

The importance of modulatory input for V1 activity and perception

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Abstract: To conduct well-controlled studies of visual processing in the laboratory, deviations from natural visual situations must generally be employed. In some regards, the reduced visual paradigms typically used are adequate for providing an accurate description of visual representations. However, the use of fixation paradigms and stimuli isolated within a receptive field may underestimate the richness of visual processing in area V1. Experiments ranging from lightness encoding and perception to paradigms involving natural scenes and saccades used to examine the relationship between V1 activity and perception are reviewed in this chapter. Using more complex and natural visual stimulation, V1 responses have been detected that are significantly different from responses obtained in more reduced paradigms. A feature common to the findings of different experiments is that the scale of the activated neural population and circuitry appears to play a key role in the correlation between V1 activity and perception. More complex and natural visual stimulation brings into play extra-receptive field modulatory input not involved with stimulation localized to the receptive field. The results suggest that rather than subtly sculpting the response, modulatory input coming from intra- and/or intercortical sources is fundamental in establishing perceptual response patterns in natural visual situations.

Introduction

A principal goal of visual neuroscience research is to understand the computations that take place in the human brain under natural visual conditions. To reach this goal, one approximation frequently made is the use of animals as human surrogates. At present there is no alternative for the examination of neural processing at the single-cell level. Other simplifications are also typically made in the type of visual stimuli employed and the visual behavior of the animal. Rather than complex real-world scenes, animals are presented with unnatural stimuli such as 2D Gabor patches or small bars of light. Rather than

exploring a scene for the purpose of foraging, an animal fixates for an extended period of time while a stimulus is flashed on its peripheral retina. Without a doubt, a tremendous amount has been learned about vision and the brain with the reductionist approach. However, there is that nagging tacit assumption behind virtually all experiments that in natural visual situations, neurons would act the same as in reduced laboratory paradigms.

No one has seriously suggested that everything we know about visual neuroscience from simplified experiments is wrong. However, there are studies that have examined both stimulus complexity and visual behavior that hint that there is more to V1 processing than the reduced paradigms reveal.

Complex stimuli often uncover effects of context that are missed with small stimuli on a blank background. A large literature exists on the effects of

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context, both perceptual and neural. Demonstrations, some dating back hundreds of years, show that the lightness, color, motion, and other perceived properties of objects are powerfully influenced by the attributes of neighboring objects. Well known examples are color and motion contrast effects. Neural activity also shows powerful contextual influences. A considerable number of experiments have shown that the response of a neuron to a stimulus in its receptive field can be strongly modulated by other stimuli located outside the receptive field (Allman et al., 1985; MacEvoy et al., 1998; Albright and Stoner, 2002). For example, uniform illumination outside the receptive field (RF) suppresses responses to a stimulus in the receptive field (MacEvoy et al., 1998; Rossi and Paradiso, 1999). This is consistent with the suppressive effect seen perceptually in which a gray patch looks dimmer if it is surrounded by a brighter patch. If an optimal bar stimulus is in the receptive field, the response is modulated by the orientation of a bar or grating outside the receptive field (Blakemore and Tobin, 1972; Maffei and Fiorentini, 1976; Fries et al., 1977). This sort of line contrast effect seen in neurons may be related to perceptual effects including figure-ground segregation (Lamme, 1995; Zipser et al., 1996), popout (Knierim and Van Essen, 1992; Nothdurft et al., 1999) and tilt illusions (Paradiso, 1988; Gilbert and Wiesel, 1990). These contextual influences coming from beyond the receptive field presumably arise from lateral or feedback connections. Despite the large number of studies of perceptual and neural contextual effects, there are relatively few cases where it has been established that there is a direct relationship between the two. The contextual studies do not imply that measurements obtained with stimuli confined to the receptive field are incorrect. Rather, the simplified experiments may miss some of the richness of natural processing.

