Context-dependent interactions and visual processing in V1

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Summary — We examined the influence of stimulus context on the response of cells in primate V1 utilizing both concentric and spatially discrete stimuli. The majority of cells (63/71) showed marked patch suppression, including non-oriented cells. This suppression was reduced or lost if there was an orientation discontinuity in the stimulus overlying the receptive field. Cross-oriented stimuli could exert strong facilitatory effects so that a cell’s response to an optimally oriented stimulus over its receptive field was increased by the presence of an adjacent cross-oriented stimulus. This increase appeared to involve both disinhibition as well as a direct facilitation. The strength of the cross-orientation effects was such that for some cells it seemed appropriate to define a cross-oriented stimulus configuration as the ‘optimal’ stimulus. Effects following from orientation context could be strongly influenced by stimulus direction. Subcortical as well as cortical interactions may contribute to these observations. It is suggested that the properties of the network as a whole define the responses of individual cells and that the representation of discontinuities is an important component of network function in V1.

visual cortex / receptive field / minimal discharge field / orientation contrast / horizontal connectivity / center/surround

Introduction

Both the pattern and complexity of the circuitry in the primary visual cortex argue for processing mechanisms that have the capacity to integrate different levels of analysis in the system and draw local ‘retinotopic’ processing into the broader context of the surrounding image. Of particular interest is the way the extensive cortical circuitry interacts with those effects that follow from the constraints of the direct feedforward excitatory connections relaying the thalamic input. On one level these direct excitatory feedforward connections may seem to determine the operational characteristics of cells in V1. However, it has long been recognised that cells in V1 can be influenced by visual stimuli that lie outside their classical receptive field (Maffei and Fiorentini, 1976; Fries et al., 1977; Nelson and Frost, 1978; Gilbert and Wiesel, 1990; Born and Tootell, 1991; Knierim and Van Essen, 1992; DeAngelis et al., 1992; Grinvald et al., 1994) and it is this type of effect that might be expected to reflect those operations that do not derive from the action of the direct feedforward connections. An element of caution is needed here because thalamic input to the cortex may itself not be neutral to events outside the immediate local retinotopic focus. We and others (Murphy and Sillito, 1987; Sillito et al., 1993, 1994; McClurkin et al., 1994; Cudeiro and Sillito, 1996) have previously shown that the extensive feedback from cortex to lateral geniculate nucleus modulates both response magnitude and the temporal distribution of spikes in a stimulus context-dependent fashion. Particularly, in its presence, cells show a sensitivity to the orientation and direction context of bipartite stimuli overlying their receptive field (Sillito et al., 1993; Cudeiro and Sillito, 1996; Jones et al., 1996).

Thus for example, in the presence of feedback LGN cells give a larger response to a circular patch of drifting sinusoidal grating overlying their receptive field when it is surrounded by a cross as opposed to an iso-oriented annulus of drifting grating. These effects seem to be compatible with the response properties and subcortical connectivity of layer 6 cells (Grieve and Sillito, 1991a, 1995b; Murphy and Sillito, 1996).

It is important to emphasise that the axonal arborization of layer 6 cells in the LGN extends substantially beyond the retinotopic focus corresponding to their classical receptive field (Murphy and Sillito, 1996) and thus enables them to bring context relevant to the cortical level of analysis to bear on local processing in the LGN. Equally interesting is the fact that the same layer 6 cells send a collateral up to layer 4 and these constitute some 45% of the excitatory input to spiny stellate cells in layer 4 (Anderson et al., 1994), which contrasts with the 4–9% received from the LGN. Even allowing for significant variation in synaptic weighting it seems that layer 6 cells might be expected to bring considerable influence to bear on the processing of visual information in layer 4, via subcortical and cortical routes. Indeed selective blockade of layer 6 can produce a substantive reduction in the visual response of cells in the overlying layer 4 (Grieve and Sillito, 1991b, 1995a). In the sense of the potential importance of intracortical excitatory circuits in building the visual response this is very compatible with the suggestions of Douglas and Martin regarding the canonical microcircuit (Douglas and Martin, 1991). However, in underlining the fact that layer 6 cells can have a large influence on the responses of layer 4 cells it also implies that the range of excitatory influences converging on layer 6 will in turn be able to influence layer 4.
cells. This includes input from layer 5 and feedback influences which in the primate for example, include a projection from MT (Shipp and Zeki, 1989). Here, we have systematically explored the responses of cells in primate V1, with special emphasis on layer 4, to stimulus context to attempt to determine effects that might be linked to the 'cortical circuitry' whether local, horizontal, feedforward or feedback.

