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Report

V1 Response Timing and Surface Filling-In

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Huang X, Paradiso MA. V1 response timing and surface filling-in. *J Neurophysiol* 100: 539–547, 2008. First published May 28, 2008; doi:10.1152/jn.00997.2007. There is ample evidence from demonstrations such as color induction and stabilized images that information from surface boundaries plays a special role in determining the perception of surface interiors. Surface interiors appear to "fill-in." Psychophysical experiments also show that surface perception involves a slow scale-dependent process distinct from mechanisms involved in contour perception. The present experiments aimed to test the hypothesis that surface perception is associated with relatively slow scale-dependent neural filling-in. We found that responses in macaque primary visual cortex (V1) are slower to surface interiors than responses to optimal bar stimuli. Moreover, we found that the response to a surface interior is delayed relative to the response to the surface's border and the extent of the delay is proportional to the distance between a receptive field and the border. These findings are consistent with some forms of neural filling-in and suggest that V1 may provide the neural substrate for perceptual filling-in.

INTRODUCTION

There is considerable uncertainty about the manner in which the brain represents visual surfaces. Neurons in the primary visual cortex (V1) usually respond vigorously to luminance contrast within their receptive fields (RFs), but early studies reported that V1 neurons generally do not respond to areas of uniform luminance (Hubel and Wiesel 1962). Subsequent studies found that a subset of V1 neurons do respond to uniform surfaces covering their RF (Friedman et al. 2003; Kayama et al. 1979; Kinoshita and Komatsu 2001; Lee et al. 1998; MacEvoy et al. 1998; Peng and Van Essen 2005; Roe et al. 2005; Rossi and Paradiso 1999; Rossi et al. 1996; Squatrito et al. 1990; Wachtler et al. 2003) and responses sometimes correlate with perceived surface brightness (Kinoshita and Komatsu 2001; MacEvoy and Paradiso 2001; Reid and Shapley 1989; Roe et al. 2005; Rossi and Paradiso 1999; Rossi et al. 1996). The subject of this report is the cortical representation of surfaces with uniform luminance; the related topic of surface texture is not considered.

Psychophysical experiments with stabilized images (Krauskopf 1963; Riggs et al. 1953; Yarbus 1967), the Craik–O'Brien–Cornsweet effect (Davey et al. 1998), masking (Paradiso and Nakayama 1991), dynamic brightness induction (DeValois et al. 1986; Rossi et al. 1996), and temporal luminance ramps (Paradiso and Hahn 1996) suggest that surfaces fill-in over time based on information at the boundaries of uniform areas. Thus it appears that normal surface perception may involve a filling-in process akin to visual completion at the retinal blind spot. Surface filling-in might be neurally implemented in any number of ways. Some models of brightness perception incorporate a more-or-less isomorphic mechanism in which neural brightness signals spread from surface boundaries to surface interiors (Arrington 1994; Cohen and Grossberg 1984; Gerrits and Vendrik 1970). Such models are in marked contrast to proposals that surface perception is an automatic interpretation not requiring explicit filling of any kind (e.g., Dennett 1992). In between the isomorphic and automatic extremes are filling-in processes that are not isomorphic (for a discussion of possible mechanisms, see Komatsu 2006; Pessoa et al. 1998). Neurophysiological and functional imaging studies argue against the idea that uniform surfaces have an isomorphic representation in V1 (Cornelissen et al. 2006; Friedman et al. 2003; Rossi and Paradiso 2003; von der Heydt et al. 2003), although in some situations, filling-in has been observed in human visual cortex (Mendola et al. 2006; Sasaki and Watanabe 2004).

Strong evidence that surface filling-in is not an automatic interpretation comes from a variety of studies indicating that a temporally protracted process is involved (Davey et al. 1998; DeValois et al. 1986; Paradiso and Hahn 1996; Paradiso and Nakayama 1991; Rossi et al. 1996). These experiments suggest that the brain's representation of surface interiors takes longer to complete than the edge representation and the larger the surface, the longer filling-in takes. Combining all the available data, it appears probable that the brain mechanism underlying surface perception is a nonisomorphic but temporally protracted and scale-dependent process.

It is the issue of response timing that the present study aims to address: Is the V1 surface representation delayed relative to the edge representation? Moreover, is there a space/time tradeoff, consistent with filling-in, such that RFs embedded in uniform surfaces respond at progressively later times because they are positioned further from the luminance boundary? Here we show for the first time that there is a temporal progression to activity in area V1 consistent with psychophysical studies of filling-in. We found a variety of V1 response types to uniform surfaces but, on average, responses to surface interiors were slower than those to contours.

METHODS

Two types of experiments were performed. One type examined the temporal response pattern of V1 neurons to uniform surfaces. The other type compared response timing with stimulus borders at different locations relative to the RF.

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General

Our neurophysiological methods have been described in detail previously (Huang and Paradiso 2005) and are summarized here. Experiments were performed on two macaque monkeys (*Macaca mulatta*), weighing 5.0–6.3 kg. Before recording, under isoflurane anesthesia, each monkey was surgically implanted with a head post and a recording chamber overlaying the operculum of area V1. All procedures were approved by Brown University's institutional animal care and use committee and were in accordance with the National Institutes of Health *Guide for the Care and Use of Laboratory Animals*.