It also appears that visual behavior influences neural coding. A small number of studies have used free viewing paradigms to study receptive fields without enforcing prolonged fixations at specific locations in the visual field. In one study of area IT, free viewing elicited responses indistinguishable from those of fixation paradigms (DiCarlo and Maunsell, 2000). However, there are hints from other experiments that in natural visual situations

brain activity in V1 may be different from what is typically seen in the laboratory. Livingstone et al. (1996) found that it was surprisingly difficult to discern a V1 receptive field from the firing of a neuron during free viewing. To locate a receptive field it was necessary to use a burst filter tailored to the neuron under study. In a series of experiments, Gallant and his coworkers have examined the effects that free viewing has on responses in V1 and later areas. They found that responses in free viewing are often lower and more sparse compared to common flashed-stimulus paradigms (Gallant et al., 1998; Vinje and Gallant, 2000, 2002).

Introducing complex visual stimuli and more natural visual behavior into experiments pose great challenges, but several labs have taken up this challenge. The initial forays into this realm suggest that reduced paradigms may underestimate or mischaracterize neural computations in natural situations (Livingstone et al., 1996; Vinje and Gallant, 2000; David et al., 2004). This may be particularly true in early cortical areas that can appear to be entirely driven by feedforward input (Ferster, 1986; Reid and Alonso, 1995; Kara et al., 2002). The experiments described here are examples from our research showing that neural responses sometimes change significantly as stimulus or behavioral complexity is increased and made more natural. Indeed, in some cases this complexity may be essential for making the V1 response perceptually correlated. The findings have implications for the role and importance of recurrent or modulatory connections in visual cortex. The findings are discussed in terms of their implications for the circuitry underlying perception and the importance of modulatory input to V1 neurons.

Spatial integration and lightness constancy

The great majority of experiments in primary visual cortex employ stimuli that place high contrast features in receptive fields. Indeed, most textbook descriptions state that this is a requirement for evoking a significant response. While this is true for many cells, for many others significant responses can be elicited when the receptive field is covered by a patch of uniform luminance (Kayama et al., 1979; Komatsu

et al., 1996; Rossi et al., 1996; Rossi and Paradiso, 1999; Wachtler et al., 2003). The significance of this observation relates to the importance of surface lightness and color in object recognition.

Of particular interest is the finding that many V1 neurons actually respond in a manner better correlated with perceived lightness than with luminance (Rossi and Paradiso, 1999; Kinoshita and Komatsu, 2001; MacEvoy and Paradiso, 2001). It appears that the basis for this neural correlate of perception in primary visual cortex is spatial integration arising from lateral and/or feedback interactions (MacEvoy et al., 1998; Rossi et al., 2001).

There is ample evidence that stimuli located outside the classical receptive field modulate the response to stimuli within the receptive field. For example, the response to an optimally oriented bar in the RF is generally greater when surrounding bars outside the RF are orthogonal and less when the surrounding stimuli are parallel (Blakemore and Tobin, 1972; Gilbert and Wiesel, 1990). Significant surround interactions are also found when the stimuli are surfaces rather than lines (Schein and Desimone, 1990; MacEvoy et al., 1998; Wachtler et al., 2003). One indication of the potential importance of these interactions is the numerous lightness and color illusions that are based on context (e.g., simultaneous contrast). Most often when a uniform patch covers a receptive field, light in the surrounding area has a suppressive effect, though there are cells for which surrounding light enhances the response. The range of the spatial interactions can be quite large, often extending many times the size of the classical receptive field (MacEvoy et al., 1998; Wachtler et al., 2003). This large range is consistent with the large scale over which perceptual interactions occur.

A reasonable hypothesis is that the extensive spatial integration observed in V1 serves some valuable purpose and perceptual illusions are a harmless side effect. It appears that lightness constancy may be one such purpose. Over the course of a day and across the seasons of the year, the illumination coming from the sun varies considerably. Humans, and animals that have been tested, perceive the lightness of objects to be stable despite large variations in illumination. This perceptual constancy for lightness, and related color constancy, was presumably of great evolutionary value. For example, in

the absence of perceptual constancies, there might not be reliable cues upon which to select ripe fruits to consume.

