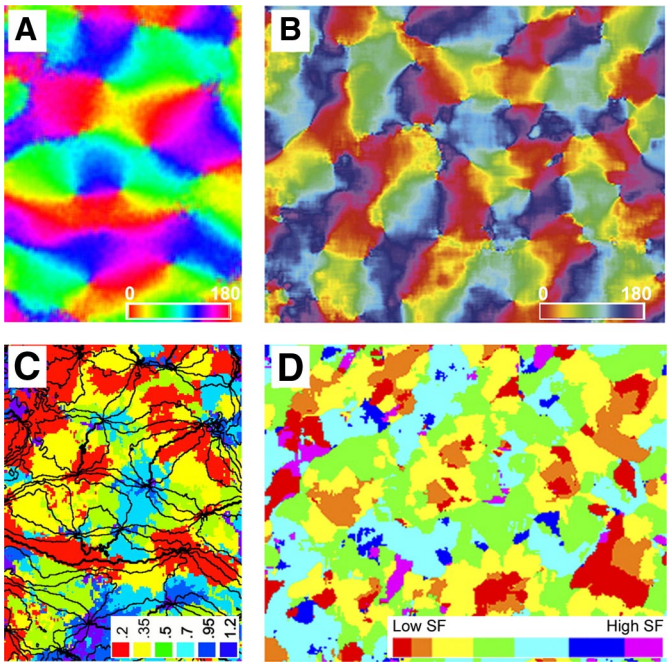


FIG. 1. Example functional maps in primary visual cortex (V1). Orientation maps in cat (*A*) and bush baby (*B*) show classic pinwheel structures. Spatial frequency (SF) maps in cat (*C*) and bush baby (*D*) both show less overall structure, but exhibit a "target" pattern with high and low domains separated by areas preferring intermediate frequencies. Iso-orientation lines in *C* show that pinwheel centers (where several iso-orientation lines intersect) overlie high and low SF domains. (*A* and *C* adapted by permission from *J Neurosci*, Issa et al. 2000; *B* and *D* adapted by permission from Wiley: *J Comp Neurol*, Xu et al. 2007, © 2003.)

SPATIOTEMPORAL FILTERING AND ENERGY MODELS

Spatiotemporal energy models treat a neuron as a series of filters, each selective for a small range of orientations, spatial frequencies, and temporal frequencies (Adelson and Bergen 1985; Baker and Issa 2005; Mante and Carandini 2005; Nielsen et al. 1985; Reichardt 1961; van Santen and Sperling 1985). They were named "energy models" because their output is closely related to the amount of Fourier power or "energy" in the stimulus at the spatiotemporal frequencies preferred by the modeled neuron. The activity of each neuron therefore reports the contrast of (energy of) an image component with a specific mix of orientation, SF, and temporal frequency.

By applying the spatiotemporal energy model originally described for neurons to cortical domains, two theoretical treatments reconciled the requirement for mapping spatiotemporal energy, as suggested by Basole et al. (2003), with previous maps of individual parameters like orientation and SF (Baker and Issa 2005; Mante and Carandini 2005). The six required parameters of the energy model can be determined from the orientation, SF, and temporal frequency tuning curves of a given location on the cortical surface (Fig. 3). The traditional orientation and SF preference maps give two of the six parameters (orientation and SF preference). Adding temporal frequency parameters (preference and bandwidth) as well as maps of orientation and SF bandwidths to maps of orientation and SF preference is enough to predict all the response patterns found in the data of Basole et al. (2003) (Baker and Issa 2005; Mante and Carandini 2005). The spatiotemporal energy description that Basole et al. (2003) proposed is therefore completely compatible with previous maps, but requires that temporal frequency tuning also be represented to predict distributed cortical activity patterns (Figs. 2 and 3).

According to the spatiotemporal filtering model, a unified description of the organization of V1 consists of several maps of filter properties: orientation preference, SF preference, temporal frequency preference, the associated bandwidths, and supporting features including retinotopy, ocular dominance, and contrast sensitivity. Much of the work needed to characterize these responses has been done, both with optical imaging and targeted electrophysiology, but there are still significant open questions about the functional organization of primary visual cortex. In subsequent sections we review important structural features of these maps, relationships among the maps, and how well this combination of maps can predict responses in V1 to complex images.

SPATIOTEMPORAL PARAMETER MAPS

Orientation preference

There is little controversy over the general structure of the orientation preference map. The original descriptions showed small domains that were selective for a narrow range of orientations and that these domains were arranged around point singularities (Blasdel 1992b; Blasdel and Salama 1986; Bonhoeffer and Grinvald 1991). Many studies have since confirmed the orientation pinwheel structure and added details that relate the map structure to receptive field properties. For example, the size of orientation domains varies with receptive field size, both within and across cortical areas. Within Area 17, orientation domain size increases with eccentricity (pinwheel density decreases), just as receptive field size increases with eccentricity (Xu et al. 2007). A similar pattern is observed crossing from Area 17 to Area 18. Within the portion of cat Area 17 that represents the central visual field, the average orientation domain width is 0.54 mm (Rao et al. 1997) and receptive fields subtend an angle of approximately 1.2° (Hubel and Wiesel 1962; Tusa et al. 1978), whereas in Area 18, the average domain width increases to about 0.83 mm (Bonhoeffer and Grinvald 1993) and the average receptive field diameter increases to 3.3° (Tusa et al. 1978, 1979).

Results from electrophysiological studies had differed on the question of whether neurons at orientation pinwheel centers are sharply tuned for orientation. Intrinsic signal imaging experiments show poor orientation selectivity around pinwheel centers, but this could be caused either by poorly tuned neurons or by averaging, at low spatial resolution, the responses from a variety of sharply but differently tuned neurons (Blasdel and Salama 1986; Bonhoeffer and Grinvald 1991). Maldonado and colleagues (1997) targeted electrode penetrations in adult cats to pinwheel centers identified by optical imaging. Their results, as well as subsequent intracellular recordings (Schummers et al. 2002), suggested that neurons near pinwheel centers were nearly as sharply tuned for stimulus orientation as neurons far from pinwheel centers, but it was not clear whether cells were randomly ordered near the pinwheel center. A separate study in juvenile cats using tetrodes came to the opposite conclusion that neurons at pinwheel centers were broadly tuned (Ruthazer et al. 1996). This lingering controversy has recently been