During training and recording, animals performed a simple fixation task. Eye position was measured at 60 Hz using an infrared video system (ISCAN) with spatial resolution of 0.2–0.3°. The width of the fixation window was 0.7–1.0°. Fixation locations and stability were found to be similar in different experimental conditions. After the animal held fixation for about 300 ms, a visual stimulus was presented on the screen for about 550 ms. The monkey was required to maintain fixation during stimulus presentation and an additional 500 ms after stimulus offset. The animal received juice rewards for successfully maintaining fixation. The monkeys were free to move their eyes during the intertrial interval, which was about 1.5 s.

The behavioral paradigm and data acquisition were controlled by REX software (Hays et al. 1982). Extracellular potentials were recorded using tungsten microelectrodes (FHC) and action potentials of single neurons or a small cluster of neurons were discriminated with a template-based software system (Alpha-Omega). We have no histology on the brains we studied to confirm recorded lamina, but electrode depths and subjective impressions based on experience suggest that the recordings were from superficial layers of V1. RF properties were determined initially with a computer-generated bar of light whose parameters were varied manually. The classical receptive field (CRF) was defined as the minimum response field mapped with an optimally adjusted stimulus bar. The CRFs of the V1 neurons were located in the lower contralateral visual field with eccentricities of 3–6°.

In experiments examining the temporal response patterns to uniform surfaces, we recorded in an unbiased fashion from V1 neurons responding to surfaces and/or contours.

In the other experiments, we were specifically looking for neurons responding to uniform stimuli larger than the size of the CRF; thus these samples were biased. Note that the neurons responding to uniform surfaces also generally responded to contour stimuli.

Visual stimuli

Visual stimuli were presented on a 27-in. video monitor, which subtended 33 × 25° at the viewing distance of 93 cm. The monitor was driven by a graphics board with 640 × 480 pixel resolution at a refresh rate of 60 Hz (Number Nine).

In the experiment examining the temporal response patterns to a uniform surface, we randomly interleaved trials showing a uniform surface covering the whole video screen with trials showing an oriented bar of light. The luminance of the full-screen stimulus was 8.6 cd/m^2. The stimulus bar (18.0 cd/m^2) was presented in the CRF on a gray background (8.6 cd/m^2). The length of the bar was comparable to the size of the CRF and its width was 0.15°. It was presented at six orientations (0–180° in 30° steps). The luminance of the display prior to the stimulus onset was 0.2 cd/m^2.

In the experiment comparing response latencies to surface interiors and boundaries, a large uniform disk was used. The diameter of the disk was at least fivefold larger than the size of the CRF and ranged from 5.4 to 13.6° (mean diameter = 11.9°). The luminance of the disk was 12.0 cd/m^2. The disk was presented on a background of 0.2 cd/m^2. In the "boundary" condition, the disk boundary passed through the center of the CRF at an angle matched to the preferred orientation of the neuron. In the "center" condition, the same disk was centered on the CRF. "Boundary" and "center" conditions were randomly interleaved.

In the experiment comparing response latencies to uniform disks of different sizes, we centered a uniform disk (12.0 cd/m^2) over the CRF. The diameter of the "small" disk was comparable to the size of the CRF; the diameter of the "medium" disk was at least threefold larger than the size of the CRF and ranged from 4.3 to 13.0°; the diameter of the "large" disk was at least tenfold larger than the size of the CRF and was ≥12.3° larger than the "small" disk and ≥5° larger than the "medium" disk in each experiment session.

In all experiments, we typically presented 20 trials per condition.

Data analysis

For the data in Fig. 1, the raw poststimulus time histograms (PSTHs) with a bin width of 10 ms were normalized to the maximum