Experiments were conducted in cat V1 to test responses for lightness constancy (MacEvoy and Paradiso, 2001). Stimuli consisted of monochromatic patches (i.e., a monochromatic “Mondrian” stimulus) on a computer monitor simulating surfaces with a wide range of reflectances (Fig. 1A). One patch of the stimulus encompassed the receptive field and the rest composed the background. Changes in the luminance values of the patches were made in a manner either consistent (illumination conditions) or inconsistent (control conditions) with overall changes in illumination. Comparisons were made between the two situations when the patches covering the receptive field in each case were identical.

In control conditions only the luminance of the patch covering the receptive field increased, a situation in which the perceived lightness of the patch increases with luminance. By contrast, in the illumination conditions the lightness percept is stable. While there is considerable cell-to-cell variability, on average the responses of V1 neurons to identical stimuli in their receptive field are significantly different in the two conditions (Fig. 1B, C). In the control condition the average V1 response correlates with the luminance of the RF patch. Since perceived lightness also correlates with the luminance, the neural response also correlates with lightness. In marked contrast, in the illumination conditions there is essentially no change in the average V1 response as the luminance of the RF patch increases. This mirrors the perceptual constancy of the patch. These results are reminiscent of the constancy demonstrations of Land (Land and McCann, 1971; Land, 1986). In these demonstrations, the color of patches in a Mondrian were shown to be constant when the overall illumination was varied, but viewing any single patch in isolation (for instance, through a tube) revealed that the patch luminance changed dramatically. The context provided by the changes in the larger area is essential to normalize the local percept. In our physiological studies, in both the illumination and control conditions the response correlates with lightness, but only in the illumination conditions does the response exhibit lightness constancy.

