# Cortical Representations of a Class of Subjective Contours

by

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M.S., Computer Science, University of Southern California, 1991

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SUBMITTED TO THE DEPARTMENT OF BRAIN AND COGNITIVE SCIENCES IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

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## ABSTRACT

Contours that are perceived under stimulus configurations where the stimulus lacks any physical discontinuity (such as a luminance border) are termed subjective or illusory contours. We investigated responses to end-stopped subjective contours in visual cortical areas V1 and V2 in adult cats using optical imaging of intrinsic signals and single-unit recording. The imaging experiments demonstrate that V2 contains a map of the orientation of subjective edges characterized by a modular representation of orientation domains and singularities at the intersection of orientation domains similar to that for luminance gratings. Neurons that prefer similar subjective and luminance orientations are clustered separately from neurons that prefer different orientations, leading to an elaborate pinwheel-like representation of neurons with adjacent orientation differences. V1, on the other hand, contains neurons that combine responses to the subjective as well as the luminance edges (inducing lines) in the subjective grating and these are also organized in modular fashion. Using novel end-stopped subjective stimuli with the same luminance component, an unambiguous V1 response to subjective edges alone is seen. The data suggest that there does not exist a special subset of cells that respond to subjective stimuli. Most, if not all, cells in early visual cortex convey some information about the orientation of subjective contours. The data suggest that a strong response to subjective edges does not arise *de novo* in V2; instead, considerable processing of the perceptual signal takes place in V1.

Responses to line terminations cannot account for the response to end-stopped subjective contours. More complex and sophisticated mechanisms must be invoked. On a broader note, our study shows, for the first time, that even complex visual attributes (subjective contour orientations) can be systematically represented in early visual cortex. The presence of a significant response in V1 as well as V2 to subjective stimuli suggests that several areas must participate in the processing of a visual stimulus and ascribing a single function to a particular area or, conversely, stating that a particular stimulus is processed by a single area alone may not be entirely correct.

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# BACKGROUND

The study of contours that are perceived under stimulus configurations lacking any discontinuity have formed a large and growing body of literature in the field of visual perception (Schumann '00). Contours that are perceived in the absence of physical discontinuities such as luminance or chromatic gradients are termed subjective contours. A number of investigators have proposed that subjective contours are an epiphenomenon, an artefact of a process that prevents the emergence of visual illusions in the environment (Gregory '72, Rock and Anson '79, von der Heydt and Peterhans '89). The premise is that real-world images are noisy and full of spurious features and false combinations (Peterhans and von der Heydt '91). Parts of different objects attach to consitute new features i.e.' mergers', and parts of an object are detached from the rest of the object i.e. 'deserters', are commonly found when three-dimensional objects occluding one another are projected onto a two-dimensional retina. Object structures have to be seperated and assigned to the occluding foreground object and to the occluded background. Visual systems have evolved to overcome this problem of occlusion and are adept at delineating objects in real-world situations. Contour definition based solely on contrast is incomplete since luminance and chromatic gradients are sometimes undetectable due to surface texture, shadow, lighting and so on. One device that prevents spurious combinations from forming may actually be the cause for the famous visual illusions such as the Kanizsa triangle (Kanizsa '55) or the border between two abutting gratings offset by half a cycle (Figure 1). The study of subjective contours and the mechanisms responsible for them form a key component of our understanding of visual perception.

Bravo et. al. ('88) have demonstrated that cats can perceive subjective contours. The performance of the cats used in the study for detection of a moving Kanizsa square remained consistently above chance in their experiments. Furthermore, humans and cats displayed comparable performance in perceiving shapes defined by subjective contours i.e. cats performed a task accurately that humans found possible and failed in perceiving a subjective square under stimulus conditions in which humans also performed at the level of chance. de Weerd et al. ('90) have shown that cats can discriminate the *orientation* of subjective contours. In an experiment using phase-shifted inducing semi-circles, they have shown just noticeable differences in subjective orientation (73.5 % correct level) to be in the order of 17 degrees. Control experiments performed to reduce the salience of subjective contours (such as in which they scrambled the contour, or decreased the density of inducing patterns forming the subjective contour or lowered the contrast of the inducing lines ) decreased discrimination thresholds (i.e. increased the JNDs), thus minimizing the already remote possibility that these cats used some local cue to discriminate the orientation of the subjective contour. To summarize, there is sufficient psychophysical evidence to warrant the physiological study of subjective contours in cats.

*The common types of subjective contours.*

One of the most compelling illusory configurations is the Kanizsa triangle (Kanizsa, '55, '79) where three pacmen (sectored inducing disc-like elements) produced a clear illusory triangle. The phenomenon is not confined to triangles, but can be made to yield squares, curves and other shapes. The defining characteristic is that a solid element seems overlain by a part of a shape. The inducing elements in this class of subjective contours are solid figures.

Edge-stopping illusory contours form another important category. The inducing elements are composed of line segments. There are several variants of this class. The first configuration is arranged such that the elements are similar to the Kanizsa solid element configuration. The solid pacman is replaced by a series of concentric circles (or concentric whatever the element is) with a corner, sector or wedge or curved element removed. This produces a contour that has an appearance of overlay and is phenomenologically similar to the original Kanizsa figure. The second edge-based variant also has the appearance of overlay. An interrupted set of radiating or even random lines gives rise to the appearance of an occluded surface over the line set (Gillam '87, Day and Jory '80). The Ehrenstein and Koffka illusions ('35) belong to this class. A third variant of illusory contours induced by lines consisting of displays in which line segments abut in a manner similar to that used when tesing vernier acuity. This generates a sharp curved or straight edge between the misaligned line segments and there may be a sense of two adjoining surfaces. Three-dimensional versions of these configurations also exist (Ware and Kennedy '78). Finally, in the domain of spatial Fourier analysis, illusory contours can be generated by changes in any three of the following fundamental sine wave grating parameters: phase, orientation, and spatial frequency.

The illusory contours described above the inducing elements are usually achromatic. There also exist illusory contours based on hue, assimilation of brightness, and transparency (Varin '71, Ware '80, Meyer and Senecal '83, Van Tuijl '75, Redies and Spillman '81). These contours form an impression of filled extent (Parks, '84). There is a film of transparent or translucent gray or of some color that starts at the inducing

elements and spreads through the illusory contour area. The illusion is usually generated by filling-in the empty area of a typical illusory contour-inducing element with a chroma or value. This leads to the perceived extension of that chroma or value across the illusory surface.

One possible factor in the induction of illusory contours can be the motion of the display elements. There are several well-defined motion-induced illusory contours. Thus, it is possible to produce illusory contours that are made visible only when the figure is in motion. There are several variants of this type of illusory contour. The kinetic optical occlusion effect (a pattern of dots is moved such that the pattern seems to pass under an edge giving a clear sense of a contour at the border; Andersen and Braunstein, '83, Kellman and Loukides, '87). Bradley and Lee ('82) found that an illusory triangle persisted even when the rotating configuration did not contain any apices of the illusory triangle. Thus, illusory contour inducement is dependent on an analysis of motion. Visual phantoms (Tynan and Sekuler, '75) are another example of a motion-based illusory contour.

Finally, differences in textural qualities can also be used to induce the perception of a border or a surface. In texture segregation displays one can have the impression of a bounded area and see an edge surounding the textured patch (Triesman and Gelade, '80, Julesz and Bergen '83). Thus, these displays qualify as illusory contours for some in the field (Meyer and Fish, '87).