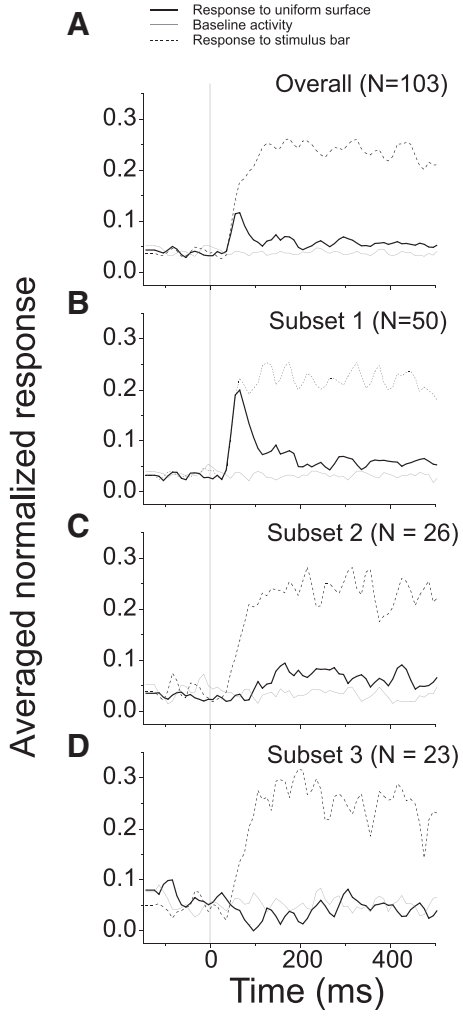

FIG. 1. Responses to large surfaces with uniform luminance. *A*: averaged normalized poststimulus time histograms (PSTHs) of 103 primary visual cortex (V1) units in response to a large uniform surface (solid black line) and an optimally oriented stimulus bar (dashed black line). Baseline activity is indicated by the gray dotted line. The average response to the uniform surface had a large early transient component followed by lower sustained activity. Average response latency to the surface was comparable to the optimal stimulus bar latency. Within the total population, 3 distinct response types were observed. *B*: in response to the uniform surface, 50 of the 103 units showed the early transient response. *C*: 26 of the 103 units showed a delayed and slow-rising response. *D*: 23 of the 103 units were suppressed by the uniform surface.

response across the stimulus bar and uniform surface conditions. The normalized PSTHs were then averaged across the neuronal sample. The averaged PSTHs were smoothed using a Savitzky–Golay (SG) filter with a second-degree underlying polynomial and a window size of five bins. The SG filter is a least-squares moving average that preserves features better than simple adjacent bin averaging. The optimal orientation for each neuron was determined as one of the six orientations that gave rise to the largest response. For PSTHs shown in Figs. 3 and 4, raw PSTHs with a bin width of 10 ms were smoothed with the same SG filter mentioned earlier.

To calculate the latency of the excitatory response for each neuron, a PSTH with a bin width of 5 ms was generated and then smoothed using an SG filter with a window size of five bins. Since we never encountered neurons whose response latencies were <20 ms, we used the time window of −150 to 20 ms relative to stimulus onset to determine the background activity. The response latency was measured with a method adapted from Maunsell and Gibson (1992) and Raiguel et al. (1999). Latency was taken to be the middle time point of the first of three successive bins whose firing rates all exceeded a criterion. The criterion was a firing rate with a probability of $P = 0.01$ based on a Poisson distribution of the background activity. To calculate the latency of an inhibitory response, the same latency measure was used except that the firing rates of three successive bins were all significantly smaller than the baseline firing rate ($P \leq 0.01$). The algorithm we used to quantify latency gave measurements that agreed well with those assigned by human visual inspection. Friedman and Priebe (1998) compared four different procedures for computing response latency and assessed their relative merits. Although the measures yield latencies that are quite similar (i.e., within 2–3 ms), there are advantages to procedures different from that used here. The measure we used was chosen because it is good at determining whether there is a response and it is comparable to the procedure used in many other visual neurophysiology studies.

RESULTS

Temporal patterns of responses to uniform surface

We recorded from 103 V1 neurons or small clusters of neurons in two awake macaque monkeys. Of these, 74 were single units and 29 were multiunits. Single and multiple units displayed similar response properties and response latencies recorded for single and multiple units were comparable; they were combined in the analyses. Henceforth when the term "units" is used, it is meant as shorthand for either single-unit or multiunit data.

The solid black line in Fig. 1*A* shows the average normalized responses of 103 units to a full-screen uniform gray stimulus. The maximum responses of the individual units to the full-screen uniform gray stimulus ranged from 0 to 22.2 spikes/s, with a median of 5.3 spikes/s. The averaged response to this uniform surface shows an early transient component starting about 40 ms after stimulus onset. The timing of the transient matches the early response of the same cells to an optimally oriented bar stimulus (dashed line). The initial transient of the surface response lasts for about 100 ms (extending from 30 to 130 ms on average), followed by lower sustained activity lasting for the duration of the stimulus presentation. Although small, the average sustained activity (calculated 200 to 500 ms after stimulus onset) across the 103 units was significantly greater than the baseline activity (one-way Student's *t*-test, $P < 0.01$). The averaged transient (calculated 30 to 130 ms after stimulus onset) and overall (calculated 30 to 500 ms after stimulus onset) responses were also significantly greater than baseline activity (one-way Student's *t*-test, $P < 0.001$). The significant surface response is consistent with previous results showing V1 neurons respond to uniform luminance (Kayama et al. 1979; Kinoshita and Komatsu 2001; MacEvoy et al. 1998; Peng and Van Essen 2005; Roe et al. 2005; Rossi and Paradiso 1999; Rossi et al. 1996; Wachtler et al. 2003).

Our visual inspection of PSTHs suggested that surface responses with latencies shorter and longer than about 90 ms were qualitatively different. Therefore we used 90 ms as a dividing point for data analysis (importantly, the findings were relatively unchanged if a dividing point 10–20 ms shorter or longer than 90 ms was used). For each neuron we used the statistical latency measure (see METHODS) to categorize the response as positive and early (i.e., before 90 ms), positive and late (after 90 ms), or negative. Fifty of our 103 units had response latencies <90 ms; they all showed increasing activity. The averaged normalized PSTH of these units is shown in Fig. 1*B*. The average early transient response of the short-latency neurons was nearly as large as the average response to an optimal bar in the same neurons. In contrast, 26 units had response latencies >90 ms and slowly increasing activity (Fig. 1*C*). Another 23 units had decreasing activity (Fig. 1*D*). We did not find any systematic difference in orientation tuning widths across the three subsets of neurons with different temporal response patterns. The responses of the remaining 4 (of the 103) units failed our latency measure.

