Responses of Primate Visual Cortical Neurons to Stimuli Presented by Flash, Saccade, Blink, and External Darkening

TIMOTHY J. GAWN AND JULIE M. MARTIN
Department of Physiological Optics, University of Alabama at Birmingham, Birmingham, Alabama 35294

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Gawn, Timothy, J. and Julie M. Martin. Responses of primate visual cortical neurons to stimuli presented by flash, saccade, blink, and external darkening J Neurophysiol 88: 2178–2186, 2002; 10.1152/jn.00151.200. Our visual experience constitutes an unending chain of transient events, including those caused by saccadic eye movements, by blinks, and by localized or global changes in the external world. The categorical perception of objects is maintained across different classes of transient events, suggesting that the neural circuitry underlying visual perception responds to different transient events in a similar manner. However, different sorts of transients do have different perceptual impacts: for example, the sudden changes in a scene due to a saccade or a blink do not disturb our perceptual continuity of a visual scene as much as an external change does. We recorded the responses of 103 single visual cortical neurons in two rhesus monkeys (V1: \( n = 19 \), V2: \( n = 24 \), V3V/VP: \( n = 38 \), V4V: \( n = 16 \)) to the onset and offset of a visual stimulus that was elicited by four different conditions: 1) stimulus flashed on and off while the eyes remain fixed; 2) stimulus turned on and off along with the entire scene (external darkening); 3) stimulus constant, onset and offset induced by rapid saccadic eye movements; and 4) offset induced by an eyeblink. For most neurons the onset and offset of a visual stimulus elicited qualitatively similar responses regardless of condition. We found no systematic effect of different conditions across the neuronal population. Previously we have shown that when the visual scene is occluded by a blink V1 neuronal firing declines in a similar manner as when the external scene is darkened and the eyes left open. Here we show that this is also the case in V2, V3V/VP, and V4V. However, for a substantial minority of neurons, the response varied strongly as a function of the transient event. This overall pattern was the same in all four cortical areas studied here. We hypothesize that most neurons in visual cortex constitute a passive “filter bank”, analyzing the scene for specific details regardless of condition. However, there are neurons that respond in a qualitatively different manner depending on how a stimulus is presented, and we hypothesize that these signals may be important for determining the perceptual salience of a visual event.

Introduction

Transient visual stimulation is essential for vision: indeed, if transient changes are eliminated by stabilizing an image on the retina, the visual scene fades and there is no perception (Ditchburn and Ginsberg 1952). We easily see and recognize objects no matter what class of transient event is used to begin or to end a visual stimulus, and given the inherently expensive nature of image processing, this suggests that the same neural circuits are used to analyze a visual scene under all conditions.

However, it does matter how a visual scene is presented. For example, the sudden changes in an image due to saccades or blinks do not interfere with our subjective experience of continuity, and an isolated change in a small part of a scene draws attention to it in a way that does not occur when the change is part of a change in the entire scene (Riggs et al. 1981; Ross et al. 2001; Volkmann et al. 1980). Therefore, while it might seem reasonable that the visual system processes all transient changes in a similar manner, in at least some respects the system must also process different kinds of transient events differently. How does the visual system handle these apparently conflicting demands?

Recordings from single neurons in both visual cortical area V1 (Richmond et al. 1999) and inferior temporal cortex (Di-Carlo and Maunsell 2000) have determined that for most neurons there is little difference between stimuli that are flashed on with the eyes unmoving and stimuli that are stable and brought into the receptive field of a neuron by a saccadic eye movement. Another study has demonstrated that V1 neurons show similar orientation selectivity during saccades as during static vision and that the pattern of firing of bursts of action potentials is similar in the saccade as in the static flashed case.(Livingstone et al. 1996). There is previous evidence that visual cortical neurons can be sensitive to how a stimulus is presented: for example, recordings in cortical area V3A have shown diverse effects of eye movements (Nakamura and Colby 2000), and studies have shown suppressive effects on neuronal responses in V1 and V2 during both saccades (Battaglini et al. 1986) and in V1 during blinks (Gawne and Martin 2000).