We have studied a variant of just one class of subjective contour in which line segments abut and are offset by half a cycle. This particular stimulus has been used previously in

other physiological studies (von der Heydt and Peterhans, '89, Redies et al. '86) and it has been found that cats are able to discriminate between end-stopped inducing circles of different orientations (de Weerd et al. '90).

*The perception of subjective contours.*

Several psychophysicists have argued that the perception of subjective contours is a higher-level, cognitive process (Rock and Anson '79, Gregory '72). As Gregory notes, " .. a description of processes postulating objects from sensory evidence seems to require concepts beyond those of classical physiology-cognitive concepts." Rock and Anson regard subjective contours as a solution to the problem posed by the stimulus input as to what it might represent in the world. Subjective percepts are the result of a multi-stage process that, according to them, selects the most plausible perceptual hypothesis that provides an explanation for the data. The presentation of displays that did not immediately or necessarily invoke a subjective contour percept in some observers (cf. Figures 3,5 and 7b, Rock and Anson '79) and the effect of a prior set (or expectation, cf. Figure 3, Rock and Anson '79) is, according to them, a very strong argument against a possibility that edge detectors or contrast mechanisms might play a role in the percept of subjective contours and shapes. Curvilinear subjective contours (cf. Figures 3 of Gregory '72) and other subjective contours formed by a combination of broken lines and *dots* (cf. Figure 2 of Gregory '72) are considered insufficient to activate edge-detector cells in primary visual cortex.

Several points against such arguments based on cognition may be provided. Cognitive theories and 'lower-level' theories are not mutually exclusive in explaining any given psychophysical phenomenon. Some aspects of subjective contour perception may not be

explainable by stimulus-driven low-level processing. However, some of the cognitive processing may be subserved by low-level visual cortical processes that have evolved to incorporate a great deal of information about the environment (Peterhans and von der Heydt '91). Moreover, there is considerable evidence (Kennedy '78) that the orientation of the inducing lines plays an important role in the perceived strength of the subjective contour (cf. Figure 20 and 21 in von der Heydt and Peterhans '89, see below) and it is generally known that orientation information contained in real contours are processed first in 'low-level' visual cortices (V1, V2)[1]. Subjective contours produced tilt aftereffects just like real contours (Smith and Over '75) and these effects were shown to transfer, suggesting yet again, that subjective and real contours are processed by the same group of cells in visual cortex. Preattentive (presumably low-level) visual processing of real contours was demonstrated by the now-famous pop-out experiments (Treisman '88). Analogously, a horizontal anomalous bar popped out from an array of vertical anomalous bars with a reaction time that was independent of the number of such contours presented (Grabowecky and Treisman '89). A study to determine increment thresholds, a pre-attentive phenomenon, on either side of one of the subjective contours of a Kanizsa square, found that threshold elevations were lower or even absent on the subjective contour itself (Dresp and Bonnet '91). These observations lend added support to low-level explanations of subjective contour perception that involve "automatic" processing. This pre-attentive, early processing may occur in V1 and V2.

*Cortical responses to subjective contours.*

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1. Lesions involving V1 and large parts of V2 produced a marked deficit in orientation discrimination (Vandenbussche et al. '91), that included a loss in retention, and after retraining, a substantial increase for upto 3 years were tested with long bars. There was no recovery of discrimination when the animals were tested with short bars. These studies indicate that the cortical representation of bar orientation used for discrimination is distributed within V1 and V2.

Lesions of V1 and V2 in cats destroy the capacity to discriminate the orientation of subjective contours (abutting phase-shifted inducing circles; de Weerd et al. '93), and also cause an important, though less severe, deficit in bar orientation discrimination. The deficits induced by these lesions are permanent. Thus, areas V1 and/or V2 are necessary in the processing of at least one class of subjective contours (edge-stopped subjective contours)in the brain and form a critical component of the processing pathway[2] for these subjective contours.

Several neurophysiological studies have provided evidence against explanations that invoke higher-level cortex as being exclusively responsible for subjective contour perception. Recordings from V2 of awake monkeys (Peterhans et. al. '86, von der Heydt and Peterhans '89, Peterhans and von der Heydt '89) and from visual cortex (V1 and V2) of anesthetized cats and monkeys (Redies et. al. '86, Grosof et. al. '93, Sheth et al. '95) show convincingly, using techniques ranging from single-unit extracellular recording to optical imaging, that subjective contours are indeed, at least initially, processed in low-level visual cortex.

In one of the first experiments done to study cortical responses to subjective contours (abutting phase-shifted inducing circles), Redies et. al. ('86) recorded from the LGN, V1 and V2 of anesthetized,paralyzed cats. They investigated responses of cells in these regions to subjective contours. A response was noted by observing a response to the phase shift in a phase-shifted abutting lines stimulus. They found that in both V1 and

2. This is not to say that V1 and/or V2 are solely responsible for subejctive contour perception. Lesions in areas that receive projections from V1 and V2 (such as areas of lateral supersylvian cortex) also cause a profound deficit in orientation discrimination of subjective contours, but only a neglible deficit in bar orientation discrimination (Vandenbussche et al. '91). Thus, other areas in addition to V1 and/or V2 must be involved in subjective contour processing.

V2, S cells and B cells responded very slightly or not at all to the subjective contour, whereas C cells (n = 5) in both areas responded strongly to the phase shift. The authors did not find any marked difference in the response of all cell classes across the two areas. Geniculate cells also responded to the phase shift in the subjective pattern. They proposed that S and C cells served complementary perceptual functions: S cells are sensitive to borders containing luminance gradients, whereas C cells respond strongly to the borders with a luminance gradient.

Von der Heydt and Peterhans studied responses to subjective contours such as in Figure 1) in areas V1 and V2 in the awake, alert rhesus monkey using extracellular recording. They compared the orientation preference and tuning bandwidth of subjective contours to those of real contours. The rationale was that if this class of subjective contours are processed like real contours, the response of a cell in cortex should depend both on the oriented inducing lines and on the orientation of the subjective contour. Using this criterion (cf. page ), the authors found a remarkable difference in the responses of V1 and V2 to subjective contours. Only one out of 60 neurons recorded from V1 signaled the anomalous contour. In contrast, 45 of 103 neurons (44%) recorded from V2 signaled the orientation of the subjective contour; 16 did so (16%) without signaling the orientation of the inducing lines. They also found some physiological correlates to perception in their V2 recordings. With oblique inducing lines, the orientations signaled by the cell were biased towards the orientation orthogonal to the lines, as in the Zöllner illusion (wherein subjective lines that intercept horizontal lines appear to be rotated towards the vertical, cf. figure 20 in von der Heydt and Peterhans '89). Moreover, in 6 of 8 subjective contour cells of V2, the response to the oblique pattern was found to be less than the response to the orthogonal line pattern which is again analogous to perception (cf. Figure 21 in von

der Heydt and Peterhans '89). Again, similar to perception, neuronal response to subjective contours increased with an increase in the density of inducing lines until a threshold was reached after which the response did not increase any further (cf. De Weerd et al. for an analogous psychophysical test in cats).