Downloaded from jn.physiology.org on June 11, 2008

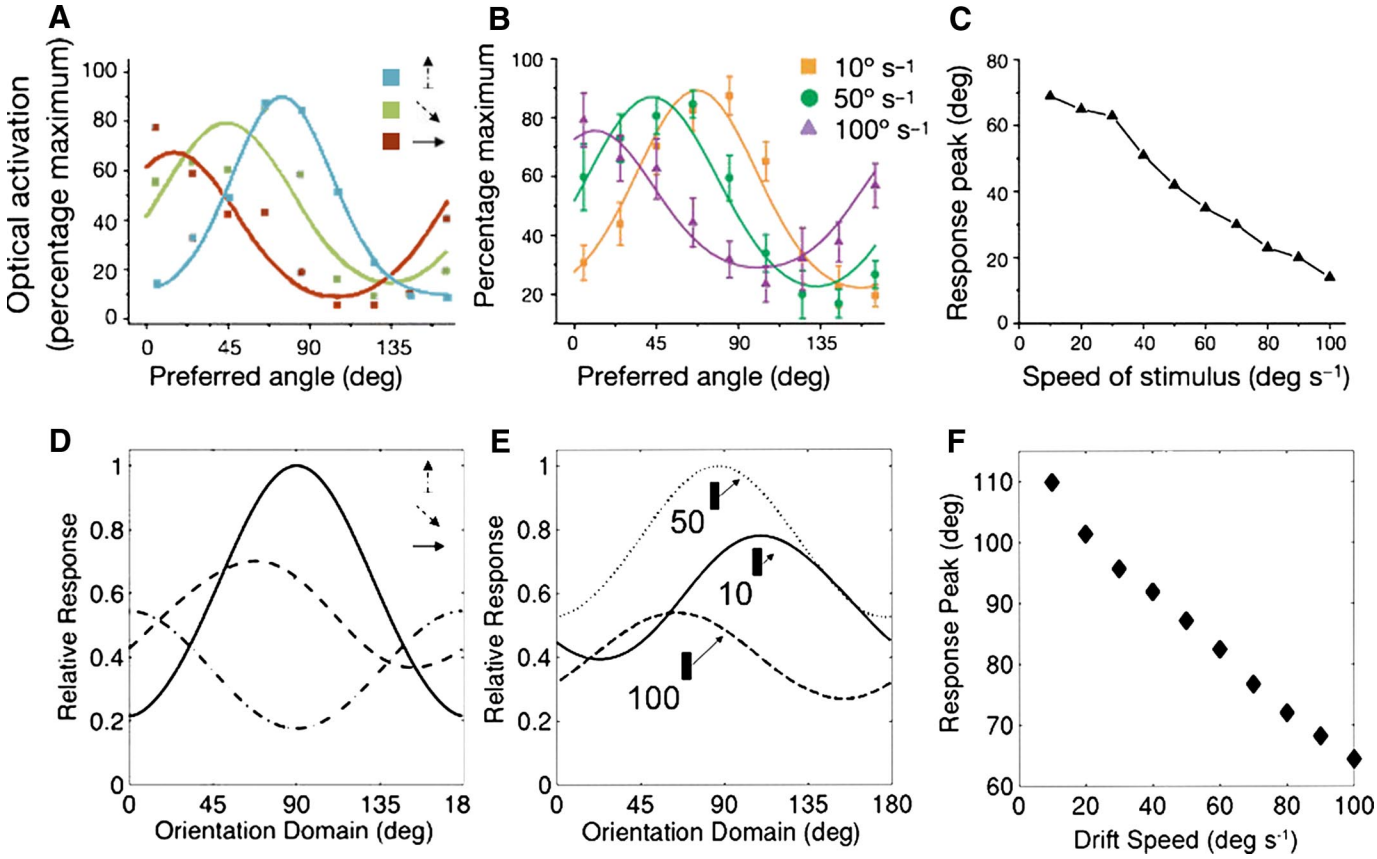


FIG. 2. Role of temporal frequency in determining spatial activity patterns in V1. A visual stimulus activates different orientation domains depending on the direction and speed with which it is moving. *Top row*: figure adapted from Basole et al. (2003) shows responses in different orientation domains plotted as a function of stimulus drift angle (*A*) and drift speed (*B*). (Adapted by permission from Macmillan Publishers Ltd: *Nature*, Basole et al. 2003, © 2003.) The effect of changing drift speed on which orientation domain is maximally activated is summarized in *C*. *Bottom row*: model predictions from Baker and Issa (2005) show that a spatiotemporal filtering model qualitatively predicts the shifts with stimulus drift angle (*D*) and drift speed (*E* and *F*).

resolved in adult cat Area 18 with a series of two-photon calcium imaging experiments, which showed that neurons at pinwheel centers were quite selective for stimulus orientation and that there was a well-ordered progression of orientation selectivity around the pinwheel center (Ohki et al. 2006).

Spatial frequency preference

Unlike maps of orientation selectivity, the structure of SF maps has been quite contentious. Claims from optical imaging studies range from no organization whatsoever to a clear organization with specific relationships to other maps (Everson et al. 1998; Hubener et al. 1997; Issa et al. 2000; Shoham et al. 1997; Sirovich and Uglesich 2004; Xu et al. 2007). There are several reasons why optical mapping has provided less consensus on SF maps. First, clustering by SF preference is weaker than that by orientation or ocular dominance. DeAngelis et al. (1999) considered pairs of single units found at the same recording site and measured how similarly tuned they were for several features. As the summary figure (Fig. 4) shows, nearby neurons were very likely to have similar orientations, less likely to have the same SF preference, and even less likely to have similar temporal frequency preferences.

Spatial frequency maps also appear weaker than orientation maps because the stimuli used to generate them have fewer frequency components (less power) than do stimuli used to generate orientation maps. Orientation maps are typically generated using square-wave gratings (the sum of many sinusoidal gratings), so they have power over a wide range of spatiotemporal frequencies at the same orientation. Because these stimuli contain multiple frequencies, they are poorly suited for isolating single spatiotemporal frequencies, as required to construct a SF map. It is thus tempting to increase the power of SF stimuli by adding components at different orientations but at the same spatial frequency. However, theoretical, single-unit, and optical imaging studies all show that SF tuning can change with orientation (Daugman 1985; Issa et al. 2000; Webster and De Valois 1985). These considerations indicate that even though sinusoidal gratings elicit weaker responses than stimuli with multiple components, their use is required to isolate individual SF domains and properly assess their tuning bandwidth (Issa et al. 2000).

Finally, because the distribution of orientation preference is uniform over neurons, orientation domain size is roughly constant regardless of preference [with the exception of a small bias toward larger domains for the cardinal orientations (Dragoi et al. 2001; Muller et al. 2000)]. Spatial frequency domains, by comparison, can have very different sizes since far fewer neurons are selective for very low and very high spatial frequencies (Issa et al. 2000; Movshon et al. 1978; Xu et al. 2007). As a result, postprocessing, like the nearly ubiquitous high-pass filtering of images, can have differential effects on small, medium, and large SF domains. Taken together, these

Downloaded from jn.physiology.org on June 11, 2008

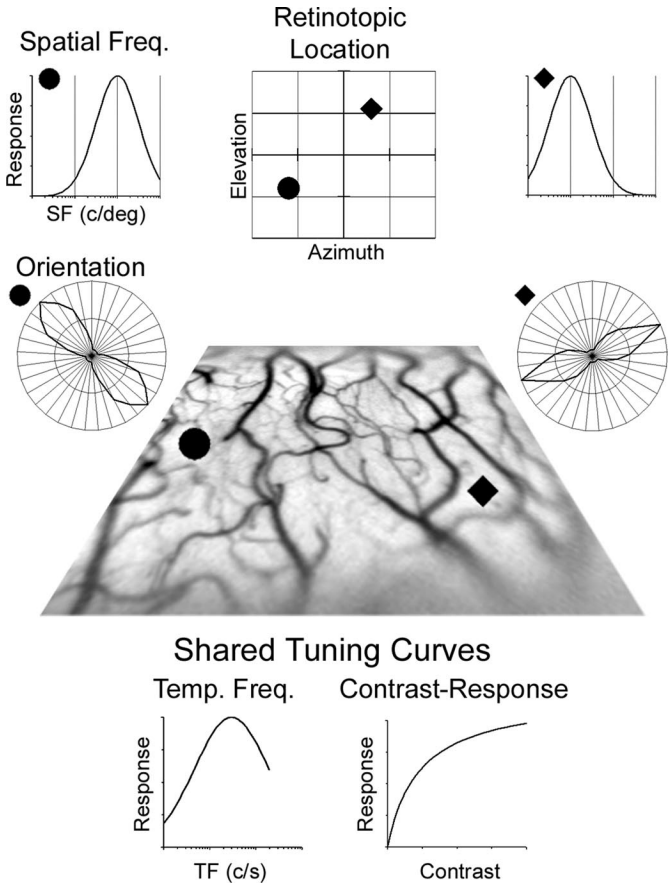


FIG. 3. The spatiotemporal filtering model. Each location on the surface of V1 has filtering properties characterized by orientation, SF, and temporal frequency tuning curves. Orientation and SF tuning curves are schematized for 2 locations, marked by the circle and diamond, that represent different parts of the visual field (plot of retinotopic location). Temporal frequency tuning and contrast response functions do not appear to vary much across the surface of V1. The response of each location is determined by how much of the visual stimulus falls within the measured tuning curves.

features of neuronal response properties conspire to make the mapping of SF preference more challenging than the mapping of orientation preference.