However, the limited number of different conditions used in the previous studies and the difficulty of comparing studies in different visual cortical areas that used different experimental paradigms makes general conclusions difficult. In particular, you cannot combine studies using blinks with studies using saccades and determine if blinks and saccades have the same effects on the same neurons: you need to use all combinations of transient events on the same neurons to do this. The purpose of this study was to examine the effects of different kinds of transient events on the same neurons and in several visual cortical areas using the identical paradigm.

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Address for reprint requests: T. J. Gawne, University of Alabama at Birmingham, Dept. Physiological Optics, 924 South 18th St., Birmingham AL 35294 (E-mail: Tgawne@icare.OPT.UAB.EDU).
METHODS

We recorded from 103 single visual cortical neurons in two awake rhesus monkeys (Macaca mulatta). The monkeys were prepared for single-unit recording under sterile surgical conditions using halothane anesthesia. A recording chamber was implanted on the posterior dorsal surface of the skull, allowing access of fine parylene-insulated tungsten microelectrode (Microprobe) via 23 gauge stainless-steel guide tube to the more ventral cortical areas. A coil of Teflon-coated stainless-steel wire (Cooner Wire) was implanted under Tenon’s capsule of one eye so that the eye position could be monitored by the magnetic field coil technique (Robinson 1963). Eyelid position was monitored by gently positioning a small (2.5-mm diam) coil to the outside upper surface of one eyelid using a 2 × 6 mm strip of masking tape. Unlike the main eye-position coil, which was permanently implanted, this lid coil was attached each day before the start of each experiment. These lid coils are very comfortable (in wearing them ourselves we found that one rapidly ceases to notice them) and the animals gave no evidence that they were in any way affected or irritated by them.

Recordings were made from neurons in response to a patterned visual stimulus that was presented under four different conditions (Fig. 1). The monkeys were trained to fixate for juice reward a small spot on a computer display while high-contrast (87%) black-and-white patterns were presented on a uniform gray background (luminance 33 cd/m²) on a video monitor running at 85 Hz. Stimuli were flashed on by replacing a square patch of the uniform gray background with a black-and-white pattern, and flashed off by making everything uniform gray again. All stimulus timings were checked with a photocell taped to the video monitor, and we used this technique both to ensure accurate timing and to avoid having a stimulus cutoff by changing it partway through a video scan.

We also presented stimuli by blanking the video signal of the video monitor, causing the entire scene to become dark (external darkening), thus approximating the short dark gap caused by eye blinks. In this condition the onset of the external darkening caused stimulus offset, and the offset of external darkening caused stimulus onset. We ensured that the video blanking occurred during the vertical retrace interval so that there were no partial video frames displayed.

Saccades were induced by shifting the fixation point 15° horizontally. Saccade start and stop were determined by the time at which the eye position was 0.5° away from the initial or final position. During the saccade condition, stimulus onset was defined as the saccade bringing the neuron’s receptive field onto the stimulus, and stimulus offset was defined as the saccade moving the receptive field away from the neuron. Neuronal responses were aligned about saccade end for stimulus onset and aligned about saccade beginning for stimulus offset. Stimuli were never changed during a saccade. When a stimulus was brought into the receptive field of a neuron it was always previously visible to the monkey but well outside the neuron’s receptive field. Saccade trials were always initiated from a fixed starting point. The stimulus was turned on, and then the program waited for the eye position to fall within a starting window. An interval of 300 ms was then allowed to elapse to allow for a corrective saccade and to increase the accuracy of the starting eye position. It was always the case that, when a saccade moved the receptive field of a neuron onto the stimulus, the stimulus had always been visible and stable elsewhere in the visual field. This is the most common occurrence in normal scanning eye movements, where it is rarer for parts of a visual scene to change during or immediately before a saccade.