Materials and methods

These data are drawn from recordings of 71 cells in the primary visual cortex of anaesthetized (sufentanil 4 μg/kg/h or halothane (0.1–0.4%) in 3:1 N₂O/O₂), paralysed (vecuronium bromide 0.1 mg/kg/h) primates (macaque) using methods described in detail elsewhere (Cudeiro and Sillito, 1996). End-tidal CO₂, the ECG waveform, intersystolic interval and EEG waveform were monitored at all times throughout the experiment. Any perturbations of these parameters commensurate with a decline in the level of anaesthesia were immediately compensated for by increasing the dosage of anaesthetic agent.

We have explored the interaction between an inner stimulus patch centred over the classical receptive field and an outer stimulus. The responses of cells were quantitatively documented using a range of stimuli (including concentric annular and circular patches of drifting gratings and discrete gratings patches positioned at various XY coordinates) to map the classical receptive field (CRF) and its surround. The stimuli were drifting sinusoidal gratings and we kept the contrast, spatial frequency, phase (for concentric stimuli) and drift rate constant in both inner and outer stimuli but varied orientation and direction of drift. Outer stimuli consisted either of an annulus of grating surrounding the inner patch, or a small patch of grating positioned in various locations over the surrounding area. For the former, when the orientation and direction were the same the two stimuli appeared as a single patch of grating. Individual cells were studied for 6–12 h. All the effects could be observed with simultaneous stimulation of CRF and surrounding areas at the same contrast.

Results

Sensitivity to orientation context was seen in many (~60%) but not all oriented and non-oriented cells and the effects could be marked. The majority of cells in our sample (63/71) taken from layers 2–5 showed marked patch suppression as has been previously reported (Born and Tootell, 1991; Sillito et al., 1995). Non-oriented layer 4Cβ cells showed a pattern of influence of orientation context that was very similar to that seen in LGN cells (Sillito et al., 1993; Cudeiro and Sillito, 1996; Jones et al., 1996), where an iso-oriented stimulus overlying centre and surround mechanisms minimised the output of the cell but as the orientation of inner and outer sections of the stimulus deviated the output of the cell increased. An example is given by the surface plot in figure 1. The effect of stimulus context on orientation-tuned cells could be profound (Sillito et al., 1995) as illustrated by the tuning curves in figure 2. For this cell its output to a cross-oriented stimulus configuration exceeded that to any single stimulus. Our data also show a clear variation in the magnitude of the effect with the diameter of the ‘window’ marking the interface of the inner and outer stimuli.

The locations that elicit the interactions are not necessarily uniformly distributed around the CRF. They can be strongly constrained in a circumscribed zone of visual space, which may be asymmetrical distributed around the receptive field. Further, different outer stimulus parameters can elicit modulatory effects from different locations as illustrated in figure 3. We were particularly interested in links between the classical receptive field (CRF) and the mechanisms mediating context-dependent effects. Both orientation and direction context-dependent effects were observed within, on the edge of, and significantly beyond the apparent confines of the CRF. The modulatory effect of a 1–2 second stimulus patch on the response to a stimulus overlying the CRF could be observed up to 3° or more away from the CRF. As this applied to receptive fields within 5° of the fovea with classical field dimensions in the range of 0.2–0.5°, it reflects a very significant horizontal convergence. We also observed strong directional influences on orientation contrast, as shown in figure 4. These effects were seen even in non-directional cells, suggesting that the influence of stimulus direction pervades more of primate V1 than the response to single stimuli indicates.

Discussion

Speculatively the data could be thought to derive from four mechanisms. Firstly a core mechanism of variable strength for all cells that exert a non-orientation specific orientation contrast influence, minimizing the output of the cell for extended iso-orientation contours. This generates the suppressive surround and depends on coactivation of centre and surround mechanisms. It was seen in non-oriented 4Cβ cells, and in some oriented cells when the inner/outer stimulus boundary was well within the confines of the CRF. Subcortical mechanisms may contribute to this. Secondly, in orientation tuned cells, a mechanism that seems to be best explained as a cross-oriented (with respect to the cell's
Fig 1. This surface plot shows the response of an S type layer 4Cβ cell to varying the orientation of an inner patch of grating (0.5° diameter) in the presence of an outer annulus (inner border diameter was set to 0.5°) of drifting grating also of varying orientation (orientations were varied in a randomized interleaved sequence). The diagonal running from bottom left to top right represents all those points where the orientation of the inner and outer stimuli were the same, over a complete sequence of absolute orientations. The magnitude of the cell’s response (computed as the mean response rate averaged from the full stimulus cycle for 20 stimulus repeats) is shown by the height and shading of the contour. The cell gave a vigorous response to all those conditions where the orientation of the inner and outer stimuli differed, but an absolutely minimal response to all the conditions where the orientation of the inner and outer stimuli were the same (as defined by the diagonal trough). Thus, the output of the cell does not provide information regarding the absolute orientation of a stimulus but rather signals the presence of a discontinuity at any orientation (20 stimulus repeats, grating contrast 0.36, drift rate 3 Hz, spatial frequency 2 cycles/degree (cpd), randomized interleaved presentation. Scale bar in upper right corner shows response gray scale values from 1 to 100 where responses are scaled to 100% (as defined by the maximal response seen)).