In another series of experiments, Peterhans and von der Heydt ('89) showed subjective contours that appeared as continuations of the inducing elements (parallel induction), in contrast with the subjective contours shown before (von der Heydt and Peterhans '89) that appeared as orthogonal to the inducing elements (perpendicular induction). The stimulus consisted of a moving pair of notches in two spatially seperate, bright rectangles that mimicked an overlaying black bar. To determine whether a neuron responded to the subjective contour, the two parts of the stimulus (bright rectangles) were positioned on either side of the neuron's response field and outside it (response field is, by their definition, the visual field outside which no responses can be evoked by rectangles of light) and the subjective "bar" was then moved back and forth and the response recorded. This response was then compared to the response when the notches in the stimulus were closed by thin lines which had the effect of reducing the bar percept considerably. Using the criterion described above, once again they found a similar result as in the first experiment. 23 of 72 (32%) neurons recorded from area V2 responded to the subjective bar and when the notches were closed, responded much less or not at all. Likewise, when half of the figure was removed, the neurons usually failed to respond. These response properties, they argued, could not be explained by linear-summation models. Thin lines added to the stimulus changed the overall luminance by a negligible amount and yet the response was practically abolished. Moreover, the sum of the responses of the cells to each of the two parts individually was almost always (3 of 4

cells) less than the actual response to the subjective bar stimulus which was, a sum of the two individual parts (part = bright rectangle). V1 neurons failed to show such non-linear response properties (despite a reduction in the gap width commiserate with the smaller receptive fields of V1 neurons) and even though 6 of 26 V1 neurons (23%) responded to the subjective bar, only one showed the reduction effect with the addition of the thin lines to the stimulus. Even though the stimuli used in the two experiments were quite different, 9/15 V2 cells (60%) they tested that showed a response to the abutting line grating stimulus showed a response to the subjective bar stimulus. 22/23 cells that did not respond to the abutting line grating did not respond to the subjective bar as well. Both these observations showed that the two tests are related, an important point which we shall return to later.

Grosof and his colleagues (Grosof et al. '93) showed, using a different stimulus, that V1 cells in anesthetized monkeys do seem to respond to 'subjective' contours.The stimuli they used were sinusoidal luminance gratings offet by half a cycle and half-screen patches of sinusoidal luminance. Although summed over the entire stimulus, the gratings have the same mean luminance on either side of the contour, luminance-defined contours exist locally across the entire length of the contour. Hence, there is nothing subjective at all about these contours. Moreover, one might argue (see below) that the mechanisms to process and recognize such contours are different from the ones invoked to explain subjective contours used by other investigators.

In summary, a few studies have been done to investigate physiological responses in early visual cortex to subjective contours. Several questions still remain, however. Does cat visual cortex show response to subjective contours? Can subjective contours elicit an

orientation-specific response in area V1 neurons? Cats and monkeys have different anatomical connectivities. In monkey, the lateral geniculate nucleus (LGN) projects almost exclusively to V1 in cortex whereas, in cat, the LGN sends projections to areas V1 and V2 (Talbot '42, Rosenquist et al. '74, Gilbert and Kelly '75, Geisert '80, Bullier et al. '84). It has been shown that X cells project to V1 alone, whereas both areas V1 and V2 receive input from Y cells (Hoffman and Stone '71, Stone and Dreher '73, Singer et al. '75, Humphrey et al. '85) in cat. These differences in input projections between cat and monkey may be responsible for important differences in the responses of V1 and V2 in cats vs. monkeys to subjective contours. One of the principal features of early visual cortex is the grouping of neurons into columnar clusters that share preference for the same orientation of a bar/edge of light (Hubel and Wiesel '63, '74). If subjective contours are processed in the same way as real contours, there must exist cortical columns for different orientations of subjective contours. How is the cortex organized for subjective contours and how does the organization for subjective contours relate to the functional architecture for luminance contours? Finally, what are the mechanisms behind such subjective contour-dependent response in visual cortex?

*Theories/models for response to subjective contours*

Several theories have been proposed to account for subjective contour percepts. These theories range from the phenomenological to the neural and some theories make experimentally testable predictions. Most of all, it is important to remember that these theories are not mutually exclusive.

The first theory (Rock and Anson '79, Gregory '72) regards subjective contours as the result of a top-down, cognitive solution to the problem posed by the stimulus. While the

involvement of top-down, cognitive processes cannot be ruled out, they are at best, a part of the solution. Also, cognitive theories of subjective contours do little to further our understanding of the underlying neural circuitry and mechanisms behind the subjective contour percept.

Another cognitive theory originally proposed by Kanizsa ('55) suggests that a Gestalt tendency for completion (principle of closure) is responsible for the percept. While this theory has some merit, it too has run into problems. In perceiving the Kanizsa triangle, the primary percept is that of a triangle and it is only later that we infer that the pacmen forming the triangle might actually be discs that may be occluded by a triangle. The principle of closure can explain the edges of the pacmen 'closing off' to form discs, but the primary percept of a triangle is not so easily explained. There are many examples of irregular figures that are unlikely to have prior representations in the brain (cf. 12.27 and 12.28 in Kanizsa '79). Moreover, there exist classic examples in the literature (cf. Figure 8B in Coren '72) of figures that are explained by the principle of closure and yet do not evoke a subjective percept. Also,this principle offers no explanation for the enhancement of brightness perceived in some subjective stimuli (e.g. the Ehrenstein illusion, Kanizsa triangle). Lastly, this principle fails to provide any clue regarding the neural underpinnings behind the principle of closure.

Another theory also based on top-down processing (Coren, '72) states that the subjective stimulus contains depth information and the percept of an subjective contour arises as a by-product of the depth organization. The author illustrates his point with several figures that contain depth cues (e.g. interposition, texture, perspective etc.). Lately, this theory has received a lot of criticism (cf. Rock and Anson '79). According to these critics,

the proponents of the 'depth theory' are confusing effect with cause. Prior to the perception of the subjective contour, there is nothing in the stimulus pattern that could provide any depth cues to the observer. Moreover, the examples Coren uses (cf. Figure 6,8B in Coren '72) can be explained by other mechanisms such as brightness contrast and filling-in (Grossberg and Mingolla, '85). These mechanisms may, in turn, be used to explain other kinds of subjective figures (cf. Figure 1) that provide no depth even after the subjective shape is perceived. In summary therefore, one cannot rule out the possibility of depth cues playing a role in the perception of some subjective contours; however, its significance may be somewhat limited and marginal.

A theory inspired by signal-processing (Ginsburg, '75, Becker and Knopp, '78) proposes to derive the subjective contour percept as being the result of a low-pass filtering process of the visual system and the brain. Geometric illusions such as the Kanizsa triangle and Hering illusion could be explained by biurring the object with various low-pass filters (cf. figure 1e in Ginsburg '75). However, it is impossible to reveal a subjective triangle with sharp edges by using low-pass filtering alone (Tyler '77) since high frequency components are necessary to form sharp edges. While it is possible to explain the Kanizsa triangle with the use of filters containing both low-frequency components and straight edges (cf. figure 5b in Becker and Knopp '78) for each of the three sides of the Kanizsa triangle, there is no evidence for frequency domain filtering in the visual system of the kind required to explain the result. Phase information from the original image must be retained (Lim '85) in order to obtain a final post-processed *triangle*. Even otherwise, for figure 1, there exist no Fourier components along the subjective contour since the mean luminance on either side of it was equal. Local spatial frequency analysis may provide an explanation since patterns containing an odd number of inducing lines

do not have the same mean luminance on either side of the subjective contour. However, recordings (n = 10) by von der Heydt and Peterhans showed no indication at all of this "odd-even" effect (cf. Figure 13 in von der Heydt and Peterhans '89). Stimuli with an odd number of inducing lines did not evoke greater response from contour cells in V2 than stimuli with even numbers of inducing lines. Hence, it seems unlikely for spatial filter theories to be able to explain some of the subjective contours in the literature.