Relex blinks were elicited via gentle air puffs, and eyelid position was monitored via a 2.5-mm-diam coil of wire gently taped to one upper eyelid. Blink onset was determined as the point at which the lid crossed the central pupil (Fig. 2). We have blink data from only 81 of 103 neurons and could reliably determine the neuronal responses only during blink onset. We blink all the time in response to transient dryness or minor irritation and rarely even notice: an air-puff-induced eye blink is not dystonic if it is gentle enough. We carefully titrated the level of air puff to the minimum that elicited blinks more often than not (this is a level at which we could not easily feel it with our bare hands). We used a 2.5-gallon air tank fed through a computer-controlled solenoid valve and connected though ⅛-inch ID tubing to a ¼-inch ID metal tube that projected to within 1 inch of the cornea on one side, well out of the field of view of the monitor. The air tank was pressurized by hand before each experiment, which avoided the possibility of a regulated high-pressure air source accidentally discharging too strongly. The monkeys evidenced no signs of distress, they did not vocalize or shake or stop working, and they required no periods of acclimatization or extra training.

A blink is a remarkably rapid cessation of light: not only is the pupil
Neuronal signals were digitized at a rate of 31.25 kHz and spikes were sorted off-line using a standard technique (Abeles and Goldstein 1977). Only well-isolated neurons with absolute refractory periods were used. The neuronal responses were aligned about the different events (start and stop of flashing stimulus on, start and stop of blanking the video signal, start of a blink) and then converted to smoothed poststimulus histograms by convolving with a Gaussian pulse $\sigma = 3$ ms. (Heller et al. 1995; Silverman 1986).

All stimulus conditions were repeated from 30 to 40 times each in a shuffled random order. The stimulus conditions were all performed exactly once in a random order. The error trials were then added to a list of all stimulus conditions, the order was shuffled again, and the sequence repeated. This ensured both that the different trials were not performed in any fixed order and that there would be nearly equal numbers of successfully completed trials of the different conditions.

Because a saccade toward a target is on average less precise than stable fixation, these trials were pruned to include only those in which the eye position at the end of the saccade fell to near that of the mean of the stable fixation eye positions, to match the mean and SD of eye position under these different conditions (the higher-order moments could not be so matched).

The visual stimuli consisted of 128 black-and-white two-dimensional stimuli based on the Walsh functions. These stimuli were used because they are easy to generate and have been shown to be good stimuli for a large fraction of the visual neurons in multiple visual cortical areas. The single stimulus that gave the strongest response for each neuron was selected and presented at a size that varied from 0.5 to 2° square, either just covering or (mostly in V4V) smaller than each neuron’s receptive field. In all cases the saccade was sufficiently large to move the stimulus either completely onto or completely away from the stimulus.

Recordings were made in visual cortical areas V1 (n = 38), V2 (n = 19), V3 (n = 30, also referred to as VP) (Hung et al. 2001), and V4V (n = 16), which together constitute a significant portion of the ventral “stream” of cortical areas that is critical for form vision (Van Essen and Gallant 1994). Determination of cortical site was made by a combination of comparing stereotaxic coordinates with a standard atlas (Paxinos et al. 2000) comparing receptive field location and size and, in one animal, by making 40-μm coronal sections and Nissl staining. The recording sites for V1 and V2 were located in the calcarine fissure and for V3V and V4V on the adjacent inferior/lateral surface of cortex.

The purpose of this study was not to precisely duplicate the same pattern of light on the retina under the different conditions but to explore the range of neuronal responses to different classes of transient events as they actually occur. All of the transient events used here effect rapid changes in a stimulus, but they do not result in identical patterns of light on the retina. Thus a saccade-induced onset and offset will have some short period where the stimulus is shifting and accelerating within a receptive field while a flashed stimulus does not, and a blink and an external darkening will have overall luminance changes while saccade and flashed do not, and during a blink there will be a very brief period in which there is a weak vertical gradient of luminance across the retina (weak because the lid is far removed from a plane of image focus). This is the range of events to which the visual system is typically exposed, these are events for which we see objects perfectly clearly, the categorical perception of shape does not change depending on whether we move our eyes or blink or turn the lights on or off, and yet these different sorts of transients do have different perceptual consequences. The purpose of this study is to explore the range of neuronal behavior in visual cortex to the actual ecological range of stimuli to which we are adapted.