Analysis of the data in Fig. 1*A* shows that in the averaged V1 response both the early transient and the later sustained responses to uniform surfaces were significantly above baseline. In Fig. 1, *B–D* we show the average patterns of what appeared to be three distinct response types. However, the responses in Fig. 1, *B–D* are not necessarily significant for the *entire* early or late response epochs. For example, a neuron could satisfy the latency measure showing statistically significant upward activity, but the activity could fall back to baseline shortly thereafter. Thus we were interested whether individual neurons showed activity significantly different from baseline activity over the duration of the entire early (30–130 ms), late (200–500 ms), or combined response epochs. These response epochs were chosen based on the averaged response to a uniform surface shown in Fig. 1*A*. We found that for 52 of the 103 units, neither the early nor the late response was sustained significantly above baseline (i.e., the response deviated significantly from baseline at some points, but averaged over the entire response epoch the difference was not significant). However, 21 units had early responses that were sustained significantly different from baseline, 16 showed late responses that sustained significance, and 14 showed both early and late responses that sustained significance (Wilcoxon signed-rank test, $P < 0.05$). These results are summarized in Table 1. For

TABLE 1. *Comparison of transient and sustained responses and baseline activity*

Number of Units (Percentage)	Early Transient Response (Greater/Less) Than Baseline	Late Sustained Response (Greater/Less) Than Baseline
14 (13.6%)	9/5	8/6
21 (20.4%)	13/8	0
16 (15.5%)	0	12/4
52 (50.5%)	0	0

the overall response period (30–500 ms), 32 units showed sustained responses that were significantly different from baseline. It is interesting to note that across the different response patterns, some cells showed significantly greater early or late responses than baseline and others showed lower responses. We cannot say whether the increases and decreases relative to baseline came from recordings of excitatory and inhibitory neurons. Nonetheless, the critical point is that across all neurons, there is a strong positive response compared with baseline (Fig. 1*A*).

Comparison of response latencies to uniform surface and stimulus bar

The averaged data in Fig. 1 might indicate that response latencies to bar and surface stimuli are similar, a finding that would seem inconsistent with a temporally delayed surface representation or filling-in. However, the latency of the averaged PSTHs can be misleading because the fastest neurons may make it appear that there is no latency difference between bar and surface even though many individual neurons may exhibit differences. We therefore analyzed individual neuron responses to uniform and bar stimuli. We found that for neurons that gave excitatory responses to the surface stimulus, the mean response latency to a uniform surface was significantly longer than that to an optimally oriented bar stimulus (paired *t*-test, $P < 0.001$). Figure 2 shows the scatterplot of response latencies of the 76 units that showed excitatory responses to the uniform surface stimulus (i.e., cells in Fig. 1, *B* and *C*). The points in the scatterplot appear to be stretched horizontally along the surface response axis. Consistent with the subjective appearance of the plot, the mean response latency to the surface stimulus was 85 ms and that to the bar stimulus was 67 ms (indicated by the star in Fig. 2).

For the 23 units that were suppressed by the uniform surface (Fig. 1*D*), the suppression occurred early. The mean response latency of the 23 units was 51 ms, which was shorter than the mean latency of the same units in response to the bar stimulus (mean = 84 ms, paired *t*-test, $P < 0.01$). The mean response latency of the 23 units to the uniform surface was also significantly shorter than the mean latency of 72 ms to the bar stimulus averaged across all 103 units in the sample (Student's *t*-test, $P < 0.01$).

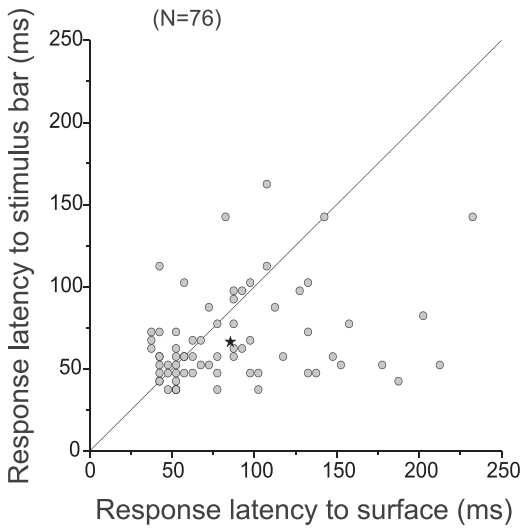

FIG. 2. Response latencies to optimal bars and surfaces with uniform luminance. The horizontal stretch in the distribution shows that response latencies tended to be longer for the uniform surface than for the optimal bar. Each dot represents one of the 76 (out of the 103) units that gave an excitatory response to the uniform surface. The solid star indicates the mean response latencies to the surface and stimulus bar.

These results show that, although many V1 neurons have latencies similar to those of bar and surface stimuli, the average excitatory V1 surface response is delayed compared with the bar response.