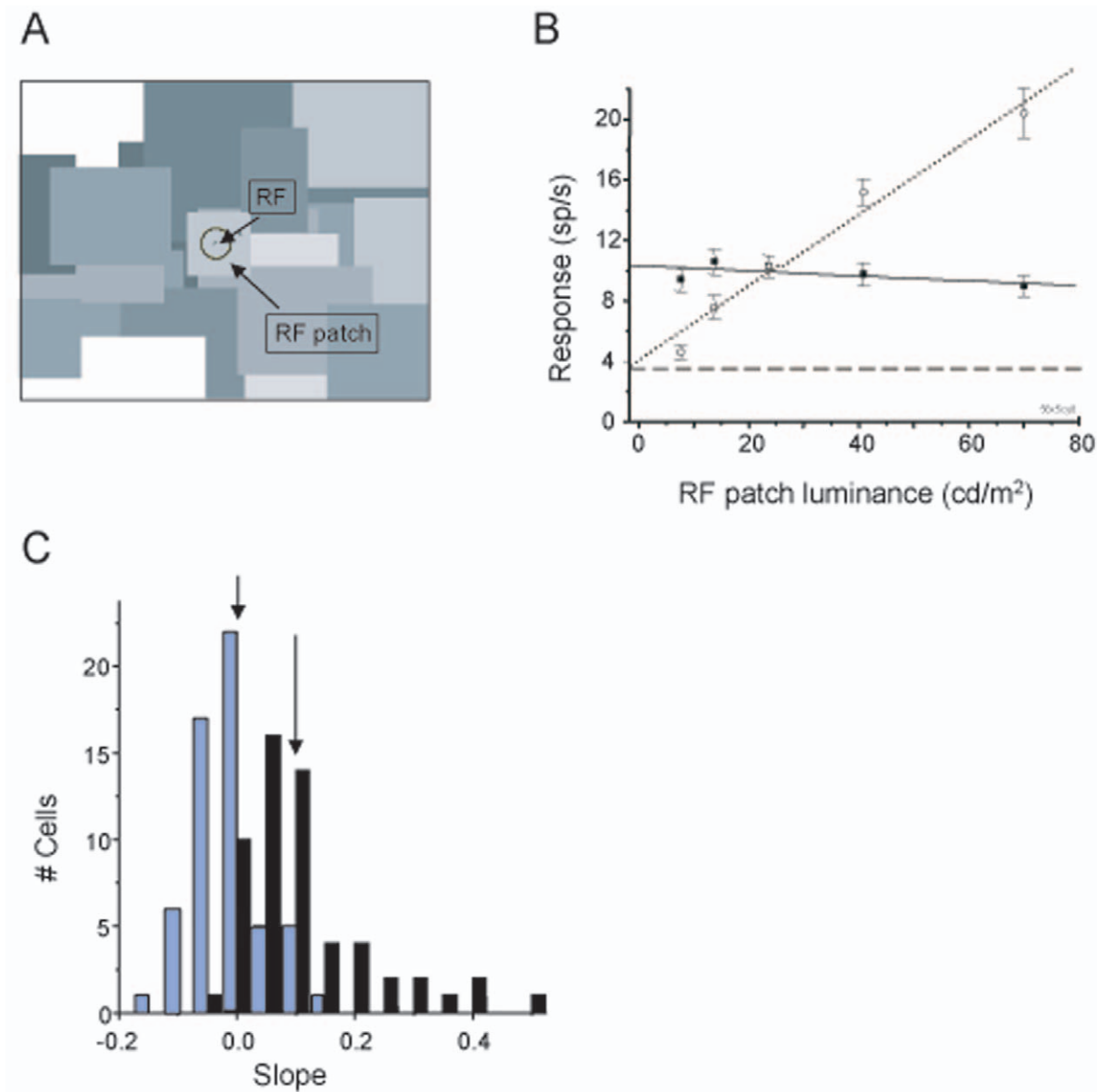


Fig. 1. V1 response to lightness constant stimuli. A. The receptive field was positioned on one patch of a monochromatic Mondrian pattern. B. The dashed line shows that the response of one neuron increases as the luminance of the RF patch increases. When the luminance of all Mondrian patches increases in a manner consistent with an illumination change, the response is unchanged (solid symbols and line). C. Using plots as in 1B, slopes were computed for each cell in illumination and control conditions. The average slope in the control condition was 0.11 indicating that the average response increases with RF patch luminance (black bars). In the illumination condition the average slope was -0.01 , nearly invariant (gray bars).

A likely basis for the response invariance in the illumination conditions is the predominant surround suppression seen with uniform patches of light (Schein and Desimone, 1990; MacEvoy et al., 1998; Wachtler et al., 2003). Evidently in the illumination conditions the increased response of the neuron that comes from more light in the RF is counterbalanced by increased suppression from the surround. What is somewhat surprising is that on average the net input to V1 neurons balances the added RF drive with increased surround suppression.

The effects of natural scenes and saccades on V1 activity

The results described above suggest that in the domain of lightness, modulatory inputs from lateral or feedback connections play an important role in making V1 activity lightness constant. Although Mondrian's paintings can be viewed in museums, flashing similar pictures to a fixating animal can hardly be considered a natural visual situation. Visual stimulation in the real world typically involves complex arrangements of light, color, and contrast, quite unlike the simple stimuli usually used in the laboratory. Moreover, natural stimuli fill the visual field whereas many experiments are conducted with small RF stimuli isolated on a large blank display. Another obvious difference between typical experiments and natural vision is behavioral. In a natural setting, the eyes move to bring new stimuli into view; typical fixations are about 300 ms with brief intervening saccades. In most experiments, animals are trained to hold fixation (or anesthetized) while stimuli are flashed into the receptive field.

To explore the significance of stimulus complexity and saccades on V1 responses, we conducted an experiment in alert macaques in which the same stimulus was presented to a neuron under four different conditions, varying with respect to how natural the visual situation was. In the first condition, the animal fixated a point on an otherwise gray visual display and a small bar was flashed into the receptive field. In the second condition the animal fixated the same point and the bar was flashed, but in this case the background was a grayscale outdoor scene (van der Schaaf and van Hateren, 1996) with the same

mean luminance as the gray background. In the third and fourth conditions the background image was a uniform gray or a grayscale photo, respectively. However, in these conditions the fixation of the animal was guided such that a saccade brought the bar stimulus into the receptive field rather than it being flashed on.