All experimental procedures and care of the animals were carried out in compliance with guidelines established by the National Institute of Health and were approved by the University of Alabama at Birmingham Animal Care and Use Committee.

Results

Figure 3 shows four examples of the most common response pattern. The neurons respond with an essentially identical transient burst of activity to the onset of a visual stimulus regardless of how that onset was achieved, and, when the stimulus goes away, after a latency similar to the onset latency the neuronal firing stops, again largely independent of condition. The example shown from V4V has a relatively long latency and a slow onset; we also found neurons in V4V that had more abrupt transients, as in the other cortical areas, but whether short and brisk or slow and gradual they all generally responded in a similar manner to all conditions. We term these neurons passive because they are driven by the visual stimulus regardless of condition.

However, a significant minority of the neurons had very different properties, which we term event related because their
responses are not just a function of the visual stimulus but also of the specific event that started or ended a visual stimulus. There is considerable diversity among this class of neurons. As a partial list of the wide variety of response patterns, we present one neuron displaying transient responses to the offset of a stimulus by every condition except flashed, but no responses to the onset of a stimulus (Fig. 4A); a neuron exhibiting a transient pulse to the offset of a stimulus caused by sudden darkening, whether by a blink or external darkening (Fig. 4B); another that exhibits transient responses for the offset of a stimulus for flashed and saccade cases (Fig. 4C); and another that only exhibits transients at the offset of a flashed stimulus (Fig. 4D). At least in principle, it would take only a small number of neurons with complementary properties to allow a local region of cortex to determine exactly how any particular visual stimulus had been presented.

Figure 5 shows the peak firing rates for the responses to the different conditions against each other. There is a large spread in the magnitude of the peak rates, because some neurons had which we had valid blink data for the four visual cortical areas, comparing the responses to the sudden darkening caused by a blink with the sudden darkening caused by blanking the video monitor signal. Overall there is little sustained firing across the "temporal scotoma" of either a blink or an external darkening: when the visual scene goes away, after some latency, the neuronal firing of most visual cortical neurons in these four regions goes away as well. We had previously demonstrated this finding in V1 (Gawne and Martin 2000) and now extend it to V2, V3/V/VP, and V4/V. The intuitively appealing notion of the nervous system interpolating its activity across blinks (Billock 1997) does not appear to hold: apparent continuity does not require actual continuity of neuronal activity in, if not all, certainly much of, visual cortex.
strong transient pulses while others did not and because for any given condition there were usually at least a few neurons in which the response was very weak (even though more robust in other conditions). Fig. 6, A and B, are for the ON responses, and while there is considerable scatter, there is an overall strong correlation between the magnitude of the ON response to one condition and the ON response to another. Nevertheless, there are some neurons that have quite different responses to the different conditions. Fig. 6, C, D, E, and F, are for the OFF responses. Here many more neurons had responses that were weak or absent, and of those neurons that did respond strongly to the offset of a stimulus, there was a much greater proportion that had different responses to different conditions.