Comparison of response latencies to the boundary and center of a uniform disk

The above-cited data show that V1 responses are often slower to a uniform surface than an optimal bar, but the data do not directly address response timing to the border and interior portions of a uniform stimulus. To determine the relationship between interior and boundary responses, we recorded from 34 V1 neurons with a large uniform disk stimulus. All but 2 of the neurons used in this follow-up experiment were distinct from those illustrated in Fig. 1. The neurons were selected for study with an admittedly biased procedure in which we tested neurons that tended to respond to uniform stimuli larger than the CRF. In the "boundary" condition, the disk boundary crossed the CRF at the optimal orientation of the neuron. In the "center" condition, the disk was centered on the CRF. These two experimental conditions are illustrated in Fig. 3*A*. Figure 3, *A* and *B* shows results from two exemplary neurons that gave robust responses to large uniform disks. The response latencies in the "center" condition were longer than those in the "boundary" condition. We were able to obtain response latency measures for all 34 cells in the "boundary" condition but only 21 neurons in the "center" condition. The mean response latency in the "center" condition (for these 21 neurons) was 96 ms, which was significantly longer than the mean response latency of 74 ms in the "boundary" condition of the 34 neurons (Student's *t*-test, $P < 0.05$), and was also longer than the mean latency of 72 ms in the "boundary" condition for the same 21 neurons (paired *t*-test, $P < 0.05$). These results suggest that V1 responses to the interior of a uniform surface are slower than those to the boundary of the same stimulus.

Comparison of response latencies to uniform disks with different diameters

We next measured response latency in 37 V1 neurons to uniform disks of various sizes. The question to be addressed was whether responses to the center of a uniform area were progressively later as the boundary of the surface moved further from the CRF. Disks of all sizes were centered on the CRF. Based on the size of the stimulus disk, we defined three experimental conditions: small-, medium-, and large-sized disks (see METHODS). Consistent with previous data, we found that V1 neurons responded less to larger uniform stimuli than smaller uniform stimuli (MacEvoy et al. 1998).

Figure 4*A* shows PSTHs from an exemplary neuron in response to uniform disks of three different sizes. This neuron responded to disks of all sizes, but gave a progressively lower response as disk size increased, indicative of surround suppression. Importantly, the response latency increased as the disk

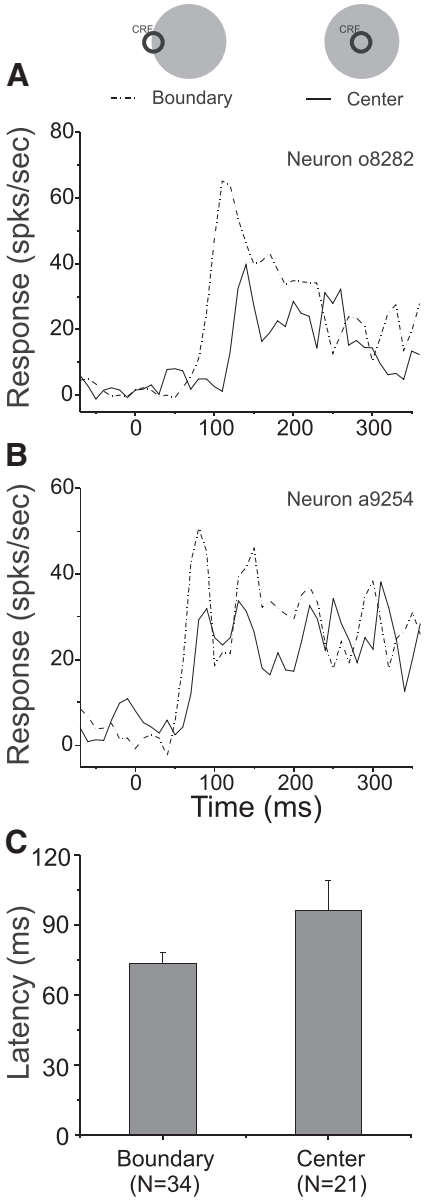

FIG. 3. Responses to the boundary or interior of a large uniform disk. *A*: the response had a shorter latency when the classical receptive field (CRF) was at the boundary of the disk (dashed black line) than when the CRF was centered on the uniform disk (solid black line). The stimulus disk was 13.6° in diameter. *B*: responses of a second neuron showing a delayed response to the surface interior. The stimulus disk was 13.0° in diameter. *C*: mean latencies of "boundary" and "center" responses (error bars show SEs).

size became larger. Figure 4*B* shows responses of another neuron in response to disks of different sizes. This neuron gave a vigorous response to the small disk with a very abrupt response onset. As the disk size increased, the response magnitude decreased and the temporal onset was more gradual.

With our latency measure, we were able to obtain response latencies of 20 neurons in the medium-disk condition and 19 neurons in the large-disk condition. The mean response latencies to the small, medium, and large disks were 73, 89, and 99 ms, respectively (Fig. 4*C*). The mean response latency to the large disk was significantly longer than that to the small disk (Student's *t*-test, $P < 0.05$). The mean response latency to the medium disk compared with the small and large disks fell just short of significance with a *t*-test and ANOVA, but there was a trend of increasing latency across the medium disk size. Although we found significantly different response latencies in the population average, a cell-by-cell comparison fell short of statistical significance (comparing the mean latencies of the responses to the small and large disks gave a *P* value of 0.075 using a paired *t*-test). Nonetheless, the population results imply that, as the size of the surface stimulus increases, V1 responses to the center of a uniform surface become slower.