Despite these challenges, commonalities can be extracted from the results of several studies. First, SF preference is organized into functional domains. Both electrophysiological and imaging studies show consistent clusters (DeAngelis et al. 1999; Everson et al. 1998; Hubener et al. 1997; Issa et al. 2000; Shoham et al. 1997; Thompson and Tolhurst 1979; Tolhurst and Thompson 1982; Tootell et al. 1981; Xu et al. 2007), although it is not clear whether SF preference is organized in radial columns with the same frequency preference from pia to white matter (Maffei and Fiorentini 1977). Second, a range of SF domains are arrayed across the cortical surface. Although the pioneering imaging studies found only low and high SF domains (Hubener et al. 1997; Shoham et al. 1997), subsequent studies identified a variety of preference domains (Everson et al. 1998; Issa et al. 2000; Xu et al. 2007). The discrepancy between the early and later studies is likely due to both the choice of stimuli and technical differences in image postprocessing. When the data of the later studies were processed like the data of the original studies, they generated similar maps, suggesting that both data sets carried similar information (for details of the technical differences see Issa et al. 2000).

One outstanding issue regarding SF maps is whether they have a repeating modular structure. Shoham et al. (1997) initially suggested that, like ocular dominance columns, SF maps consisted of alternating patches of low and high spatial frequency preference. Everson et al. (1998) subsequently proposed that, like orientation columns, SF preference was organized into pinwheels, in which the extreme low and extreme high SF domains abut. Issa et al. (2000) proposed that rather than pinwheels, SF preference is organized in target patterns, with low- and high-frequency domains usually separated by intermediate frequency domains—similar to the patches suggested by Shoham et al. (1997) but with intermediate frequency domains intercalated between the peaks of the high and low SF domains. Xu et al. (2007) suggest from their images in bush baby primary visual cortex that SF preference maps are not comprised of tightly packed repeating units and are less regular than orientation maps, having both target-like and pinwheel-like patterns that can be seen in the same area.

A recent analysis raises two challenges to the idea of an organized map of SF preference. The first challenge, raised by Sirovich and Uglesich (2004), is that SF response profiles of pixels can be estimated by the weighted sum of two independent basis functions, one with a positive peak at low SFs and the other with a positive peak at high SFs. They argue that these two basis functions are consistent with Y- and X-type inputs from the lateral geniculate nucleus (LGN) and therefore it is not necessary to invoke a map of SF preference to describe cortical responses; rather, it is necessary to describe only a mixture of X- and Y-type input at any given location. Although there might be a bias in the distribution of X- and Y-type inputs to different regions of Area 17 (Boyd and Matsubara 1996; Shoham et al. 1997), cortical neurons derive their narrow SF tuning curves from their elongated, opponent receptive field subunits, not from the broadly tuned LGN inputs to Area 17 (Jones and Palmer 1987a,b; Jones et al. 1987; Lampl et al. 2001). Despite the ability to fit cortical responses to X- and Y-like basis functions, the tangential organization of cortical SF tuning is nonetheless not primarily a function of X- and Y-cell projection patterns. Equally important, the spatial pat-

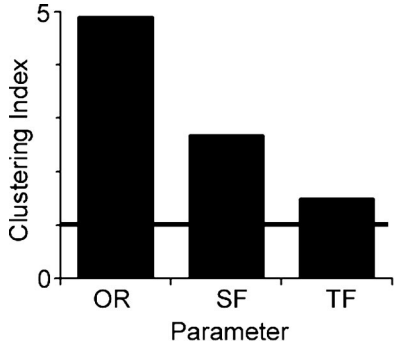


FIG. 4. Neuronal clustering by receptive field parameter. DeAngelis et al. (1999) measured the likelihood that neighboring neurons would have similar receptive field properties. The chance probability (solid line) has a clustering index of 1. Neighboring neurons were nearly 5-fold more likely than chance to have similar orientation preference, 2.5-fold as likely to have similar SF preference, and nearly chance probability to have similar temporal frequency preference. Values were averaged across both adult and young animals, which were reported separately in DeAngelis et al. (1999).

Downloaded from jn.physiology.org on June 11, 2008

terns of X- and Y-like regions calculated by Sirovich and Uglesich are similar to SF preference maps detailed in other optical imaging studies (Everson et al. 1998; Issa et al. 2000; Xu et al. 2007): there are regions dominated by the Y-like basis function (low SF preference), regions dominated by the X-like basis function (high SF preference), and regions that are best fit by a combination of X- and Y-like basis functions (intermediate SF domains).

The second challenge to a tangential organization of SF preference is that intrinsic signal imaging is often contaminated by vascular artifacts and that these artifacts might be misinterpreted as SF domains. The analysis reported by Sirovich and Uglesich (2004) suggested that, other than orientation-specific responses, the only stimulus-driven modulation in images was over vasculature and was not specific to SF domains. To address this concern directly, our lab has recently remapped SF preference using autofluorescence imaging (Mallik et al. 2008). Cortical autofluorescence likely derives from flavoproteins in neuronal mitochondria, so it has a significantly better spatial resolution than that of intrinsic signal imaging and is far less susceptible to vascular artifacts since it does not rely on blood flow or oxygenation signals (Husson et al. 2007; Reinert et al. 2004; Shibuki et al. 2003; Tohmi et al. 2006). The SF maps in cat Area 17 generated by autofluorescence were similar to intrinsic signal maps of SF in the same animals, suggesting that variations in SF preference are genuine features of cortical organization.

Temporal frequency preference

Attempts to map cortical temporal frequency preference are only now beginning. Temporal frequency is defined as the number cycles of a drifting sinusoidal grating that pass a point in 1 s. A V1 neuron responds to a limited range of temporal frequencies and, unlike neurons in "speed-tuned" cortical areas like middle temporal Area MT (Perrone and Thiele 2001; Priebe et al. 2003), its temporal frequency preference typically does not change with the SF of the stimulus (Priebe et al. 2006). Although there is a 4-octave range of temporal frequency preferences among V1 neurons (Movshon et al. 1978), there is little evidence for a systematic variation in temporal frequency preference across V1.

Electrophysiological recordings suggest that V1 neurons do not cluster together based on temporal frequency preference. DeAngelis and colleagues (1999) reported that the likelihood of finding neighboring neurons with similar temporal frequency preferences was almost at chance level and was about one third the probability of finding neighboring neurons with similar orientation preferences (Fig. 4). A recent mapping study in bush baby Area 17 using intrinsic signal imaging similarly found no clear evidence for clustering by temporal frequency (Khaytin et al. 2007). In an attempt to identify temporal frequency domains, Khaytin et al. analyzed single-condition images in several ways, including: comparing the positions of domain centers activated by different temporal frequencies, averaging responses over orientations to see whether temporal frequency domains are accentuated, and calculating the similarity among different single images. Regardless of the analytical approach, no temporal frequency domains were apparent. By comparison, both orientation and SF maps in the same species were both reproducible and consistent (Xu et al. 2007). The graded strength of functional maps (strong orientation maps, weaker SF maps, and "flat" temporal frequency maps) is reminiscent of the clustering index of DeAngelis et al. (1999; Fig. 4), so both imaging and electrophysiological results suggest weak clustering by temporal frequency preference.

A recent functional magnetic resonance imaging (fMRI) study in humans, however, argues for variation in temporal frequency preference across V1 (Sun et al. 2007). In this study, Sun et al. mapped responses to annular checkerboard patterns whose contrast reversed either slowly (0.75 Hz) or rapidly (15 Hz), and found that small domains within V1 were differentially activated by the two flicker speeds. Although there is definitely a temporal frequency difference between the two stimuli, the use of checkerboard patterns makes the interpretation of the cortical responses challenging. As is the case for drifting texture stimuli, checkerboards are composed of multiple sinusoidal components, with a range of different orientations, spatial frequencies, and temporal frequencies. So although the overall pattern flickers at either 0.75 or 15 Hz, the components are actually moving with a range of temporal frequencies. Moreover, a wider range of spatial frequencies should be visible in the slowly flickering stimulus than in the quickly flickering stimulus: optical imaging experiments show that both low and high SF domains can be activated by slowly moving complex stimuli, whereas quickly moving stimuli activate only low SF domains—even when the different domains have similar temporal frequency tuning curves (that is, when there is no variation in temporal frequency preference across the cortical surface) (Zhang et al. 2007). It is thus possible that the organization identified by fMRI actually represents different SF domains rather than temporal frequency domains. Given the lack of clustering by temporal frequency in cat and bush baby cortex and the dependence of SF responses on flicker rate, it is likely premature to conclude that variations in activity observed by fMRI in human V1 represent a map of temporal frequency preference.