We note that there is a relatively strong correlation between the responses to the offset of a stimulus caused by a blink and that caused by an external darkening (Fig. 6F). Presumably this is due to the fact that both of these conditions involve large luminance changes. There are, however, exceptions (see Fig. 4D), and we further note that, in Fig. 6D, comparing flashed offset with saccade offset, neither condition involving net luminance changes, it is still the case that of those cells that had a large OFF response a larger fraction differentiated between condition than for the stimulus onset case. Finally, we note no such asymmetries between high- and low-luminance conditions for stimulus onset. Thus, while some neurons displaying similar strong OFF responses to large overall decrements of light appears to be part of the pattern here, it is not an explanation for the full diversity of behavior nor for the general observation

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**Fig. 4.** Example responses from 4 event-related (i.e., qualitatively different responses to the different conditions) neurons in the 4 different visual cortical areas (A–D). A: no strong ON responses for any condition, but strong OFF responses to all conditions except for that where the stimulus was removed from the receptive field via a saccade. B: responds similarly to all stimulus onsets, but only gives a strong transient pulse to stimulus offset caused by external darkening and blink (delayed pulse in saccade offset is actually an ON response to a target at another location). C: neuron with no strong ON responses, but strong OFF responses to flashed and saccade (delayed pulse in the second row is due to end of the trial). D: neuron with a strong OFF response only to the flashed condition.
that OFF responses, when they are present, are more likely to differentiate between conditions than the ON responses.

To make it easier to visualize the response patterns across all conditions we first took the highest value of peak rate across all seven conditions for each neuron, categorized responses as positive or negative based on whether they were more than 50% of this value, and then listed the numbers of all the permutations (Fig. 7). The blink condition was not included in this graph because ON responses could not be reliably determined for this condition and because we only had reliable blink data for 81 out of 103 neurons. There is nothing especially critical about using the 50% level to categorize responses; this method was chosen only to illustrate qualitative presence or absence of relatively strong transient responses across all conditions simultaneously.

For the ON responses, most of the neurons had relatively strong transient responses for all conditions, but 29% had responses that varied with the condition. For the OFF responses, most neurons also had qualitatively similar responses to all conditions, but only because most did not have strong transient OFF responses at all. For the neurons that had at least one positive response to the offset of a stimulus, 93% had responses that varied with condition. Thus when they are present, the transient responses to the offset of a visual stimulus are far more likely to differentiate strongly between conditions than the ON responses.

For those neurons that had strong responses to the onset of a stimulus by both flash and saccade conditions, we computed the response latency by taking the point at which the spike density waveform reaches half of peak value (Gawne et al. 1996). Response latencies were not always identical for the different conditions (see Fig. 3, top right, where the response latency of a V4V neuron for the saccade condition appears significantly delayed relative to the response latency for the flashed condition). However, in general, the response latencies are similar for different conditions (see Fig. 8). Response latency increases as one goes from V1 to V4V, but there is substantial overlap (it has been demonstrated elsewhere that the variation of response latency within a visual cortical area is greater than the variation between areas) (Nowak et al. 1995). There was an overall tendency for the response latency to be slightly longer for the saccade condition than for the flashed, which was statistically significant for areas V1 and V4V ($P < 0.05$, paired $t$-test). Other than for V4V, these small differences in latency could be due to our definition of saccade ending: there is no absolute agreed on point at which a saccade may be judged to be over, and different definitions will result in alterations in measured latency (although the rapid deceleration of the eye means that different definitions can only change the estimation of latency by a few milliseconds). The latency differences seen in V4V frequently had the appearance of a

**FIG. 5.** Mean firing rates as a function of time for the four different visual cortical areas (rows) for when the stimulus was occluded by an eyeblink (left column) or by blanking the video monitor (right column). There was only valid blink data from 81 out of the 103 neurons used in this study. While there is considerable variability between neurons, overall there is no strong sustained neural activity during the blank period of either a blink or an external darkening, and this overall pattern is true for all four visual cortical areas studied here.

**FIG. 6.** Plot of peak firing rate in an 80 ms duration interval starting after shortest response latency (this interval was sometimes shortened to avoid including the on-transient when a saccade brought a second stimulus into the receptive field, as in Fig. 2B second panel from the bottom). Gray lines represent $\pm$SE. A: stimulus onset: flash vs. external darkening. B: stimulus onset: flash vs. saccade toward target. C: stimulus offset: flash vs. external darkening. D: stimulus offset: flash vs. saccade away from target. E: stimulus offset: flash vs. start of blink. F: stimulus offset: external darkening vs. start of blink.
period of suppression before the response onset, but it is difficult to apply statistics on suppression for neurons with low spontaneous firing rates and we could make no firm conclusions. We never saw any predictive or noncausal behavior in any of the neurons studied here; in particular, we never saw a neuron respond to the presence of a stimulus in its future receptive field before the saccade was initiated.