It was found that the response to a bar stimulus in the receptive field is influenced by both stimulus complexity and the method by which the stimulus comes into the RF (flash or saccade). Examples are shown in Fig. 2. The cell illustrated in Fig. 2A shows

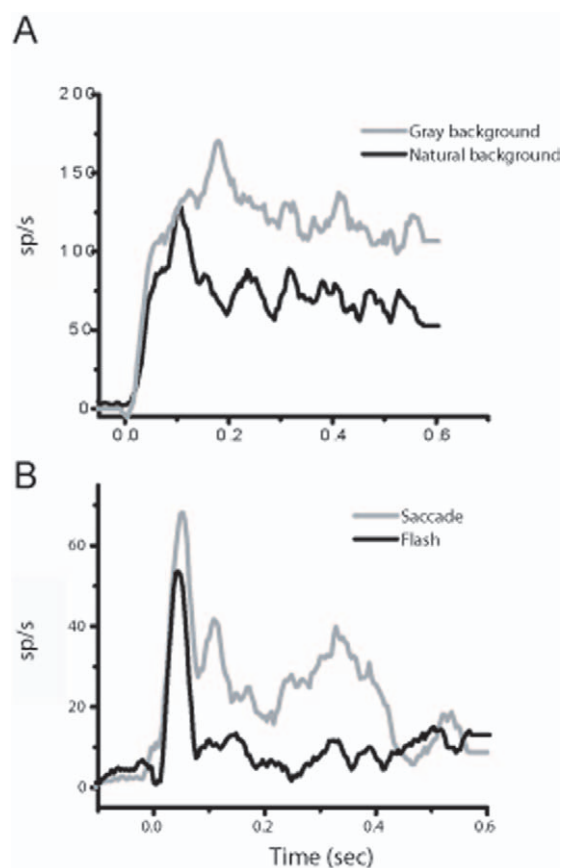


Fig. 2. Stimulus and behavioral context influence the response of a V1 neuron. A. After similar initial responses, a small bar in the receptive field gives a greater response on a uniform gray background (gray curve) than on a grayscale natural image background. B. Responses to the same stimulus are initially similar whether the bar appears in the RF by being flashed or swept in via saccade. After a delay the saccade response is significantly greater.

the difference in response associated with the gray and natural scene backgrounds. The response to a small bar is significantly higher when the background is a uniform gray than when it is a grayscale picture. In this case the response was roughly 50% greater when the bar was presented on a gray background compared to a natural scene. This response difference is found regardless of whether a saccade or flash introduced the bar into the receptive field. Also interesting is the delay in the separation of the two curves. The initial response with gray and natural backgrounds is similar but after about 50 ms there is a reduction in the natural scene response. It is not possible to say why the response differs between the two conditions, but the natural scene obviously has contrast and structure not present with the gray background. Previous studies have reported the suppressive effect of contrast outside the receptive field (Allman et al., 1985) and the present result can be interpreted in that context. The delay in the background effect suggests that different circuitry may be involved.

More surprising is the influence of presentation method shown in Fig. 2B. When a saccade brought the bar stimulus into the receptive field the initial response was similar to a flashed stimulus, but after about 50 ms the response in the saccade condition was much larger (more than 100% greater). The neuron shown in this figure has a particularly pronounced difference, but even in the population average, the saccade response with the natural scene background was 15% higher than the flash response on the same background. Several factors were considered to account for the response difference when a stimulus appeared in the receptive field via saccade versus flash. For example, we considered the possibility that the stimulus present in the receptive field prior to the saccade might affect response magnitude. While there was a hint of this in some cells, it could not account for most of the response difference. We also considered the possibility that stimuli swept across the receptive field during the saccade might make the saccade response greater. Again, this was not able to account for the response difference. These and other factors were considered (MacEvoy et al., 2002), and while several factors have small effects on response rate, no single factor has yet been found that can account for the bulk of the response difference.

The combined (and opposed) effects of scene complexity and saccades suggest that it is impossible to predict responses in natural situations from responses to small stimuli flashed into the receptive field.

Background changes and delayed form information

The experiments in which saccades on a natural scene brought stimuli into receptive fields represent a more natural visual situation than flashing a bar isolated to a receptive field. However, the use of complex scenes and saccades complicates interpretation of the results. For example, natural scenes had a suppressive effect on V1 activity relative to a uniform gray background, but the scene complexity made it difficult to ascertain what aspect(s) of the picture was responsible for the suppression.