Retinotopy

Electrophysiological mapping has so far provided the cleanest description of the retinotopic organization of primary visual cortex. For cat, the map of Tusa et al. (1978) is the most accepted reference, showing the basic retinotopic organization over all of Area 17. Optical imaging methods typically produce incomplete maps of retinotopy because large segments of the primary visual cortex are often buried in sulci. Exceptions to this include lissencephalic species, like the mouse and tree shrew, in which all of primary visual cortex is found on the surface and optical maps show a relatively smooth retinotopic progression at the resolution of a few hundred micrometers (Bosking et al. 2002; Husson et al. 2007; Kalatsky and Stryker 2003). fMRI now provides good maps of retinotopy in primates (Fize et al. 2003; Logothetis et al. 1999), including humans (Engel et al. 1997; Tootell et al. 1998), and ultra-high-field (9.4 T) fMRI can produce retinotopic maps with 1-mm resolution in cat primary visual areas (Olman et al. 2003). With the exception of electrophysiologically measured maps, however, retinotopic maps are too sparsely sampled or are at too low a resolution to show whether the map is smooth at fine spatial scales.

Downloaded from jn.physiology.org on June 11, 2008

Contrast

A priori, one might expect contrast–response parameters to vary across Area 17 in conjunction with SF preference. Anatomical studies in the cat found that Y-type cells from the C-lamina of the LGN, which have a contrast-sensitivity profile different from that of X-cells (Enroth-Cugell and Robson 1966), project preferentially to so-called cytochrome oxidase (CO) blobs in primary visual cortex (Boyd and Matsubara 1996). Shoham et al. (1997) subsequently found that low SF domains, but not high-frequency domains, also lie over CO blobs in cat Area 17; therefore if there is a spatial segregation of X- and Y-cells into high and low SF domains, these domains should show different contrast–response curves.

Two imaging studies, however, have failed to find variation in contrast–response curves across Area 17. Carandini and Sengpiel (2004) mapped the parameters of the contrast–response curve and showed that they do not vary in a statistically significant manner across Area 17. More recently, Zhang et al. (2007) measured contrast–response curves in identified low and high SF domains and, again, found no substantial difference in contrast–response curves between the two types of domains. Together, these studies suggest that contrast–response functions are relatively constant across Area 17.

How can the flat maps of contrast–response parameters be reconciled with SF maps? The most likely resolution is that low and high SF domains receive mixed input from X- and Y-type LGN inputs. Although the labeling study of Boyd and Matsubara (1996) showed that cells from the C-layers (W- and/or Y-cells) of the LGN project to CO blobs, the study was not designed to rule out inputs to CO blobs from other cell types in the LGN. Early studies in which axonal projections were individually labeled after electrophysiological characterization suggest that both X- and Y-cells project to the same regions within cat Area 17, with some sublaminar differences in termination sites (Humphrey et al. 1985a,b). The flat contrast–response maps suggest that even if there is a bias in the tangential input pattern of X- and Y-cells, the two channels are mixed together within the supragranular layers.

We can rule out an alternative explanation—that nonlinearities in intrinsic signal imaging mask differences in contrast–response curves among SF domains– by comparing contrast-response curves in areas 17 and 18. Area 17 receives a mixture of X- and Y-type inputs, whereas Area 18 receives little or no X-type input (Humphrey et al. 1985b; Stone and Dreher 1973). Consistent with the different type of LGN input, the areas have different average contrast–response curves: optical responses in Area 18 saturate at much lower contrasts than do responses in Area 17 (Carandini and Sengpiel 2004; Zhan et al. 2005; Zhang et al. 2007). Because optical imaging can detect differences in contrast sensitivity across areas 17 and 18, it would likely detect substantial spatial variations in contrast response across Area 17, if they existed.

RELATIONSHIPS AMONG MAPS

Although characterizing the topography of individual feature preference maps is important, it is also revealing to characterize the relationships among these maps. The study of the coordination of feature maps began with microelectrode recordings and the ice-cube model of the V1 hypercolumn (Hubel and Wiesel 1962, 1968). In this model, ocular dominance is mapped into parallel bands that run orthogonally to orientation preference bands. Although optical imaging has revealed that the relationship between orientation and ocular dominance is more complicated than originally proposed, the basic principle of that model was confirmed. As suggested, iso-orientation contours tend to cross ocular dominance boundaries at right angles (Blasdel 1992a; Blasdel and Salama 1986; Hubener et al. 1997; Obermayer and Blasdel 1993). In primate species, this tendency may be stronger than that in the cat (Blasdel 1992a; Hubener et al. 1997), whereas in the ferret, these tendencies are weaker (Issa et al. 1999; White et al. 2001; Yu et al. 2005). These studies also suggest that there is a bias for pinwheel centers to be found toward the center of ocular dominance domains.

Similar relationships have been identified between maps of orientation and spatial frequency. For example, orientation pinwheel centers tend to be located more in the center of high and low SF domains (Hubener et al. 1997; Issa et al. 2000). Iso-orientation lines also tend to cross the borders of SF domains at right angles, although this relationship is weaker than that between iso-orientation lines and ocular dominance domains (Farley et al. 2007; Hubener et al. 1997; Yu et al. 2005).

Why are there relationships among the maps? If features were encoded independently we might not expect any organization, no less to find that feature maps are coordinated. Indeed, in rodent visual cortex there is no clear long-range tangential organization of orientation preference, despite good neuronal selectivity (Kalatsky and Stryker 2003; Niell and Stryker 2007; Ohki et al. 2005; Van Hooser et al. 2005). In the carnivore visual system, by comparison, the organization of multiple feature maps seems nearly optimal to ensure coverage uniformity (Swindale et al. 2000), which refers to the goal of representing all combinations of parameters across the cortical sheet. For example, because less cortical area is dedicated to the extreme spatial frequencies than intermediate frequencies, one method of ensuring that all orientations are represented at these frequencies (thus improving coverage) is to align orientation pinwheel centers with domains sensitive to extreme spatial frequencies (Fig. 5*A*). The finding in cat Area 17 that orientation pinwheel centers tend to lie within domains of extreme spatial frequency (Issa et al. 2000) is consistent with this topological constraint. The effect of having the extreme SF domains shifted away from orientation pinwheel centers can be seen in Fig. 5*B*: the extreme spatial frequencies would be represented in only a few orientation domains, rather than having the full range of spatial frequencies represented at all orientations. Essentially, this would leave the cortex blind to certain combinations of spatial frequency and orientation.