A biologically inspired, reductionist model to explain the response to end-stopped subjective contours is based on a response to the line ends (Livingstone M., personal. communication). According to this model, the line terminations in the subjective contour stimulus account for the cell's response and its orientation preference for end-stopped subjective contours. Hence, the response of a cell in cortex to subjective gratings must follow the response to a grating composed of dots. If a cell responds to subjective contours, it is because of the presence of line terminations in the stimulus and the response to a stimulus reduced to these line ends (dots) alone can account for most, if not all, the cell's response to the subjective grating. This hypothesis can be tested experimentally (cf. Chapter 4 for experiments and results).

The most popular model to explain cortical response to subjective contours, using neural substrates and biological mechanisms invokes end-stopping as the key (von der Heydt and Peterhans ' 89, Peterhans and von der Heydt '89, Finkel and Edelman, '89). An end-stopped (also called end-inhibited, length-tuned or hypercomplex) neuron's response declines when the optimally oriented bar is lengthened beyond a certain length. Thus, these neurons are length-tuned or end-inhibited and, for this reason, end-inhibition is

generally believed to come about because of the presence of an inhibitory region at the ends of the cell's receptive field (along the optimal orientation axis), often termed an inhibitory end-zone. In this model, end-stopped cells in area V1 have receptive fields that are scattered along the subjective contour axis and oriented perpendicular to it. These cells project to a cell that responds to subjective contours, thus accounting for its orientation sensitivity to subjective contours (cf. Figure 15 in Peterhans and von der Heydt '89). The input receptive fields are lined up in a row with their orientations approximately perpendicular to it. The excitatory subregions of the input cells stop just at the subjective edge and the inhibitory zones at the line ends project out to cross the subjective border into the opposite side occupied by the neighboring inducers. The spatial arrangement of the input fields accounts for the sensitivity of the target cell to subjective contours and for the summation behavior (the greater the number of line ends, the more robust the response; Figure 12, von der Heydt and Peterhans '89). The end-stopped fields must be oriented roughly orthogonal to the preferrred orientation of the target contour cell since the response to orthogonally induced subjective contours has been shown to be stronger in single-unit recordings (von der Heydt and Peterhans '89) and psychophysically (the Ehrenstein illusion, Jung '78, Fuld and O'Donnell '84). This model explains several psychophysical and physiological phenomena, such as the biasing effect of tilted inducing lines, the Zöllner illusion and other contour figures (Peterhans and von der Heydt '89). However, one of the implications of their model is that cells having orthogonal orientations should be connected in V2 and that a part of the connections should be excitatory. While Matsubara et al. ('86) have argued for connections between orthogonal orientation columns in V2, most others have argued for iso-orientation connections (Gilbert and Wiesel '89, T'so et al. '86, Weliky et al. '95). No one has shown evidence for excitatory connections between cells having orthogonal

orientation preference. This, and several other restrictive assumptions (such as end-stopped cells whose RFs slightly displaced from one another all projecting to a contour neuron, the precise lining up of receptive fields and the inhibitory end-zones of these end-stopped cells, gating units that connect distant pairs of these fields to name a few), make their model somewhat infeasible to explain a wide host of subjective phenomena in the literature. Despite such drawbacks, it cannot explain an subjective contour percept observed with inducing lines of randomly varying orientations. At the very least, their theory of dual inputs to contour cells in V2 is an important one in its attempt to base itself on neurophysiology and in its ability to account for several psychophysical phenomena (cf. Vogels and Orban '87).

Finally, another biologically plausible theory, proposed by Grossberg and Mingolla (Grossberg and Mingolla '85a, '85b), is briefly described below. A bar or line has a non-zero but finite width. According to this model, the line end itself is an edge and should therefore weakly activate cells of other orientations (end-cutting). For example, the end of a horizontal line (if thin enough) will activate vertical and diagonal orientation detectors in cortex. Cells, whose receptive fields encompass these line ends, will be weakly activated. This activation will propagate through intracortical and corticocortical circuitry to other similarly activated cells whose receptive fields are collinearly aligned, mutually reinforcing each other's activity. Alignment of receptive fields along their orientation axis is key to eliciting a response (collinearity). Thus, when vertical and diagonal line detectors are activated in the above example, vertical detectors are aligned with other vertical orientation detectors along the vertical orientation axis, hence these detectors' responses get reinforced iteratively; the activity of the diagonal detectors (left oblique and right oblique) may die out over time. When the diagonal

detectors are aligned along the same orientation however, the diagonal edge detectors' responses get strengthened (cf. Chapter 2, Figure 1 for stimulus with diagonal inducing lines) and not the vertical detectors. Either diagonal or vertical subjective contours can be perceived with horizontal inducing lines, depending on the orientation of the alignment of the line ends. Hence, collinearity may be essential in getting the cells' responses to build up, strengthen and finally exceed firing threshold. In the absence of collinearity, the cells will be weakly activated, their activity will not get reinforced and the responses of these misaligned cells will not exceed threshold in order for the subjective contour to be perceived.

If the line end is thick enough that it forms a distinct edge itself having an unambiguous orientation, the cells preferring that orientation will be activated more strongly (for example, a thick vertical bar will activate a horizontal edge detector at its end strongly). A subjective contour formed with sufficiently thick inducing lines will activate the edge detectors at the line ends strongly. As a result the connectivity that was earlier present between the activated cells will not be mutually excitatory anymore. An oriented surround has an inhibitory effect on a strongly activated oriented cell of the same orientation. Several investigators have shown this (Lieke et al. '88, Knerim and van Essen '92, Grinvald et al. '94, Toth et al. in press,; see below for details) and this process called neural gain control has been explained by theorists modeling cortical circuitry and function as well (Stemmler et al. '95, Somers et al. '95). When a cell is weakly activated, the lateral connections will reinforce the cell's activity and cause the cell to respond more vigorously. At higher levels of activation, the neural gain control circuitry will kick in and keep down the cells' response, inhibiting it. In the case of subjective contour perception, the cells that were excited at the outset will find that their responses will not

consolidate over time and, in fact, may be suppressed thus preventing the subjective edge to be formed perceptually. There is, of course, a finite limit to the spatial extent of the lateral connections. Inducing lines that are spatially distant fom one another will excite their corresponding cells. The activation will not propagate to other cells however, because of the large distance between the cells. In such cases, a subjective edge will not be seen as strongly. The density of inducing lines is known to play an important role in subjective edge perception (de Weerd et al. '90).