In a parallel series of experiments, a somewhat less natural visual paradigm was used in order to gain greater control over the effects of image complexity and saccades (Huang and Paradiso, 2000). When an animal makes a saccade while viewing a natural scene, the “contents” of a V1 receptive field change. Perhaps a flower was initially in the receptive field and afterwards the branch of a tree. At the same time that a new local feature is introduced, the background or context usually changes. When the branch of the tree sweeps into the receptive field, adjacent areas in the RF and outside the RF might “see” other vegetation. In the present study, this natural sort of visual stimulation is simulated in the context of a well-controlled fixation paradigm. Macaques fixated a point on the visual display and bars of light or Gabor patches were presented in the receptive field. On some trials the background was static as in most visual physiology experiments. On other trials the background luminance or pattern changed simulating what would occur with a saccade. Comparisons of neural responses were made when identical stimuli were within and beyond the RF in the static and changing background trials. The only difference between the conditions was the stimulus *before* the bar and background used for response measurements.

It was found that when context changes with the introduction of a local feature (the changing background condition), the response pattern is

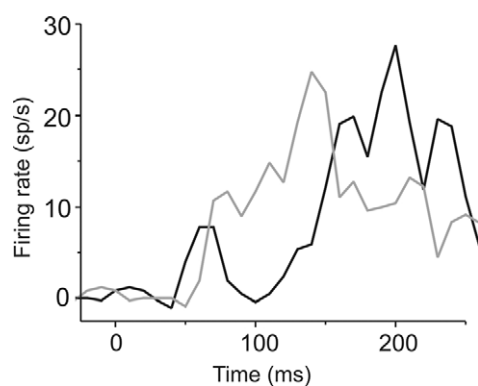


Fig. 3. The temporal response pattern and timing of feature information in a V1 neuron change with contextual changes. When a bar stimulus is flashed on a static background the response has a single peak (gray curve). To mimic the effect of a saccade the same stimulus and background were shown, but preceded by a different background. In this changing background condition the response has two peaks (black curve). With the static background, orientation is reflected in the amplitude of the initial response and contrast is anticorrelated with response latency. With the changing background the initial response carries little orientation or contrast information. Instead, these attributes are represented in the amplitude and latency of the second peak.

qualitatively and quantitatively different than the standard static background situation. An example of this is shown in Fig. 3. When a bar was introduced on a static background, the response typically showed one peak. In this case, orientation selectivity and contrast sensitivity were represented in the amplitude and latency of the earliest response, respectively. The response is quite different in the changing background situation. The data shown in Fig. 3 were obtained when a bar stimulus appeared simultaneously with a change in background luminance, but similar results were obtained with an isoluminant background pattern change. The early response in the changing background condition appears similar to that in the static condition. However, there tended to be response suppression after the initial transient followed by rebound to a higher firing rate. In other words, the average response in the changing background condition showed two peaks rather than one. Of particular interest is the observation that form information is no longer represented in the initial transient as in the static background condition. Instead, orientation and contrast sensitivity are reflected in the amplitude and latency of the delayed

second response peak. This peak occurred about 20–50 ms after the initial peak, suggesting that in the changing background condition, form information was delayed by this amount of time. Other neurons showed only this late response component.

The response differences recorded in the static and changing background conditions suggest that there might be a temporal difference in the brain's access to form information. This hypothesis was tested in a series of human psychophysics experiments (Huang et al., 2001). Bar stimuli were briefly presented and followed by a masking stimulus at various stimulus onset asynchronies (SOAs) to limit the duration of visual processing (Breitmeyer, 1984). As predicted by the physiology data, it appears that perceptual access to form information (orientation and contrast) is delayed when a background change (luminance or pattern) accompanies the presentation of a bar of light. In Fig. 4A orientation discrimination improves significantly as SOA increases with either static or changing background. However, performance saturates at much shorter SOAs with the static background. This suggests that the orientation information is present earlier in that condition. The psychophysics experiments also showed that in the changing background situation observers are able to detect that the scene has changed well before (about 20 ms) they are able to discriminate orientation (Fig. 4B). This suggests that in the changing background condition the early response signals that the scene has changed but does not carry the bulk of the information about the details of the stimulus.