The optimal relationships among maps can be derived theoretically. Dimension-reduction models use a self-organizing feature map algorithm as a numerical approach to mapping a high-dimensional parameter space of visual features onto the two-dimensional cortical surface (Durbin and Mitchison 1990; Kohonen 1982). This projection is constrained by the two competing factors of coverage uniformity (uniform representation of all parameter combinations across the cortex) and continuity (neuronal sensitivity changes slowly with distance across the cortical surface). Although coverage uniformity

Downloaded from jn.physiology.org on June 11, 2008

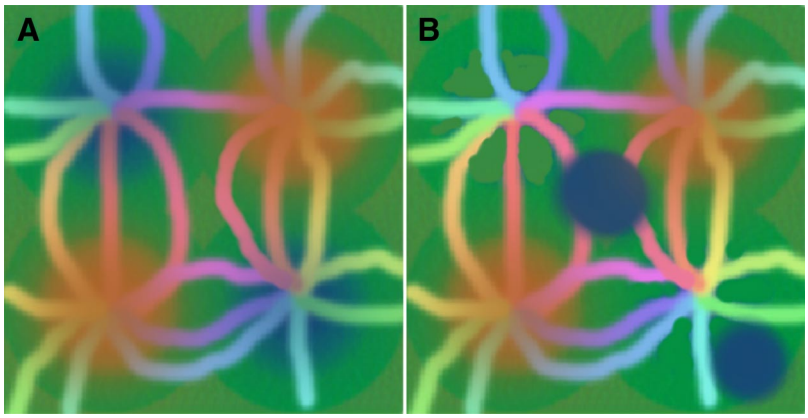


FIG. 5. Schematic of the relationship between orientation and SF domains. *A*: iso-orientation lines (colored) intersect at pinwheel centers that tend to lie over low (orange) and high (blue) SF domains. In this organization all combinations of orientation and SF are represented in the map. *B*: if a high SF domain lies away from an orientation pinwheel center, not all orientations are represented within that SF domain; in the illustrated example, only a small range of orientations is represented at the extreme high frequencies.

provides the animal with equal sensitivity to all combinations of stimulus features (Swindale 1991), continuity is thought to reflect economical use of cortical wiring (Durbin and Mitchison 1990). Without the continuity constraint, coverage uniformity could easily be achieved by a "salt and pepper" organization of receptive field parameters, like that of orientation preference in rodent primary visual cortex (Koulakov and Chklovskii 2001).

Dimension-reduction models have done a surprisingly good—albeit imperfect—job of reproducing cortical maps in different species (Fig. 6). For example, the models correctly predict that in the cat, which has a relatively isotropic retinotopic map (the representation of one degree along the azimuth takes up about the same distance on cortex as one degree of elevation) (Tusa et al. 1978), orientation domains should not be particularly elongated and orthogonal crossings of orientation and ocular dominance domains should be frequent (Fig. 6, *A*, *C*, *E*, and *G*) (Crair et al. 1997; Hubener et al. 1997). The models correctly predict a different relationship among maps in the ferret, in which the cortical magnification factor for elevation is about fourfold greater than that for azimuth. In this animal, orientation and ocular dominance domains are elongated orthogonally to the retinotopic elongation (Yu et al. 2005) and orientation and ocular dominance maps are less likely to cross at 90° angles than in cat Area 17 (Fig. 6, *B*, *D*, *F*, and *H*) (Farley et al. 2007; White et al. 2001; Yu et al. 2005). Dimension-reduction models estimate the ideal organization for a set of parameters mapped across a cortical area, constrained by uniform coverage and continuity, and it appears that the organization of primary visual cortex is largely consistent with these predictions.

It is important to note, however, that not all studies are consistent with predictions of dimension-reduction models. In the first study that examined the relationship between V1 retinotopy and orientation preference maps at single-cell resolution, Das and Gilbert (1997) found that jumps in the retinotopic map were aligned with fractures in the orientation map. That is, the gradients of both the orientation and retinotopic maps were largest at the same places and in the same directions. This result is in conflict with dimension-reduction predictions that suggest where the gradient of one map is large, the gradient of the other maps should be small and that if fractures in two maps overlap, they should tend to cross orthogonally.

TESTS OF THE SPATIOTEMPORAL FILTERING MODEL

Together the spatiotemporal filtering model and dimension-reduction models provide a conceptual framework for how sets of feature maps are organized within a cortical area and how they can be used to predict cortical responses. However, until recently it was not clear whether these maps were actually sufficient to account for cortical activity patterns.

As a quantitative test of the spatiotemporal filtering model, Zhang et al. (2007) asked whether complex images are broken down into cortical domains based on the spatial and temporal frequencies in the image. This required measuring six spatiotemporal filter parameters (preferences and bandwidths of orientation, spatial frequency, and temporal frequency) and three parameters of contrast–response curves in Area 17, and then interrogating the maps using images with multiple spatial and temporal frequencies. For three classes of stimuli moving at a variety of speeds, the filter model with no free parameters better predicted cortical activity patterns than did simpler models that had free parameters (Fig. 7 shows measured and calculated activity in low and high SF domains in response to sinusoidal gratings, square-wave gratings, and paired sinusoidal gratings). The agreement between the model's predictions and measured responses argues that the maps of spatiotemporal filtering parameters well describe the organization of Area 17.

Despite the success of spatiotemporal filtering in predicting responses in ferret orientation domains and in cat SF domains, there are several situations where spatiotemporal filtering models are expected to fail. Any nonlinear transformation will cause a deviation from the linear predictions. If, for example, the contrast nonlinearity were not explicitly included as a "preprocessing" stage in the filtering model, the measurements of Zhang and colleagues would differ from the predictions of the filtering model. A less easily handled exception is cross-orientation suppression. When two gratings of similar spatial frequency but different orientations are presented together they suppress cortical responses to each other (Benevento et al. 1972; Blakemore and Tobin 1972; Morrone et al. 1982). This nonlinearity arises from both subcortical processes (Freeman et al. 2002; Priebe and Ferster 2006) and intracortical processing (Li et al. 2005; Sengpiel and Vorobyov 2005), and cannot be accounted for by simple filtering. Linear filter models also fail to account for a number of behaviors observed in the temporal domain. For example, temporal frequency tuning depends on stimulus contrast, with neurons responding to