DISCUSSION

Consistent with previous research, we find that V1 neurons often respond to surfaces even when there is no luminance contrast within the CRF (Friedman et al. 2003; Kayama et al. 1979; Kinoshita and Komatsu 2001; MacEvoy et al. 1998;

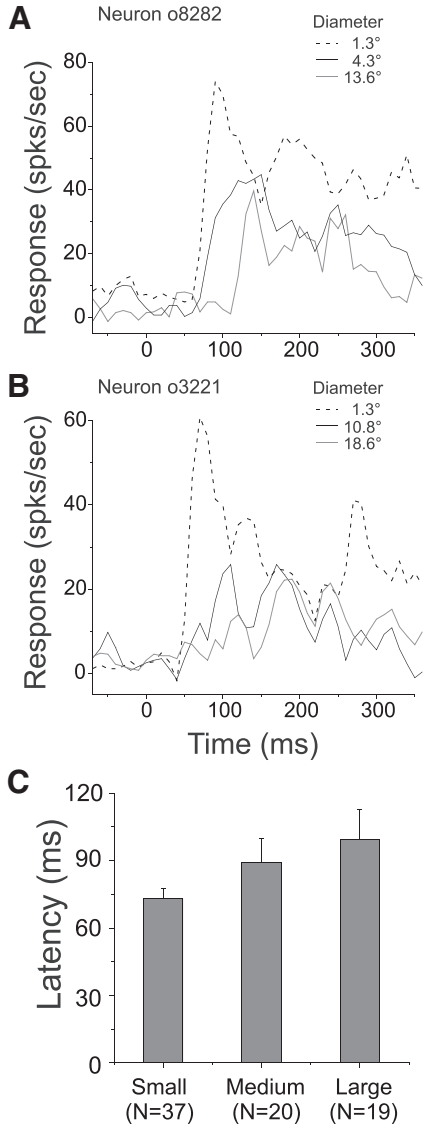

FIG. 4. Responses to disks of different sizes. *A*: PSTHs from an exemplary neuron in response to stimulus disks of 3 different sizes. Response latency increased as the distance from the CRF to the boundary of the disk increased. This neuron is the same as that shown in Fig. 3*A*. *B*: PSTHs from a second exemplary neuron showing increasing latency with disk size. *C*: mean latencies of responses to small-, medium-, and large-sized disks (error bars show SEs).

Peng and Van Essen 2005; Roe et al. 2005; Rossi and Paradiso 1999; Rossi et al. 1996; Squatrito et al. 1990; Wachtler et al. 2003). Evidently, even in the absence of spatial luminance contrast, adequate temporal luminance contrast is present to evoke a significant response in many neurons (and see Vladusich et al. 2006). This point is probably related to both classic (Broca and Sulzer 1902) and recent (Davey et al. 1998; DeValois et al. 1986; Eagleman et al. 2004; Paradiso and Hahn 1996; Paradiso and Nakayama 1991; Rossi et al. 1996) studies showing the importance of time in brightness perception.

We identified what appear to be three different temporal response patterns to uniform surfaces: early transient excitation with lower sustained excitation, delayed sustained excitation, and suppression. We found that in a cell-by-cell analysis, neurons generally respond more slowly to a uniform surface than to an optimized bar. We also found that neurons respond later when their CRF is contained within a large uniform area than when the boundary of the area crosses the CRF. Finally, when we varied the size of a uniform area we found that responses were progressively slower as the boundary of the uniform area moved further from the contained CRF.

A reasonable question is whether the response timing differences in Figs. 3 and 4 are more accurately described as timing differences, amplitude differences, or both. Because surround suppression is very common, moving a receptive field to the interior of a surface generally gives a weaker response than having the boundary of the surface run through the CRF. Despite this finding, it seems important that the responses take longer to develop when the receptive field is further from the surface boundary. Whether the neurophysiologist classifies the response difference as timing or amplitude, the fact is that any response criterion needed for perception is reached at a later time when the boundary of a surface is away from the CRF.

The timing differences we observed between the responses to surface interiors and stimulus contours suggest an important temporal component of surface filling-in. Others discuss in depth the complexities and confusions associated with the "filling-in" term and other types of filling-in such as texture filling-in, Troxler fading, and filling at the blind spot (Komatsu 2006; Pessoa et al. 1998). For the present purposes we narrow the discussion to two key points.

1) Is information at surface boundaries used to determine perception of the interior (i.e., is there filling-in)?

2) Does filling-in involve a scale-dependent process of measurable duration?