Discussion

The experiments discussed above demonstrate that neural activity in area V1 can be well correlated with visual perception. While this may not be surprising in the general sense that visual activity across the brain must play some role in perception, the correlations with perceptual constancy, detection and discrimination appear more intimate. For example, it was observed that the temporal response patterns, not just the average firing rates, in V1 predict temporal aspects of human detection and discrimination. It is also surprising that lightness constancy appears to be present in V1, as response invariance, such as scale or rotation invariance in inferotemporal neurons

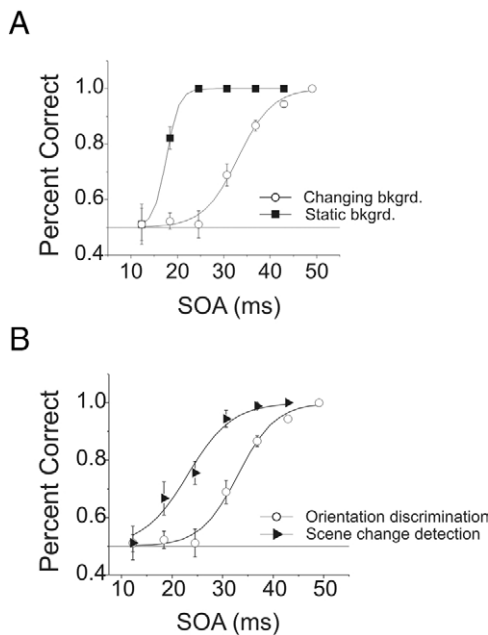


Fig. 4. Human detection and discrimination in a masking paradigm with the same stimuli used on neurons in Fig. 3. A. With a static (solid symbols) or changing (open symbols) background, orientation discrimination improves as the SOA between stimulus and mask increases. Performance saturates with the static background at shorter SOAs than with the changing background. B. With a changing background, performance at scene-change detection (solid symbols) asymptotes at shorter SOAs than orientation discrimination (open symbols).

(Logothetis et al., 1995; Booth and Rolls, 1998), is often taken as a hallmark of “higher” processing.

The data also indicate the significant extent to which an animal’s behavior and the stimulus context can alter V1 responses. The influence of behavior (i.e., using a saccade to bring a stimulus into a receptive field rather than flashing the stimulus) is intriguing and presently inexplicable. Other experiments have shown that attentional shifts associated with saccades enhance responses to visual stimuli (Motter, 1993) or alter the spatial sensitivity within a receptive field (Tolias et al., 2001) in V4, but the present experiments reveal differences even when attention is not directed to the object in the receptive field. Details of the visual stimulation associated with saccades may partly account for the effect. For example, it was found that the recent stimulation history of the

neuron and the sweep of the stimulus across the receptive field had minor influences, but these factors had not been found adequate to account for the bulk of the saccade versus flash response difference. In future experiments it will be valuable to engage the animal in different behavioral tasks, which may amplify the effect of behavior on responses. While not precisely the same thing, in the domain of perceptual learning, recent experiments have shown that task can significantly influence the response of neurons (Ghose et al., 2002; Yang and Maunsell, 2004) or extra-receptive field interactions (Li et al., 2004).

The finding that stimulus context influences neural responses in more natural situations may not seem surprising. This sounds like the earlier finding that extra-receptive field stimuli modulate the response to stimuli in the receptive field (Allman et al., 1985; Albright and Stoner, 2002). However, findings of extra-RF interactions have frequently been dissociated from any perceptual consequence or significance. The results presented here show not only that extra-RF influences exist, but also that they may be of critical importance for normal vision. When the luminance of an isolated patch increases, perceived brightness and the neural response both also increase. However, when the luminance of surrounding areas increases with the patch in a manner consistent with an illumination change, the response (averaged across V1) and perception are constant. Perceptually the area surrounding a patch is critical for normalizing the local percept. Neuronally a similar contextual normalization appears to occur. Presumably, modulatory input must be used to reach the proper interpretation of the direct (feedforward) input to a cell. For example, in the absence of contextual interactions, responses of neurons in V1 may be correlated with perceived brightness (Komatsu et al., 1996; Rossi et al., 1996; Rossi and Paradiso, 1999; Kinoshita and Komatsu, 2001), but they are not lightness constant (MacEvoy and Paradiso, 2001). This is consistent with the lack of perceived constancy found with isolated stimuli. When luminance values change in a manner consistent with illumination, there are contextual effects in neurons and perceptual constancy is found (Land and McCann, 1971; Land, 1986). More to the point for present purposes, in natural situations V1 neurons would have stimuli outside their receptive

fields and the contextual interactions would be crucial for establishing a lightness constant representation in V1. In this sense, V1 activity would commonly only correlate with normal perception in the situation where contextual interactions occurred.