Are there biological mechanisms that might underlie different aspects of the Grossberg-Mingolla model? The model described above depends on two key principles - end-cutting and collinearity - for which biological correlates have yet to be discovered. However, there have been some preliminary findings that might be of some promise. Recent demonstrations of anisotropy of intracortical axonal arborization along a cell's orientation axis may provide an anatomical substrate for collinearity (Fitzpatrick et al. '94, Sincich and Blasdel '95). Experiments have shown that when a low contrast circular stimulus of a given orientation is surrounded by a high contrast surround of the same orientation, the surround has an excitatory effect on the response of the cells whose receptive fields lie in the central area; when the same annular surround is made to circumscribe a high contrast central area of the same orientation, the surround suppresses the cell's response in the central area (Toth et al., in press). When a central area occupied by bars of a particular orientation is surrounded by an annulus of orthogonally oriented bars, the surround suppresses the cell's response (as compared to the response to the central area alone), but the degree of suppression is less than when the surround bars are of the same orientation as the central area (Kneirim and van Essen '92). When a grating of the cell's preferred orientation is surrounded by a grating of a

different orientation, the cell's response is enhanced (Sillito et al. '95). When a grating of the cell's optimal orientation is expanded to cover the area beyond the cell's classical receptive field, the cell's responses diminish. These experiments show that the same surround can have a biphasic effect (excitatory or inhibitory) depending on the relationship between it and the central stimulus and the degree of activation of the central region in the brain.

In summary, the Grossberg-Mingolla model and the end-stopping model offer biologically plausible explanations for response to subjective contours; these models need to be tested experimentally. Chapters 2 and 3 show the results of some experiments done to investigate these models and Chapter 4 discusses the relevance of the experimental results to the models and other future experiments.

*Criterion for response to subjective contours.*

A neuron (pixel from an optical map) that responds preferentially to a *vertical* subjective grating (horizontal inducing lines) and favors a vertical luminance grating is a "subjective contour" cell (pixel) (or contour cell, for short). Thus, neurons (pixels) that have the same orientation preference for luminance and subjective gratings are contour cells (pixels) since they respond exclusively to the subjective edges in the stimulus and ignore the inducing lines. In the same vein, a neuron (pixel) that responds preferentially to a *vertical* subjective grating and a horizontal luminance grating is not a contour cell (pixel) since its response is driven solely by the luminance-defined inducing lines. Such

a cell (pixel) is termed a "luminance cell" (luminance pixel).

Consider, however a neuron (pixel) that prefers a vertical luminance grating and a right oblique subjective grating (left oblique inducing lines) i.e. a neuron (pixel) whose difference in orientation preferences between luminance and subjective gratings is neither $0^{o}$ (contour cell/pixel) nor $90^{o}$ (luminance cell/pixel). Such a neuron (pixel) shows a response that is driven by a combination (a "vector sum") of both the luminance (inducing lines) and subjective (subjective edges) components of the stimulus (subjective gratings). There is negligible spectral energy along the diagonal orentations when a horizontal (or vertical, for that matter) subjective grating stimulus is shown (Figure 2). Most of the spectral energy is found along the orientation of the luminance-defined inducing lines (vertical inducing lines in Figure 1; horizontal axis in Figure 2 - the zero vertical frequency axis). Certainly, if the inducing lines are sufficiently thin, there is no energy along the orientation of the subjective edges (Figure 2, vertical axis).

## CONCLUSIONS

In summary, the study of subjective contours are important since they provide clues about how real-world images might be processed. We have examined responses of neurons in area V2 and V1 to just one kind of subjective contour (abutting lines offset by

half a cycle), and have confirmed that V2 contains neurons that respond to the orientation of *subjective* edges (von der Heydt et al .'86, '89, Redies et al. '86). We show for the first time in cats that (a) V1 also contains neurons that respond to the *same kind of subjective stimuli*, and (b) in both areas, these neurons are clustered in discrete columns and organized into *maps of subjective orientation preference*. Cortical cells' responses to line terminations may underlie the processing of these subjective stimuli in low-level visual cortex.

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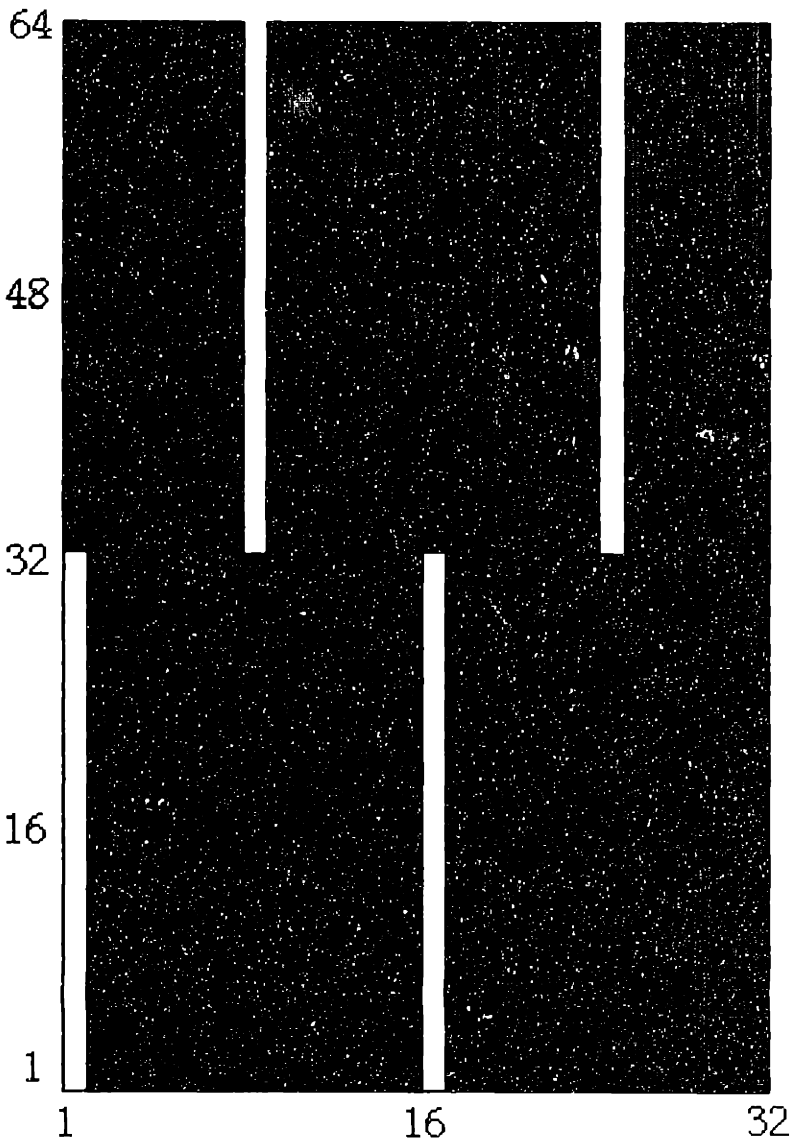
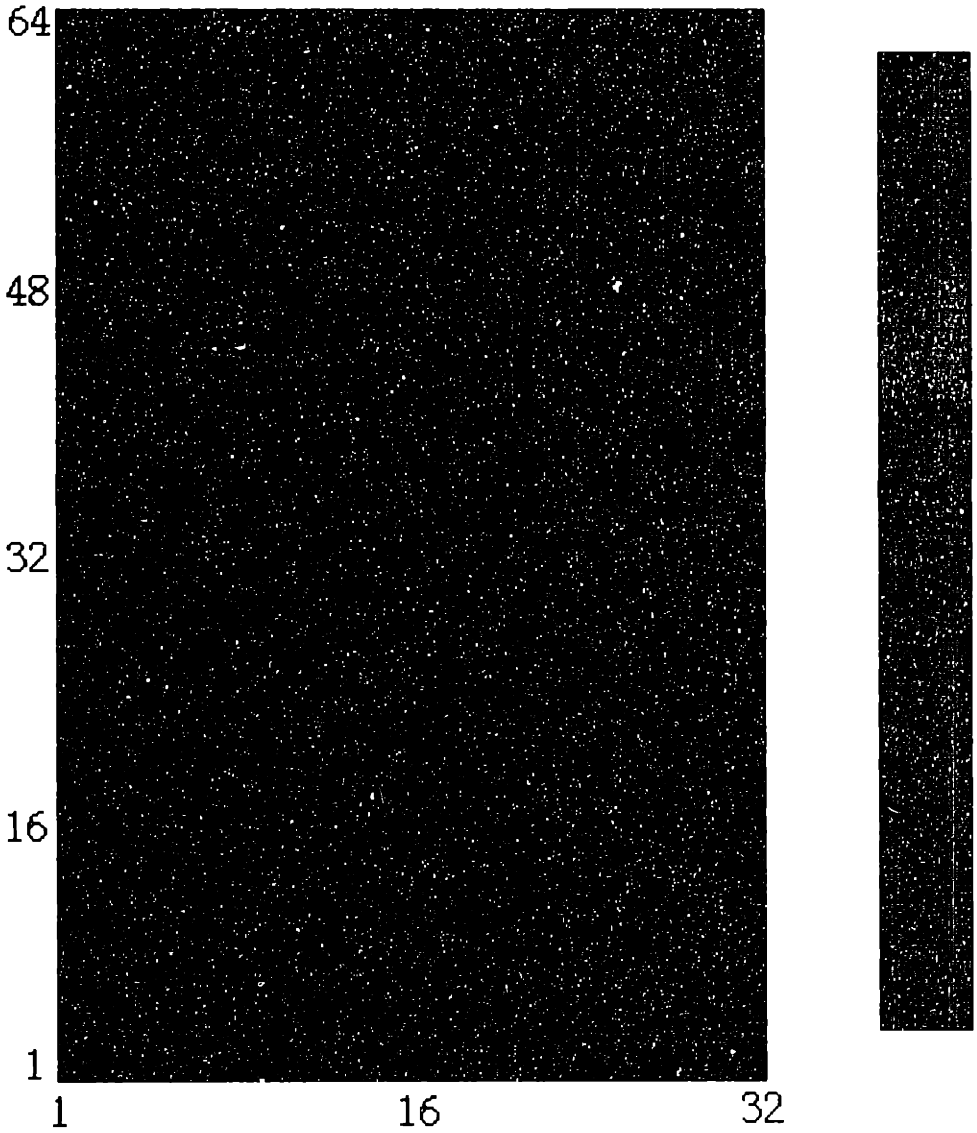