For each of these points, there are perceptual and physiological components. There are extensive perceptual data showing that surface perception is determined or influenced by information closer to surface boundaries (e.g., Craik–O'Brien–Cornsweet effect, brightness and color induction, stabilized images), so we take perceptual filling-in of surfaces as fact. There is also solid evidence that surface perception involves a scale-dependent, rather slow, process (Davey et al. 1998; DeValois et al. 1986; Paradiso and Hahn 1996; Paradiso and Nakayama 1991; Rossi et al. 1996). The physiological correlates of the perceptual observations have been harder to establish. We take the results of the present paper as evidence for the physiological component of the second point—i.e., there is a scale-dependent and relatively slow sequence of responses in V1 associated with the surface representation. As discussed below, the timing of V1 responses correlates with perceptual measures of filling-in time. What has not yet been demonstrated is the physiological component of the first point—i.e., that information (neural response) at boundaries is actually used to determine responses of surface-encoding neurons. The remainder of the DISCUSSION addresses the mechanism underlying surface perception.

Transient and sustained responses as possible neural codes for surfaces

The average surface response we observe (Fig. 1*A*) is similar to the response pattern described previously for macaque V1 (Kinoshita and Komatsu 2001) and it also appears consistent with the pattern seen with functional MRI in human visual cortex (Haynes et al. 2004). In all the reports, there is a strong initial transient followed by significantly lower sustained activity. Our data suggest, in addition, that there are three different response patterns underlying the average response. Although some neurons show the transient and sustained response, others show only a delayed excitatory or inhibitory response. Using intracellular recording, Tucker and Fitzpatrick (2006) showed that changes in uniform luminance evoke a strong delayed hyperpolarization in primary visual cortex of tree shrews that is not seen with grating stimuli. Differences in the strength and timing of inhibition may underlie the different extracellular response patterns we observe with surfaces and bars. For those neurons that did not give an early transient response to a large uniform surface despite the temporal onset of the visual stimulus, the inhibition might occur early. It is also possible that early feedforward excitation is weak for those neurons.

Conceivably, the large response transient to surfaces could suffice as the neural representation. The visual system might keep track of the sign and magnitude of each such change to maintain a running log of brightness. However, neurons that show a significant transient generally also show sustained activity that remains above baseline for the duration of the stimulus. Additionally, there are some neurons that have a low but significant sustained response without the transient. The sustained activity we observe is consistent with previous reports of "luxotonic" cells (Bartlett and Doty 1974; Kayama et al. 1979). The sustained surface response components that we and others observe suggest that surface properties are not simply encoded in the response transient. Conceivably, surface properties are represented by both transient and sustained response components, although Kinoshita and Komatsu (2001) found that brightness correlates best with the later sustained activity.

Perceptual filling-in and slow surface responses

Several human psychophysical experiments imply that there is a rather slow and scale-dependent filling-in process for surface brightness. This process is slow compared with contour detection and it appears to start near surface boundaries (Davey et al. 1998; DeValois et al. 1986; Paradiso and Hahn 1996; Paradiso and Nakayama 1991; Rossi et al. 1996). There is evidence that monkeys perceive color filling-in (Friedman et al. 1999) and since brightness perception in macaque monkeys closely resembles that of humans (Huang et al. 2002), it is likely that perceptual brightness filling-in also exists in macaques.

The fact that the perceived brightness of a surface is slow and scale-dependent does not prove that propagation of some surface signal is involved. Nonetheless, intriguing calculations of spreading speed have been made and, across various studies, they are in the same ballpark. Estimates of filling-in rates for the Craik–O'Brien–Cornsweet effect (Davey et al. 1998), texture (Lamme et al. 1999), and several brightness phenomena in our own lab (Paradiso and Hahn 1996; Paradiso and Nakayama 1991; Rossi et al. 1996) range from about 20 to 150°/s. In the present physiological study, if we assume that responses to surface interiors result from propagation of some brightness signal from the boundary, we calculate a spreading rate of about 270°/s (based on the mean response latency difference to the border and stimulus center of 22 ms and a mean disk radius of 6°). Thus the present physiological study in macaque seems to be inconsistent with the previous human psychophysical results. Further consideration, however, suggests the numbers in the two species are not irreconcilable. Let us suppose that filling-in is based on some form of signal propagation that we can express in millimeters per second, where the units are presumably millimeters of cortex. To further speculate, if propagation speeds in millimeters per second were similar in macaques and humans, one would expect different rates in degrees per second because the visual area sizes and magnification factors are different in the two species. There are complexities in precisely measuring cortical area size and magnification factor that have challenged scientists for decades (Adams and Horton 2003). Moreover even with a particular measurement technique, large interindividual variations exist (Amunts et al. 2000; Andrews et al. 1997; Dougherty et al. 2003; Stensaas et al. 1974). Nonetheless, a rough conversion can be made by noting that the V1 surface area in macaques (1,380 mm^2; Rolls and Cowey 1970) differs from human estimates by a factor of 1.5 (Stensaas et al. 1974) to 3.4 (Dougherty et al. 2003) or, alternatively, the linear magnification factors differ by a factor of about 1.6 (Tolhurst and Ling 1988). Thus if a filling-in signal spreads at the same rate in millimeters per second in humans and macaques, we would expect the rate in degrees per second to differ by a factor in the range of $\sqrt{1.5}$ to $\sqrt{3.4}$ or 1.2–1.8. Applying this conversion would mean that a speed of 270°/s in macaque is roughly comparable to a speed of 150–225°/s in human (assuming signal propagation in V1).