Also, normal vision involves background context changes (from saccades) and the results presented here suggest that data obtained without such changes may misrepresent the normal timing of form information. Form information is delayed in a situation that mimics the effects of saccades. If a stimulus isolated to the receptive field is shown, a neuron's response will show one temporal response pattern and form information is available in the earliest response (Vogels and Orban, 1991; Celebrini et al., 1993). However, if a contextual background change occurs when the focal stimulus appears, there is a different temporal response pattern and form information is delayed by about 20–50 ms. This is particularly interesting because there are perceptual changes in humans that parallel the change in the temporal responses of macaque V1 neurons. Also, in the present experiments actually using saccades, the responses in saccade and flash conditions diverged after a comparable delay.

The delay of information in the more natural situation is long enough (about 20–50 ms) that it probably results from intracortical or feedback inputs to the cell. A similar conclusion has been reached in experiments on figure-ground segregation in which a late component of the V1 response correlates with an object being perceived as figure or ground (Lamme, 1995; Zipser et al., 1996; but see Rossi et al., 2001). In V1 it has also been reported that the response to a gray patch covering the receptive field is initially the same whether the surrounding area is light or dark. However, the later part of the response correlates with perceived brightness and registers the influence of the surround (Kinoshita and Komatsu, 2001). In a different brain area, inferotemporal cortex, it has been reported that global information (e.g., is the stimulus a monkey face?) is present early in the response and detailed information (e.g., what is the facial expression of the monkey?) came about 50 ms later (Sugase et al., 1999). All of these experiments in which some perceptual information is delayed can be taken as consistent with psychophysical masking experiments. The fact that backward masking

experiments work (i.e., that a later stimulus can make a preceding one imperceptible), suggests that perception may sometimes require more than the feedforward sweep of information (Lamme and Roelfsema, 2000).

Three factors suggest that the reduced paradigms typically used in experiments may underestimate the brain circuitry involved in generating form-specific V1 responses. First, many of the findings presented here result from contextual input, whether from a Mondrian stimulus or a natural scene. As others have pointed out (e.g., Angelucci et al., 2002), the scale of perceptual interactions implicates feedback from extrastriate areas. Second, several experiments have reported that the influence of stimuli outside a receptive field is greatest when the stimulus in the receptive field is not optimal (Levitt and Lund, 1997; Hupe et al., 1998; Bullier et al., 2001). In contrast to the stimulus optimization used in many experiments, the analysis of responses associated with free viewing suggests that the great majority of the time, suboptimal stimuli are in receptive fields. Thus, the normal operating domain is one in which contextual effects may be pronounced. Third, the present data indicate that contextual effects are delayed from the initial response. When simple stimuli are flashed into the receptive field, orientation information is found in the earliest response (Vogels and Orban, 1991; Celebrini et al., 1993; Huang and Paradiso, 2000) whereas in the paradigm simulating saccades, form information is delayed by about 20–50 ms. The rapid representation of form information is consistent with the arrangement of afferents reaching V1 from the LGN, but the delay found in this study suggests that additional circuitry is involved.

Intracellular recordings show that the extent and type of visual stimulation can have a large effect on the signals reaching V1 neurons, particularly the inhibitory input (Douglas and Martin, 1991). The present results suggest that to record the natural timing of feature information in V1, stimulation of lateral and/or feedback inputs may be critical. The “canonical circuit” for natural vision may involve more widespread V1 activation, greater inhibition, and more potent contextual input. Lateral or feedback input may be called “modulatory”, but this modulation is a crucial component of the normal visual response and representation.

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