Downloaded from jn.physiology.org on June 11, 2008

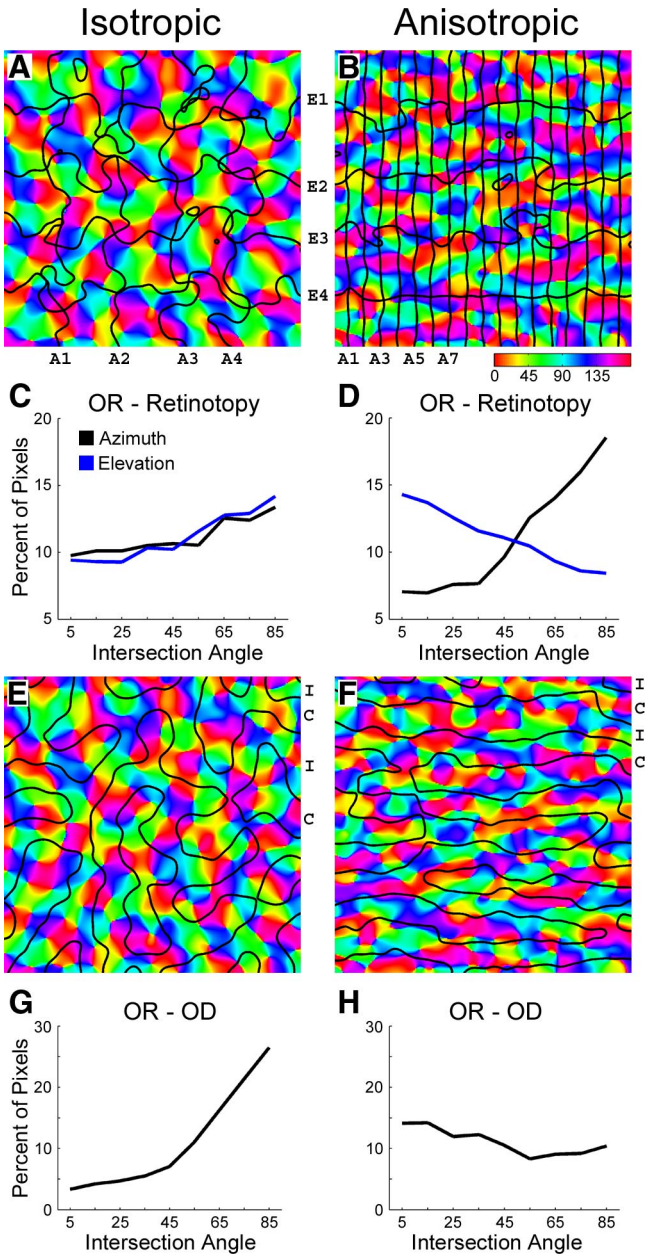


FIG. 6. Dimension-reduction models predict specific relationships among maps. These are predictions from models [based on the findings of Farley et al. (2007) and Yu et al. (2005)] for cortices that have an isotropic retinotopic mapping (*left column*) or an anisotropic retinotopic mapping (*right column*). *A*: lines of equal elevation and equal azimuth are superimposed onto the predicted orientation map when the retinotopic map is isotropic [one degree in elevation covers the same cortical distance as one degree in azimuth, similar to the map in cat (Tusa et al. 1978)]. *B*: elevation and azimuth lines are plotted on the orientation map for an anisotropic retinotopic map, in which one degree of elevation covers 3.5-fold the cortical distance as one degree of azimuth [consistent with the anisotropy measured in ferret (Yu et al. 2005)]. *C*: for the isotropic map, iso-orientation lines cross retinotopic boundaries at any angle, with a slight bias for orthogonal crossings. *D*: for the anisotropic map, iso-orientation lines tend to cross the iso-azimuth lines orthogonally. The gradient of the orientation map runs orthogonally to the largest retinotopic gradient, so iso-elevation lines tend to run parallel to iso-orientation lines. *C* and *D* show the intersection angle of the pixels with the 30% highest orientation and retinotopic gradients. *E* and *F* show the predicted relationship between the orientation and ocular dominance maps. *E*: in the isotropic condition iso-orientation lines tend to run perpendicular to ocular dominance boundaries. *F*: in the anisotropic condition iso-orientation lines do not tend to cross ocular dominance boundaries at perpendicular angles. *G* and *H* show the intersection angle of the pixels with the 30% highest orientation and ocular dominance gradients.

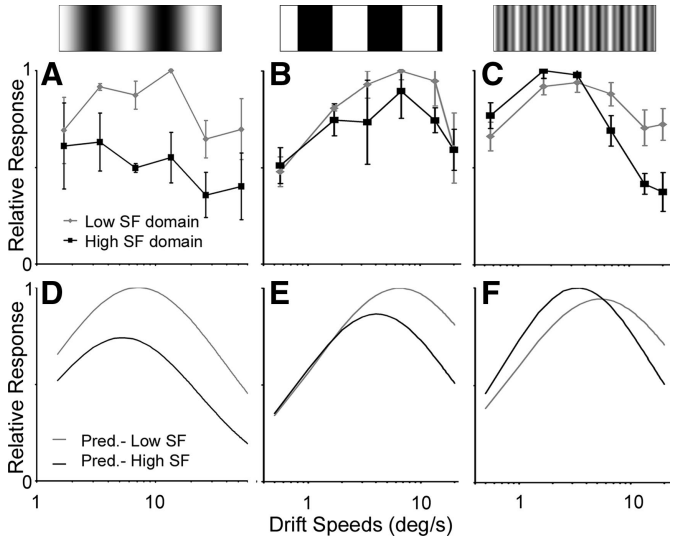


FIG. 7. Testing the spatiotemporal filtering model. Optical responses (*A–C*) and spatiotemporal filtering model predictions (*D–F*) in response to sine-wave gratings (*A*, *D*), square-wave gratings (*B*, *E*), and paired sine gratings (*C*, *F*). The spatiotemporal filtering model correctly predicts that at low drift speeds, responses to the square-wave gratings are similar in both low and high SF domains but that low SF domains are more active at high drift speeds. The model also correctly predicts that the responses to paired sine gratings in the low and high SF domains diverge at progressively higher drift speeds. All model parameters were measured experimentally. (Adapted by permission from *J Neurosci*, Zhang et al. 2007.)

higher temporal frequencies at high contrasts than at low contrasts (Albrecht 1995; Alitto and Usrey 2004). So although the linear filtering model provides a good initial description of cortical responses, it is likely to be more useful in identifying nonlinear processes that shape the distributed responses of cortex.

It is important to note that the linear filtering model of Area 17 is unlikely to apply to other cortical areas, even similar ones like cat Area 18. For example, nearly half of Area 18 neurons respond well to second-order stimuli (Zhou and Baker Jr 1994, 1996), a class of stimuli that produce perception of non-Fourier image features (Lu and Sperling 2001). Recent imaging of Area 18 shows weak but consistent responses to second-order stimulus features that, by definition, are not found after linear filtering (Zhan and Baker Jr 2006). Although the details of the linear spatiotemporal filtering model are therefore not likely to apply to visual cortical areas beyond Area 17, the general approach of identifying and mapping separable response properties may be applicable to other areas.

In conclusion, over the past several decades, the distributed encoding of image features in primary visual cortex has been studied in great detail, yielding maps of many receptive field properties. Recently, our understanding of how these individual feature maps contribute to the representation of more complicated stimuli has improved because of the theoretical framework provided by spatiotemporal filtering. The hope is that the same organizational principles will aid in our study of higher visual areas and provide a general framework for understanding the transformations that take place in visual processing. The ongoing challenge will be to define the parameters that describe the organization of higher cortical areas, which will require both novel techniques to improve the

Downloaded from jn.physiology.org on June 11, 2008

accessibility of these areas and a detailed knowledge of the first stages of visual processing.

ACKNOWLEDGMENTS

We thank Dr. Clifton Ragsdale and A. Mallik for helpful discussion.

GRANTS

This work was supported by grants from the Brain Research Foundation and Mallinckrodt Foundation to N. P. Issa and by Department of Homeland Security Fellowship DE-AC05-00OR22750 to A. Rosenberg.

REFERENCES

Adelson EH, Bergen JR. Spatiotemporal energy models for the perception of motion. *J Opt Soc Am A Opt Image Sci Vis* 2: 284–299, 1985.

Albrecht DG. Visual cortex neurons in monkey and cat: effect of contrast on the spatial and temporal phase transfer functions. *Vis Neurosci* 12: 1191–1210, 1995.

Alitto HJ, Usrey WM. Influence of contrast on orientation and temporal frequency tuning in ferret primary visual cortex. *J Neurophysiol* 91: 2797–2808, 2004.

Baker TI, Issa NP. Cortical maps of separable tuning properties predict population responses to complex visual stimuli. *J Neurophysiol* 94: 775–787, 2005.

Benevento LA, Creutzfeldt OD, Kuhnt U. Significance of intracortical inhibition in the visual cortex. *Nat New Biol* 238: 124–126, 1972.

Blakemore C, Tobin EA. Lateral inhibition between orientation detectors in the cat's visual cortex. *Exp Brain Res* 15: 439–440, 1972.

Blasdel GG. Differential imaging of ocular dominance and orientation selectivity in monkey striate cortex. *J Neurosci* 12: 3115–3138, 1992a.

Blasdel GG. Orientation selectivity, preference, and continuity in monkey striate cortex. *J Neurosci* 12: 3139–3161, 1992b.

Blasdel GG, Salama G. Voltage-sensitive dyes reveal a modular organization in monkey striate cortex. *Nature* 321: 579–585, 1986.

Bonhoeffer T, Grinvald A. Iso-orientation domains in cat visual cortex are arranged in pinwheel-like patterns. *Nature* 353: 429–431, 1991.

Bonhoeffer T, Grinvald A. The layout of iso-orientation domains in area 18 of cat visual cortex: optical imaging reveals a pinwheel-like organization. *J Neurosci* 13: 4157–4180, 1993.

Bonhoeffer T, Kim DS, Malonek D, Shoham D, Grinvald A. Optical imaging of the layout of functional domains in area 17 and across the area 17/18 border in cat visual cortex. *Eur J Neurosci* 7: 1973–1988, 1995.

Bosking WH, Crowley JC, Fitzpatrick D. Spatial coding of position and orientation in primary visual cortex. *Nat Neurosci* 5: 874–882, 2002.

Boyd JD, Matsubara JA. Laminar and columnar patterns of geniculocortical projections in the cat: relationship to cytochrome oxidase. *J Comp Neurol* 365: 659–682, 1996.