Subjective gratings

Figure 1. A horizontal subjective grating. The vertical lines that are usually 1-2 pixels thick (6-12 minutes arc of visual angle) are termed inducing lines and the horizontal perceived contours subjective edges. The total luminance across the length of any given subjective edge is balanced out on either side of the subjective edge, hence the luminance gradient is zero (summed across the entire horizontal length of the contour).




Fourier spectrum

Figure 2. The two-dimensional energy spectrum of the subjective grating shown in Figure 1. Warmer colors denote more energy. The highest amount of energy is found along the horizontal axs due to the vertical luminance lines in Figure 1; no energy is found along the vertical axis.

# Chapter 2

# Optical imaging of responses in cortical areas V1 and V2 to subjective contours

# ABSTRACT

**We investigated responses to subjective contours elicited from visual cortical areas V1 and V2 in adult cats using optical imaging of intrinsic signals. The imaging experiments demonstrate that V2 contains a map of the orientation of subjective gratings, characterized by orientation domains and singularities at the intersection of orientation domains similar to that for luminance gratings. Neurons that prefer similar subjective and luminance orientations are clustered separately from neurons that prefer different orientations, leading to an elaborate pinwheel-like representation of neurons with adjacent orientation differences. V1 contains fewer neurons that respond to subjective gratings but these are also organized in modular fashion. Single neuron responses to luminance and subjective gratings in the two areas are consistent with the imaging results. Our data suggest that a strong response to subjective edges does not arise *de novo* in V2; the presence of a significant response in V1 to subjective stimuli, as demonstrated in our optical imaging experiments, suggests that V1 and V2 work in tandem in the processing of these signals. In fact, V1 seems to be an important preprocessing stage of the subjective signal that then appears to be more widespread in V2.**

# INTRODUCTION

Subjective contours and subjective shapes can be perceived in a manner analogous to luminance contours and shapes (Kanizsa '55, Koenderink '84), suggesting that subjective and luminance contours might be processed in similar fashion, perhaps by similar neural substrates. Previous work has demonstrated that a subset of neurons in V2 of monkeys responds to subjective edges (von der Heydt et al. '84, von der Heydt and Peterhans '89). It has been claimed that cells in monkey V1 can also respond to subjective edges (Grosof et al. '93); however the stimuli used were different from classical subjective stimuli since they had a luminance gradient across the putative "subjective" edge. Thus, the question of whether or not V1 neurons respond to subjective stimuli remains unresolved. Furthermore, whether cells responsive to subjective edges are organized into maps, and how the organization relates to that of cells responsive to luminance edges, remains open. We now demonstrate that cells in both V2 and V1 of cats are responsive to subjective edges, and cells with the same subjective orientation preference are clustered to form maps which bear a systematic relationship to maps of orientation preference for luminance edges.

# METHODS

*Surgery*

Adult cats (n = 9) were used in these experiments (Figure 1). Anesthesia was induced with ketamine (15 mg/kg, i.m.) and xylazine (1.5 mg/kg i.m.) and maintained with isofluorane (typically 0.5 - 1.5% in 70/30 $N_2O/O_2$) delivered through a tracheal cannula.

Cats were paralyzed with an intravenous combination of gallamine triethiodide (3.6 mg/hr) and tubocurarine chloride (0.15 mg/hr) and artificially respired to maintain end-tidal $CO_2$ at ~4% at a partial pressure of 30 ± 3 mm Hg. The animal's EEG and heart-rate were continuously monitored to ensure adequate anesthesia. Craniotomy followed by durotomy was performed to expose visual cortex.

*Intrinsic signal imaging*

Following surgery, a stainless-steel recording chamber was attached to the skull surrounding the craniotomy, filled with silicone oil and then sealed with a quartz plate. For imaging area V2, we centered our chamber at A4 and recorded from an area that extended approximately from A3-A7 in the anteroposterior direction and between L0.5-L3.5 in the mediolateral direction. For imaging V1, the chamber was centered at P5 and a similar expanse of cortex was exposed. For imaging V1 and V2 simultaneously, the chamber was centered at A0 (Tusa et al., '78,'79). A video camera (CCD-5024N Bishke, Japan, RS-170 30 Hz, 60 dB S/N ratio) consisting of a 655 X 480 array of pixels fitted with a tandem-lens macroscope (Ratzlaff & Grinvald '91) was positioned over the cortex. The tandem-lens arrangment consisting of two back-to-back camera lenses (50 mm $f/1.2$ and 55 mm $f/1.2$) allowed both a high numerical aperture and a shallow depth-of-field. This arrangement gave a magnification of 75 pixels/mm. Initially, a reference map of the blood vessel pattern at the surface of the cortex was obtained using light filtered at 550 nm ± 40 nm (Ealing) (near-maximum absorption of hemoglobin at 550 nm wavelength so the blood vasculature is clearly seen). The camera was then focused 300–500 μm below the surface of the cortex to minimize blood vessel artifacts and to image from a cortical depth of 100-800 μm. Light from a 100W tungsten-halogen light source driven by a DC power supply (Kepco) was passed through a 610 nm filter and used to illuminate