Using a recent fit to measurements of the monkey V1 magnification factor from a variety of labs (Tehovnik and Slocum 2007), we estimated the propagation speed in V1 (m/s) that would correspond to 270°/s. Using the average receptive field eccentricity of our neurons, which was 4.5°, the Tehovnik–Slocum fit yielded an average magnification factor of 2.3 mm/deg. Multiplying this by the 270°/s rate we calculated yields an estimate of the V1 propagation speed of about 0.6 m/s. This is to be sure a rough estimate because signal propagation speed along different directions in cortex would vary and there is significant variation in V1 size. That said, the estimate of propagation speed is only slightly higher than estimates obtained with psychophysical techniques in humans (Paradiso and Nakayama 1991; Rossi and Paradiso 1996). We conclude that, although the numbers are not identical, the order of magnitude is similar and the absolute numbers are as close as one might imagine given the sources of variability in the comparison. It is interesting to note that the spreading speeds estimated psychophysically and physiologically are also similar to the rates of activity spreading from focal stimulation in optical imaging (Grinvald et al. 1994). Of course, none of the discussion above proves that spreading speeds are the same in macaques and humans, striate cortex is involved, or even that propagation occurs.

Mechanisms of slow surface responses

Our finding that the response to the surface interior was slower than the response to the surface boundary could be explained by a mechanism of neural filling-in (Arrington 1994; Cohen and Grossberg 1984; Gerrits and Vendrik 1970). It has been well established that V1 neurons are subject to potent contextual influences from beyond the CRF (Bishop et al. 1973; DeAngelis et al. 1994; Gilbert and Wiesel 1990; Knierim and Van Essen 1992; Li and Li 1994; Maffei and Fiorentini 1976; Sillito et al. 1995; for a review see Albright and Stoner 2002) and contextual modulation is thought to play important roles in surface and brightness perception (Kinoshita and Komatsu 2001; Komatsu et al. 1996; Lamme 1995; Lee et al. 1998; MacEvoy et al. 1998; Rossi and Paradiso 1999; Rossi et al. 1996, 2001; Zipser et al. 1996) and in lightness constancy (MacEvoy and Paradiso 2001). The key question here is whether the response to surface interiors is partially or completely determined by the boundary response. Even though we find some neurons with rapid surface responses, if Kinoshita and Komatsu (2001) are correct that brightness is encoded in delayed activity, it is possible that even rapidly responding surface cells could have the brightness component of their response determined by context and boundary.

In our experiments, the boundaries of the uniform disks (except in the small-disk condition) were well beyond the CRF located at the disk centers. The disk boundaries evoked robust responses in V1, which could conceivably activate other neurons representing the surface (i.e., with CRFs away from the boundary), via long-range or a series of short-range lateral connections within V1 and/or feedback connections from extrastriate cortex. This hypothetical scenario is consistent with findings from several previous physiological studies. Bringuier et al. (1999) showed that the latencies of postsynaptic potentials recorded intracellularly in cat V1 neurons increase as the stimulus is placed further away from the CRF center. Rossi et al. (2001) observed that many macaque V1 neurons respond to a texture stimulus presented beyond the CRF even when no stimulus is present within the CRF. Furthermore, they found that V1 response latency increases as the surround stimulus is moved further away from the CRF. These findings indicate that neuronal activation in V1 may spread beyond the size of the CRF. Finally, Grinvald et al. (1994) observed with optical imaging that a focal visual stimulus produces a spreading signal in V1 that moves at 0.10–0.25 m/s, extending beyond the retinotopic projection of the stimulus.

It is a challenge for future research to test whether spreading activity actually underlies perceptual surface filling-in (the physiological component of point 1 cited earlier) because this will require careful quantification of the interactions between simultaneously recorded neurons. Our results would be consistent with such a spreading mechanism, but there are alternatives. A straightforward alternative, consistent with our results, is that the response to surface interiors simply lags

behind the response to boundaries, but no spreading activity is involved. The interiors of surfaces have lower (zero) luminance contrast and it has been known for many years that V1 responses are often delayed significantly at low versus high contrasts (e.g., Albrecht et al. 2002). One problem with this explanation is our own data showing that many V1 neurons actually respond as quickly to a surface interior, with no luminance contrast in the CRF, as to a high contrast bar of light in the CRF. Additionally, if filling-in were based entirely on contrast in the CRF, one might expect more "binary" percepts in the psychophysical experiments since *all* interior points would have zero contrast. An alternative mechanism, based on spatial frequency rather than contrast, is that neurons that respond preferentially to low spatial frequencies (surface interior) have longer latencies than those responding to high spatial frequencies (surface boundary). However, single-unit recordings show that the general trend is the opposite—latency increases with spatial frequency (Frazor et al. 2004). A mechanism involving more than one mechanism is also possible. For example, the tendency for lower contrast responses to be slower may interact with some form of lateral excitation or feedback. In conclusion, although the exact mechanism is yet to be identified, the present study establishes that there are sequential responses to the border and center of surfaces with uniform luminance that correlate with perceptual filling-in results.

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