Carandini M, Sengpiel F. Contrast invariance of functional maps in cat primary visual cortex. *J Vis* 4: 130–143, 2004.

Crair MC, Ruthazer ES, Gillespie DC, Stryker MP. Ocular dominance peaks at pinwheel center singularities of the orientation map in cat visual cortex. *J Neurophysiol* 77: 3381–3385, 1997.

Das A, Gilbert CD. Distortions of visuotopic map match orientation singularities in primary visual cortex. *Nature* 387: 594–598, 1997.

Daugman JG. Uncertainty relation for resolution in space, spatial frequency, and orientation optimized by two-dimensional visual cortical filters. *J Opt Soc Am A Opt Image Sci Vis* 2: 1160–1169, 1985.

DeAngelis GC, Ghose GM, Ohzawa I, Freeman RD. Functional micro-organization of primary visual cortex: receptive field analysis of nearby neurons. *J Neurosci* 19: 4046–4064, 1999.

Dragoi V, Turcu CM, Sur M. Stability of cortical responses and the statistics of natural scenes. *Neuron* 32: 1181–1192, 2001.

Durbin R, Mitchison G. A dimension reduction framework for understanding cortical maps. *Nature* 343: 644–647, 1990.

Engel SA, Glover GH, Wandell BA. Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cereb Cortex* 7: 181–192, 1997.

Enroth-Cugell C, Robson J. The contrast sensitivity of retinal ganglion cells of the cat. *J Physiol* 187: 517–552, 1966.

Everson RM, Prashanth AK, Gabbay M, Knight BW, Sirovich L, Kaplan E. Representation of spatial frequency and orientation in the visual cortex. *Proc Natl Acad Sci USA* 95: 8334–8338, 1998.

Farley BJ, Yu H, Jin DZ, Sur M. Alteration of visual input results in a coordinated reorganization of multiple visual cortex maps. *J Neurosci* 27: 10299–10310, 2007.

Fize D, Vanduffel W, Nelissen K, Denys K, Chef d'Hotel C, Faugeras O, Orban GA. The retinotopic organization of primate dorsal V4 and surrounding areas: a functional magnetic resonance imaging study in awake monkeys. *J Neurosci* 23: 7395–7406, 2003.

Freeman TC, Durand S, Kiper DC, Carandini M. Suppression without inhibition in visual cortex. *Neuron* 35: 759–771, 2002.

Grinvald A, Lieke E, Frostig RD, Gilbert CD, Wiesel TN. Functional architecture of cortex revealed by optical imaging of intrinsic signals. *Nature* 324: 361–364, 1986.

Horton JC, Adams DL. The cortical column: a structure without a function. *Philos Trans R Soc Lond B Biol Sci* 360: 837–862, 2005.

Hubel DH, Wiesel TN. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J Physiol* 160: 106–154, 1962.

Hubel DH, Wiesel TN. Receptive fields and functional architecture of monkey striate cortex. *J Physiol* 195: 215–243, 1968.

Hubel DH, Wiesel TN. Sequence regularity and geometry of orientation columns in the monkey striate cortex. *J Comp Neurol* 158: 267–293, 1974.

Hubel DH, Wiesel TN. Ferrier lecture. Functional architecture of macaque monkey visual cortex. *Proc R Soc Lond B Biol Sci* 198: 1–59, 1977.

Hubener M, Shoham D, Grinvald A, Bonhoeffer T. Spatial relationships among three columnar systems in cat area 17. *J Neurosci* 17: 9270–9284, 1997.

Humphrey AL, Sur M, Uhlrich DJ, Sherman SM. Projection patterns of individual X- and Y-cell axons from the lateral geniculate nucleus to cortical area 17 in the cat. *J Comp Neurol* 233: 159–189, 1985a.

Humphrey AL, Sur M, Uhlrich DJ, Sherman SM. Termination patterns of individual X- and Y-cell axons in the visual cortex of the cat: projections to area 18, to the 17/18 border region, and to both areas 17 and 18. *J Comp Neurol* 233: 190–212, 1985b.

Husson TR, Mallik AK, Zhang J, Issa NP. Functional imaging of primary visual cortex using flavoprotein autofluorescence. *J Neurosci* 27: 8665–8675, 2007.

Issa NP, Trachtenberg JT, Chapman B, Zahs KR, Stryker MP. The critical period for ocular dominance plasticity in the Ferret's visual cortex. *J Neurosci* 19: 6965–6978, 1999.

Issa NP, Trepel C, Stryker MP. Spatial frequency maps in cat visual cortex. *J Neurosci* 20: 8504–8514, 2000.

Jones JP, Palmer LA. An evaluation of the two-dimensional Gabor filter model of simple receptive fields in cat striate cortex. *J Neurophysiol* 58: 1233–1258, 1987a.

Jones JP, Palmer LA. The two-dimensional spatial structure of simple receptive fields in cat striate cortex. *J Neurophysiol* 58: 1187–1211, 1987b.

Jones JP, Stepnoski A, Palmer LA. The two-dimensional spectral structure of simple receptive fields in cat striate cortex. *J Neurophysiol* 58: 1212–1232, 1987.

Kalatsky VA, Stryker MP. New paradigm for optical imaging: temporally encoded maps of intrinsic signal. *Neuron* 38: 529–545, 2003.

Khaytin I, Chen X, Royal DW, Ruiz O, Jermakowicz WJ, Siegel RM, Casagrande VA. Functional organization of temporal frequency selectivity in primate visual cortex. *Cereb Cortex* (December 3, 2007) 10.1093/cercor/bhm.210.

Kohonen T. Self-organized formation of topologically correct feature maps. *Biol Cybern* 43: 59–69, 1982.

Koulakov AA, Chklovskii DB. Orientation preference patterns in mammalian visual cortex: a wire length minimization approach. *Neuron* 29: 519–527, 2001.

Lampl I, Anderson JS, Gillespie DC, Ferster D. Prediction of orientation selectivity from receptive field architecture in simple cells of cat visual cortex. *Neuron* 30: 263–274, 2001.

Li B, Peterson MR, Thompson JK, Duong T, Freeman RD. Cross-orientation suppression: monoptic and dichoptic mechanisms are different. *J Neurophysiol* 94: 1645–1650, 2005.

Logothetis NK, Guggenberger H, Peled S, Pauls J. Functional imaging of the monkey brain. *Nat Neurosci* 2: 555–562, 1999.

Lu ZL, Sperling G. Three-systems theory of human visual motion perception: review and update. *J Opt Soc Am A Opt Image Sci Vis* 18: 2331–2370, 2001.

Maffei L, Fiorentini A. Spatial frequency rows in the striate visual cortex. *Vision Res* 17: 257–264, 1977.

Maldonado PE, Godecke I, Gray CM, Bonhoeffer T. Orientation selectivity in pinwheel centers in cat striate cortex. *Science* 276: 1551–1555, 1997.

Downloaded from jn.physiology.org on June 11, 2008

Mallik AK, Husson TR, Zhang JX, Rosenberg A, Issa NP. The organization of spatial frequency maps measured by cortical flavoprotein autofluorescence. *Vis Res* In press.

Mante V, Carandini M. Mapping of stimulus energy in primary visual cortex. *J Neurophysiol* 94: 788–798, 2005.

Morrone MC, Burr DC, Maffei L. Functional implications of cross-orientation inhibition of cortical visual cells. I. Neurophysiological evidence. *Proc R Soc Lond B Biol Sci* 216: 335–354, 1982.

Movshon JA, Thompson ID, Tolhurst DJ. Spatial and temporal contrast sensitivity of neurones in areas 17 and 18 of the cat's visual cortex. *J Physiol* 283: 101–120, 1978.

Muller T, Stetter M, Hubener M, Sengpiel F, Bonhoeffer T, Godecke I, Chapman B, Lowel S, Obermayer K. An analysis of orientation and ocular dominance patterns in the visual cortex of cats and ferrets. *Neural Comput* 12: 2573–2595, 2000.

Niell CM, Stryker MP. Highly selective receptive fields in mouse visual cortex. *Soc Neurosci Abstr* 615.4, 2007.