Fig 2. These tuning curves show the effect of varying orientation on the response of an S cell to the surrounding stimulus alone, the inner stimulus alone, and then the effect of varying the orientation of the surround whilst holding the inner at its optimal orientation. There was a marked response enhancement when the outer orientation moved out of alignment to the inner (50 stimulus repeats, grating contrast 0.36, 3 Hz, 2 cpd, randomized interleaved presentation, patch/annulus inner border 1°, layer IVB S type cell).

optimal orientation) disinhibitory influence that appears to diminish the effect of an inner stimulus encroaching on the suppressive surround. Thirdly, a facilitatory influence capable of exerting effects over a long distance, driven by orientation and direction contrast. This might also be brought into the disinhibitory category if the inhibitory mechanisms generating the suppressive surround extend through the centre of the field so that even an optimal stimulus drives them. Fourthly, two overlapping processes underpinning orientation tuning, the elongation of the central excitatory field and excitatory connections between iso-orientation columns. The dependence of the suppressive surround on coactivation of centre and surround suggests an ‘AND’ gate type mechanism for the underlying inhibition, and is why diminishing centre contrast can make a surround suddenly seem excitatory (because it actually impinges on the CRF; see also Frégnac and Bringuier, 1996 for intracellular evidence). The cross-oriented disinhibition
**Fig 3.** The plots show the effect of a second stimulus on the response to an optimally oriented square of grating overlying the cell’s receptive field centre. The second stimulus was presented at a range of locations around the central stimulus (as depicted graphically in the upper right corner). The centre of the plot represents the response to stimulation of the centre alone and the value of this is set at 100%. The centre stimulus was a 1° square patch of grating, and the plots show the effect of a second 2° patch either at the same orientation and drifting in the same direction (A), or at 90° to the optimal (B), or for the reverse direction of motion of an iso-oriented patch (C). Responses are computed from the mean response over 30 stimulus repeats and equated to 100% for that to centre stimulation alone. The iso-oriented grating had little effect on the cell’s response for either direction of motion of the outer grating (A and C) but when the second grating was oriented orthogonally there was a profound enhancement from all locations around the field (30 stimulus repeats, stimulus contrast 0.36, 3 Hz, 2 cpd, C type layer IVB cell).

seems to be exerted by a cross-oriented stimulus outside the CRF field or one overlying it, hence in some cases the effectiveness of a cross-oriented (with respect to optimal) central stimulus and iso-oriented surround stimulus.

These effects suggest that the processes underlying stimulus context dependent influences are incorporated into the processing stream at a very early stage. The pattern seen varied but the mechanisms registering stimulus context could often overlie as well as extend beyond the classical receptive field and for at least some cells, should possibly be considered part of its organisation. Given what is known of the connectivity in the ‘network’ of the cortical circuitry it is hardly surprising that stimuli that will drive adjacent areas of visual space, and higher levels in the system, should influence local processing. Indeed, it might be very surprising if this were not so. This does however introduce the idea that the role of the cell needs to be defined in the context of the network rather than just the pattern of its convergent afferent input. Our data indicate that cells registering local orientation/direction discontinuities may reflect one of the primary operations implemented in V1. One might speculate that signalling the presence of a change in orientation or direction has to be as important as registering continuity. Binding the cells registering the foci of changes (eg Sillito et al, 1995) may be as important to object recognition as binding those registering the coherence of a feature. The longer range interactions observed in some cells with spatially discrete stimuli may reflect more complex processes such as those relating to the motion of
three-dimensional surfaces in space. The state of the ‘network’ could be considered to be realigned by each new stimulus configuration and this in turn embodies shifts in the properties of the individual cells.

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References

Grieve KL, Sillito AM (1995b) Differential properties of cells in the feline primary visual cortex providing the corticofugal feedback to the lateral geniculate nucleus and visual claustrum. J Neurosci 15, 4868–4874
Jones HE, Cudeiro J, Sillito AM (1996) Context dependent visual processing in lateral geniculate nucleus (LGN) and visual cortex. Invest Ophthalmol Vis Sci 37, S1058
Murphy PC, Sillito AM (1996) Functional morphology of the feedback pathway from Area 17 of the cat visual cortex to the lateral geniculate nucleus (dLGN). J Neurosci 16, 1178–1190
Sillito AM, Cudeiro J, Murphy PC (1993) Orientation sensitive elements in the corticofugal influence on centre-surround interactions in the dorsal lateral geniculate nucleus. Exp Brain Res 93, 6–16