the cortex during data collection. Data collection was under the control of Imager 2001 (Optical Imaging Inc.) which performed analog subtraction of a stored reference image (collected during presentation of a neutral gray intensity screen) from the stimulus image. The signal from the camera, thus amplified by a video enhancement amplifier, was then digitized by an 8-bit A/D converter (Matrox) installed on a 486-66 PC. Frames were summed between 1.3-3.6 sec. after stimulus onset, corresponding to the time of maximum signal as determined by our previous experiments (Rao et. al. '94, Toth et.al. '94). Data were analyzed using in-house programs written in C++ (Borland) and IDL. Stimuli were shown to the animal on a 17 inch monitor positioned 28.5 cms. in front of it. Neutral gray intensity was 6.0 $cd/m^2$. All stimuli were shown to both eyes. Eye position and area centrali of both eyes were checked at the start of imaging by using a reverse opthalmoscope to project an image of the retinal vasculature onto the screen. The monitor was placed so as to visually stimulate the imaged area of cortex.

*Stimuli*

Since any subjective stimulus consists of a luminance component, a critical aspect of our study was to devise simple stimuli which could differentiate between components of the cortical response due to the subjective and luminance parts of the stimulus as unambiguously as possible.

De Weerd and colleagues (De Weerd et al. '90) have used phase-shifted inducing semi-circles as the stimulus in their psychophysical study. Since luminance bars or edges are absent in these stimuli, they are ideal for a psychophysical study; however these stimuli have non-zero, finite spectral energy along all orientations, and most importantly at the

subjective orientation (because of the luminance defined semi-circles). This stimulus property makes it infeasible to use such stimuli to study cells in striate and prestriate cortex of anesthetized animals. Moreover, in order to compare subjective cortical response to the cortical response from luminance square-wave gratings standardly used in optical imaging experiments, it was necessary to use subjective grating stimuli. Periodic gratings of phase-shifted semi-circles are non-intuitive in conception and impractical in design. Hence, we did not use phase-shifted inducing semi-circles in our study.

For this reason, we decided to design gratings of phase-shifted inducing lines offset by half a cycle, which will henceforth be termed subjective gratings (cf. Chapter 1, Figure 1; Figure 3). It is possible to generate subjective gratings of any (subjective) orientation and a quantitative comparison of responses (orientation preference, orientation strength, orientation column locations etc.) between luminance and subjective gratings can be done easily (cf. Figure 4).

The stimulus used for most of our experiments (abutting thin lines) has a luminance component whose orientation variesalong with the subjective edge orientation. Hence, the luminance and subjective components of the cells' response competed with one another. The presence of a luminance component whose orientation varies concomitantly with the orientation of the subjective edges (orthogonal to one another) over the subjective grating stimulus set may mask the response due to the subjective edges alone and thus weaken the effect.

It is thus better to design a stimulus which either does not have a luminance component or if it does so, is of the same amplitude and orientation across the entire stimulus set. Stimuli used (Figure 2; Chapter 3, Figure 20,21,22) in a few of our experiments had a very similar luminance component for both stimuli and hence any difference in response could thus be attributed to the subjective edges alone. However, it is not possible to obtain composite orientation preference maps (of 4,8 orientations) using these stimuli since a stimulus set spanning the entire orientation range ($0^o$ -> $180^o$) cannot be designed with inducing lines being of the same orientation for all stimuli. For this reason, quantitative comparisons with response to luminance gratings would not cover the entire orientation range (only two mutually orthogonal orientations) and hence would not prove very useful.

## RESULTS

We first imaged the response of visual cortex to a pair of stimuli that had identical inducing line orientation, identical direction of motion (orthogonal to the inducing lines) and differed in a single stimulus parameter, the orientation of the subjective edge (Figure 2; termed iso-luminance gratings since the luminance component has similar intensity and orientation in both stimuli), and found distinct dark and light patches in V2 and V1 corresponding to orientation domains for the two stimulus orientations. If the cortex did not contain columns segregated for subjective orientation preference, subtracting the response to one subjective stimulus orientation from that to the

orthogonal orientation would result in a homogeneous optical map (the signal from the inducing lines being the same for both stimuli, a subtraction of the two optical images would eliminate the common luminance signal). However, as shown in Figure 2, the resultant map consists of response clusters that are elicited by the subjective orientations.

In order to quantitatively compare cortical responses to subjective and luminance stimuli, we used luminance gratings composed of light and dark bars (or thinner lines), and subjective gratings composed of orthogonal inducing lines (Figure 3). If neurons in visual cortex signal the subjective orientation and ignore the orthogonal inducing lines, the location of orientation domains imaged with luminance and subjective gratings should match closely (Figure 4, left). (Note that the hypothetical map assumes that neurons that respond to a given subjective orientation are clustered in modular fashion). Thus, for each pixel comprising the optical map, the orientation preference for subjective and luminance gratings will be nearly identical. A histogram of pixel count showing the difference in orientation preference obtained with the two types of stimuli should therefore yield a histogram similar to that shown in Figure 4 (bottom left), with a peak at $0^{o}$ orientation difference. Conversely, if neurons respond solely to the inducing lines and ignore the orthogonal subjective edges (Figure 4, right), maps for luminance and subjective gratings should be complementary (compare, for example, the hypothetical maps at the top left and middle right of Figure 4). A histogram of pixels showing the difference in orientation preference between the two maps should therefore have a minimum at a $0^{o}$ orientation difference, and monotonically rise to peak at $\pm 90^{o}$ orientation difference (Figure 4, bottom right). The extent to which a region of cortex

responds in one fashion or the other could be used as a measure of the population response to subjective edges.

We titrated stimulus parameters so as to optimize cortical responses to subjective gratings. Since cells in V2 favor low spatial frequencies of luminance gratings in the range of 0.1-0.2 cycles/deg (Movshon et al. '78), we imaged area V2 with subjective gratings in which the spatial frequency of the subjective edges in the stimulus was kept at 0.15 cycles/deg. while the inducing lines were more densely spaced at a spatial frequency of 0.45 cycles/deg. Similarly, typical parameters for V1 imaging were as follows: spatial frequency of subjective orientation 0.5 cycles/deg., spatial frequency of inducing lines 0.45 cycles/deg., 12 deg./sec. drift velocity. Once again, to optimize responses to subjective edges, the gratings were drifted normal to the subjective edges and parallel to the inducing lines at a velocity suited for the area of cortex (whether V1 or V2) that we were recording from. In chapter 3 on single unit extracellular recording, we will see examples of the significance of the direction of motion.