Nielsen KR, Watson AB, Ahumada AJ Jr. Application of a computable model of human spatial vision to phase discrimination. *J Opt Soc Am A Opt Image Sci Vis* 2: 1600–1606, 1985.

Obermayer K, Blasdel GG. Geometry of orientation and ocular dominance columns in monkey striate cortex. *J Neurosci* 13: 4114–4129, 1993.

Ohki K, Chung S, Ch'ng YH, Kara P, Reid RC. Functional imaging with cellular resolution reveals precise micro-architecture in visual cortex. *Nature* 433: 597–603, 2005.

Ohki K, Chung S, Kara P, Hubener M, Bonhoeffer T, Reid RC. Highly ordered arrangement of single neurons in orientation pinwheels. *Nature* 442: 925–928, 2006.

Olman C, Ronen I, Ugurbil K, Kim DS. Retinotopic mapping in cat visual cortex using high-field functional magnetic resonance imaging. *J Neurosci Methods* 131: 161–170, 2003.

Perrone JA, Thiele A. Speed skills: measuring the visual speed analyzing properties of primate MT neurons. *Nat Neurosci* 4: 526–532, 2001.

Priebe NJ, Cassanello CR, Lisberger SG. The neural representation of speed in macaque area MT/V5. *J Neurosci* 23: 5650–5661, 2003.

Priebe NJ, Ferster D. Mechanisms underlying cross-orientation suppression in cat visual cortex. *Nat Neurosci* 9: 552–561, 2006.

Priebe NJ, Lisberger SG, Movshon JA. Tuning for spatiotemporal frequency and speed in directionally selective neurons of macaque striate cortex. *J Neurosci* 26: 2941–2950, 2006.

Rao SC, Toth LJ, Sur M. Optically imaged maps of orientation preference in primary visual cortex of cats and ferrets. *J Comp Neurol* 387: 358–370, 1997.

Reichardt W. Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In: *Proceedings of the Symposium on Principles of Sensory Communication, 1959*, edited by Rosenblith WA. Cambridge, MA: The MIT Press, 1961, p. 303–317.

Reinert KC, Dunbar RL, Gao W, Chen G, Ebner TJ. Flavoprotein autofluorescence imaging of neuronal activation in the cerebellar cortex in vivo. *J Neurophysiol* 92: 199–211, 2004.

Ruthazer ES, Crair MC, Gillespie DC, Stryker MP. Orientation tuning of single cells at "pinwheel" orientation singularities in kitten visual cortex. *Soc Neurosci Abstr* 22: 277, 1996.

Schummers J, Marino J, Sur M. Synaptic integration by V1 neurons depends on location within the orientation map. *Neuron* 36: 969–978, 2002.

Sengpiel F, Vorobyov V. Intracortical origins of interocular suppression in the visual cortex. *J Neurosci* 25: 6394–6400, 2005.

Shibuki K, Hishida R, Murakami H, Kudoh M, Kawaguchi T, Watanabe M, Watanabe S, Kouuchi T, Tanaka R. Dynamic imaging of somatosensory cortical activity in the rat visualized by flavoprotein autofluorescence. *J Physiol* 549: 919–927, 2003.

Shmuel A, Grinvald A. Functional organization for direction of motion and its relationship to orientation maps in cat area 18. *J Neurosci* 16: 6945–6964, 1996.

Shoham D, Hubener M, Schulze S, Grinvald A, Bonhoeffer T. Spatio-temporal frequency domains and their relation to cytochrome oxidase staining in cat visual cortex. *Nature* 385: 529–533, 1997.

Sirovich L, Uglesich R. The organization of orientation and spatial frequency in primary visual cortex. *Proc Natl Acad Sci USA* 101: 16941–16946, 2004.

Stone J, Dreher B. Projection of X- and Y-cells of the cat's lateral geniculate nucleus to areas 17 and 18 of visual cortex. *J Neurophysiol* 36: 551–567, 1973.

Sun P, Ueno K, Waggoner RA, Gardner JL, Tanaka K, Cheng K. A temporal frequency-dependent functional architecture in human V1 revealed by high-resolution fMRI. *Nat Neurosci* 10: 1404–1406, 2007.

Swindale NV. Coverage and the design of striate cortex. *Biol Cybern* 65: 415–424, 1991.

Swindale NV, Shoham D, Grinvald A, Bonhoeffer T, Hubener M. Visual cortex maps are optimized for uniform coverage. *Nat Neurosci* 3: 822–826, 2000.

Thompson ID, Tolhurst DJ. The representation of spatial frequency in cat visual cortex: a 14C-2-deoxyglucose study. *Proc Physiol Soc* 58P, 1979.

Tohmi M, Kitaura H, Komagata S, Kudoh M, Shibuki K. Enduring critical period plasticity visualized by transcranial flavoprotein imaging in mouse primary visual cortex. *J Neurosci* 26: 11775–11785, 2006.

Tolhurst DJ, Thompson ID. Organization of neurones preferring similar spatial frequencies in cat striate cortex. *Exp Brain Res* 48: 217–227, 1982.

Tootell RB, Hadjikhani NK, Vanduffel W, Liu AK, Mendola JD, Sereno MI, Dale AM. Functional analysis of primary visual cortex (V1) in humans. *Proc Natl Acad Sci USA* 95: 811–817, 1998.

Tootell RB, Silverman MS, De Valois RL. Spatial frequency columns in primary visual cortex. *Science* 214: 813–815, 1981.

Tusa RJ, Palmer LA, Rosenquist AC. The retinotopic organization of area 17 (striate cortex) in the cat. *J Comp Neurol* 177: 213–235, 1978.

Tusa RJ, Rosenquist AC, Palmer LA. Retinotopic organization of areas 18 and 19 in the cat. *J Comp Neurol* 185: 657–678, 1979.

Van Hooser SD, Heimel JA, Chung S, Nelson SB, Toth LJ. Orientation selectivity without orientation maps in visual cortex of a highly visual mammal. *J Neurosci* 25: 19–28, 2005.

van Santen JP, Sperling G. Elaborated Reichardt detectors. *J Opt Soc Am A Opt Image Sci Vis* 2: 300–321, 1985.

Webster MA, De Valois RL. Relationship between spatial-frequency and orientation tuning of striate-cortex cells. *J Opt Soc Am A Opt Image Sci Vis* 2: 1124–1132, 1985.

Weliky M, Bosking WH, Fitzpatrick D. A systematic map of direction preference in primary visual cortex. *Nature* 379: 725–728, 1996.

White LE, Bosking WH, Fitzpatrick D. Consistent mapping of orientation preference across irregular functional domains in ferret visual cortex. *Vis Neurosci* 18: 65–76, 2001.

Xu X, Anderson TJ, Casagrande VA. How do functional maps in primary visual cortex vary with eccentricity? *J Comp Neurol* 501: 741–755, 2007.

Yu H, Farley BJ, Jin DZ, Sur M. The coordinated mapping of visual space and response features in visual cortex. *Neuron* 47: 267–280, 2005.

Zhan CA, Baker CL Jr. Boundary cue invariance in cortical orientation maps. *Cereb Cortex* 16: 896–906, 2006.

Zhan CA, Ledgeway T, Baker CL Jr. Contrast response in visual cortex: quantitative assessment with intrinsic optical signal imaging and neural firing. *Neuroimage* 26: 330–346, 2005.

Zhang J, Rosenberg A, Mallik AK, Husson TR, Issa NP. The representation of complex images in spatial frequency domains of primary visual cortex. *J Neurosci* 27: 9310–9318, 2007.

Zhou YX, Baker CL Jr. Envelope-responsive neurons in areas 17 and 18 of cat. *J Neurophysiol* 72: 2134–2150, 1994.

Zhou YX, Baker CL Jr. Spatial properties of envelope-responsive cells in area 17 and 18 neurons of the cat. *J Neurophysiol* 75: 1038–1050, 1996.

Downloaded from jn.physiology.org on June 11, 2008