**DISCUSSION**

We found that, for neurons in visual cortical areas V1, V2, V3V/VP, and V4V, most neurons have qualitatively similar responses to the onset and offset of a visual stimulus. We provisionally term these neurons *passive*, in that they respond in a passive manner to the pattern of light on a region of the retina regardless of the manner in which that pattern was presented. A substantial minority of neurons clearly distinguish between the different means of stimulus presentation, and we provisionally term these neurons *event related*. We hypothesize that this division of labor is a fundamental property of visual cortical processing in these areas. The processing of visual form, which by its very nature is computationally intensive, occupies the bulk of the neural tissue. Signals relating to the manner in which a stimulus is presented, or to its context, are not multiplexed across the general population but rather are confined to a relatively small number of specialist neurons.

There did not appear to be any difference in the patterns of behavior in the different cortical areas examined here, and a $\chi^2$ test did not show significance ($P > 0.05$). However, given the limited number of neurons and the large number of different possible response patterns, this is not a conclusive result. Another study has shown differential effects of microsaccades in different visual cortical areas (Leopold and Logothetis 1998), so there is evidence that there are differences. However, Leopold and Logothetis explored microsaccades and this study explored saccades that completely removed a stimulus into and out of a receptive field. Additionally, the biggest differences found by these authors was in inferotemporal cortex, but as their stimuli did not cause any net change in firing rate in this area, it is not clear that their results are easily comparable to ours or are strong evidence for significant differences in saccade processing between areas. Determining if there are systematic differences between the various visual cortical areas will require significantly larger numbers of neurons, almost certainly requiring electrode arrays with a large number of recording sites.

We cannot rule out the possibility that those neurons with small but still significant differences in response to different conditions could also contribute to the perceptual differences seen between different conditions. However, we argue against this for the following reason: it seems likely that many of the small differences between neurons that had qualitatively similar responses to different conditions were due to small variations in the dynamics of the position of the stimuli in the receptive field. Thus these small differences would likely be unreliable in the presence of even slightly changed conditions (for example, saccades of different magnitudes or velocities), thus making any method using these small response differences either unreliable or extremely complex, requiring a simultaneous solution to the problem of form and eye-position dy-
namics of a large population of neurons. Given that there are neurons that can clearly and unambiguously discriminate between different conditions with no complex decoding at all, we feel that this is the more likely mechanism.

There is evidence that it is not just the rate of firing of neurons but also the presence or absence of transient bursts of firing that is important for the operation of the nervous system. (DeBusk et al. 1997; Lisman 1997; Martinez-Conde et al. 2000; Swadlow and Gusev 2001). We have argued that the presence or absence of transient firing around the time of a change in visual stimulus could be important for maintaining the continuity of vision, which may seem counterintuitive. Surely, if our perception is to be continuous, then the neural activity on which it is based should also be continuous? However, there does not appear to be any direct correspondence between the timing of neuronal activity and our perceptions (Eagleman and Sejnowski 2000). Continuity could be represented by the actual continuity of neuronal activity, but it could also be represented by the presence or absence of specific transient bursts of activity that are interpreted by the rest of the nervous system as meaning that something is continuous. We hypothesize that these transient bursts may act as a trigger, initiating other systems such as those that focus attention on particular locations or features. Perceptual continuity would then be represented as the absence of those transient signals that indicate change. We speculate that actual neuronal continuity across the gap of a blink may only be found in areas that require predictive motor control, for example, in the ventral premotor cortex, where neurons have been found that code for the predicted locations of targets in the dark (Graziano et al. 1997).

All of the different conditions result in very rapid (typically <10 ms) changes in the image in the receptive field; nevertheless, there clearly are differences in the detailed dynamics of the change of light on the retina under these different conditions. For example, the saccade condition involves a short period during which the stimulus is progressively shifted and blurred, whereas, in the flashed case, the image appears and disappears more abruptly. Also, there are large luminance shifts with the blink and the external darkening conditions that are not present for the saccade and flash conditions. However, it was the purpose of this study to explore the range of neuronal behavior to as broad a class of transients as possible. The visual system is exposed to all of these conditions and handles them all very well. There may be subtle differences in psychophysical performance after the different kinds of transient events, but still it is the case that we have no trouble recognizing objects no matter what class of transient event causes the image to fall on the retina.

In this study, when we used a saccade to cause a stimulus to enter the receptive field of a neuron, it was always the case that the stimulus was present in the visual field of the animal (although well outside of the receptive field of the neuron under study). It has been demonstrated in area lateral intraparietal area (LIP) that most neurons respond strongly to recently flashed stimuli, but very poorly or not at all to stable stimuli that were present before the initiation of a saccade (Gottlieb et al. 1998). Because we did not change the stimulus during a saccade, and also because we did not vary the time that the stimulus was present before a saccade was initiated, we cannot directly address this issue here. However, it was the case that the responses of neurons in V1, V2, V3V/VP, and V4V to stable stimuli found in this study were nearly the exact opposite of those found by Gottlieb et al. in LIP. Specifically, most neurons in the areas we studied respond as strongly to stable stimuli brought into the receptive field by a saccade as to recently flashed stimuli, and most neurons in LIP do not.

Recently it has been demonstrated that neurons in visual cortical areas as early as V1 can exhibit “remapping”, i.e., they can respond to the presence of a stimulus in their future receptive field even before the saccade that will move the receptive field onto the stimulus occurs (Nakamura and Colby 2002). We found no evidence for this in our data; however, we point out that in our study the stimuli were always present and stable before a saccade, while in the work of Nakamura and Colby they appear to have concentrated on recently flashed “salient” stimuli. We hypothesize that, for stable, nonsalient stimuli that are brought into the receptive field of a neuron via saccade in areas V1 through V4, the response is nearly identical to that caused by a suddenly flashed stimulus because exactly the same processing pathways from the retina are used in both cases and thus the response latencies are roughly similar. However, when a stimulus is salient, it is then and only then represented in parietal areas (such as LIP), and as parietal cortex can show clear remapping across a saccade (Duhamel et al. 1992), feedback to earlier visual cortical areas can then cause predictive effects across a saccade in visual cortical areas such as those studied here. It will be interesting to determine under a broader range of conditions whether remapping in striate and extrastriate cortex always covaries with the degree of representation in parietal cortex and whether it indeed is feedback from parietal cortex that enables the remapping to occur or whether it is feedback from some other area or a different mechanism entirely.

We were not able to gather enough data here to determine whether the event-related neurons that we found constitute a limited set with discrete properties or whether there is instead a continuum of properties. Neither were we able to determine whether there are systematic differences in the characteristics of the event-related neurons between the different visual cortical areas. Nevertheless, we have determined the overall pattern of responses of visual cortical neurons under a broad range of conditions for several areas, to our knowledge this is the first time that this has been done, and further we can make projections of the number of neurons that would be required to answer these additional questions. We project that on the order of 500 neurons per cortical area minimum would be required for random sampling of the neuronal population, which, given the technical difficulties involved in performing these experiments, seems to us to be largely impractical with current single-unit techniques. Alternatively techniques that allow the recording from specified subpopulations of neurons in awake animals could make it easier to find discrete functional subpopulations of neurons without the need of recording from massive numbers of neurons. The development of new techniques of recording from large numbers of neurons in awake animals or the ability to record from targeted subpopulations of neurons are proposed as being high-priority tasks for the investigation of the visual cortical system.
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