We recorded from areas V1 and V2 of cat visual cortex while the animal viewed subjective grating stimuli of different orientations[1]. We ensured that we were recording from a particular area (V1/V2) in two ways. Firstly, we centered our craniotomy at Horsely-Clark coordinate A4 for our V2 experiments so the imaged area had an anteroposterior extent from approximately A1 to A7 and mediolateral extent was about 0.5 - 2.5 mm from the midline (Tusa et al. '78,'79). This ensured that about 80-90% of our

1. We imaged from V1 in 4 cats, V2 in 3 cats and V1/V2 in 2 cats.

imaged area was from V2. We confirmed this by delineating the V1/V2 border using optical imaging by exploiting an important difference between V1 and V2 response properties. To physiologically assess the boundary between V1 and V2, luminance gratings with different parameters were used - a grating of high spatial frequency (0.5 cycles/deg.) and low drift velocity (4 deg./sec), which V1 neurons prefer, and a grating of low spatial frequency (0.15 cycles/deg.) and high drift velocity (1[illegible] deg./sec.), which V2 neurons prefer (Movshon et al. '78, Bonhoeffer et al. '95). By distinguishing the portion of the optically imaged region that responded preferentially to the slower drift-rate, higher spatial frequency stimulus (V1) compared to the higher drift-rate, lower spatial frequency stimulus (V2), we could locate the V1/V2 boundary accurately. Figure 5 shows an example of one such successful imaging. The physiological border coincided with the anatomical border between V1 and V2 as demonstrated by marker lesions and histology in previous studies in our laboratory (Rao et al. '94).

*Response in V2 to subjective contours.*

Figure 6A and B show responses from a patch of V2 to luminance and subjective gratings respectively [in each case, the response at a grating orientation of 90° (135°) has been subtracted from that at 0°(45°)]. Orientation domains for the same luminance and subjective orientations overlap in spatial location and extent. Figure 7A and B show the composite luminance and subjective grating maps respectively, combining the responses at all stimulus orientations. [Orientation maps obtained with luminance gratings composed of thin lines (of the same width as the subjective grating inducing lines) were identical to orientation maps obtained with thicker bars, and were independent of grating spatial frequency (data not shown)]. We determined the relative contributions of

the subjective and luminance components of the subjective grating to the cortical response by computing the difference in orientation preference between luminance and subjective gratings for each pixel (i.e. a map of "subjective signal strength"). Figure 8A shows the resultant difference map coded in shades of gray (black representing regions with an orientation difference less than $\pm 22.5^{o}$, and white representing regions with an orientation difference greater than $\pm 67.5^{o}$). The orientation difference map shows that a substantial portion of V2 (coded in black) responds strongly to the orientation of subjective edges. The orientation preference for the luminance and subjective components of the subjective grating varies smoothly across the cortical surface (darker shades of gray representing progressively stronger preference for the subjective edges relative to the inducing lines). Neurons with a given subjective response component (relative to the luminance component), and therefore having the same subjective signal strength, are clustered, and neurons with adjacent subjective signal strengths are organized, for the most part, in a radial, pinwheel-like fashion (Figure 8B shows a typical radial organization at a higher magnification). The density of pinwheels was $2.3/mm^2$. The pixel histogram (Figure 9) quantifying the difference map of Figure 8A, shows that a large number of pixels respond preferentially to identically oriented luminance and subjective gratings. These results demonstrate that many neurons in V2 respond in an orientation-specific manner to subjective gratings, and are organized into maps of orientation preference which resemble those for luminance edges (the orientation strength for subjective gratings was, on average, three-fold lower than that for luminance gratings[1]; Figure 10).

The spacing between inducing lines is important in the perception of subjective contours (de Weerd et al. '90). We doubled the spacing between the inducing lines (and also

doubled the thickness of each individual line, in order to maintain the same overall stimulus luminance), and observed a dramatic change in the response in the imaged V2 region. The same cortex that showed a clear response to subjective edges composed of a high density of inducing lines, now gave a strong response to the inducing lines with little or no response to the subjective edges in the stimulus (Figure 11). Thus, changing the density of inducing lines changed the physiological response of V2 to subjective gratings.

We designed a stimulus with abutting square-wave gratings (inducing lines) offset by half a cycle having the same inducing line frequency (0.45 cycles/deg.) as in our subjective grating stimuli (Figure 12). These stimuli differ in one important way from subjective grating stimuli in that the inducing lines are of the same width as the space between them (inducing bars). As a result, there is an actual luminance gradient, a physical contour along the entire edge seperating the inducers on both sides. The same

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1. The method for computing orientation strength is as follows: for each individual pixel, each of the *n* (*n* different orientations tested) stimulus single-condition maps are treated as vectors; a vector whose length is equal to the strength of the signal (value of the pixel), and whose angle is the stimulus orientation angle *multiplied by two*. For each pixel then, there are *n* vectors which are then summed in a vectorial fashion. Since orientation is a periodic signal whose value lies between 0° and 180° and a 0° orientation is the same as a 180° orientation, they are made equivalent in the vector sum as well. This is done by multiplying each angle by two so along the circle, 0° maps onto 0° and 180° maps onto 360° - vectors having same direction, which was the desired effect. This has the added effect of causing vectors corresponding to orthogonal orientations to point in *opposite* directions in the vector sum and to cancel one another. The resultant vector from the vector sum has a certain length and direction which correspond to the pixel's orientation strength and orientation preference (divided by 2) respectively. Orientation strength can also be obtained by computing the amplitude of the second harmonic of the Fourier spectrum of the vector consisting of the pixel's responses to different orientations.

cortex, which responded to subjective edges, with inducing lines that were 1-2 pixels thick (Figures 6-9), did not respond to the edges in the new stimulus and responded to the orientation of the thick inducing lines instead (Figure 12). Single unit recordings from area V2 (3 cells) also showed a similar result (cf. Chapter 3). Thus, thickness of inducing lines plays an important role in determining the strength of response in V2 to subjective contours.

*Response in V1 to subjective contours.*

In order to address the issue of whether or not V1 responds to subjective contours, we imaged V1 and V2 simultaneously in the same animal. The two cortical areas, which are anatomically distinct (Otsuka and Hassler '62), were first distinguished within an imaged field on the basis of responses to luminance gratings of high and low spatial frequencies respectively (Bonhoeffer et al. '95, Rao et al. '94; Figure 13 A,B). Responses to the same set of subjective gratings were more robust in V2 as compared to V1, and are summarized by the pixel histograms of Figure 13 D,E. The pixel histogram of orientation difference peaked at $0^{o}$ for V2 (Figure 13D), indicating that most pixels preferred the same orientation for both luminance and subjective gratings. The pixel histogram for V1 (Figure 13E) peaked around a $\pm 90^{o}$ orientation difference, but showed a population of pixels at and around an orientation difference of $0^{o}$ as well as local maxima at other orientation differences, signifying the presence of cells in V1 responsive to both the inducing lines as well as the subjective edges.

We examined responses in V1 to subjective gratings constructed with stimulus parameters derived from the known stimulus selectivity of V1 cells (Movshon et al. '78). Figure 14A,B show, respectively, maps of V1 in response to luminance gratings and to

subjective gratings with a high spatial frequency of inducing lines. The orientation difference map showed the presence of regions (Figure 14C, coded in shades of gray) whose response depended to varying degrees on the orientation of the subjective edges. In specific regions of the map, these cells are also organized in a pinwheel-like fashion. The density of pinwheels in V1 ($2.8/mm^2$) was slightly higher than that in V2. The pixel histogram quantifying Figure 14C had local maxima and a demonstrable number of cells within a $\pm 45^{\circ}$ orientation difference (Figure 14D). Thus, many cells in V1 also respond to subjective edges (Figure 15), though the population of cells is less than in V2 .

*Correlation between difference maps and single-unit data.*

We have confirmed the locations of domains in orientation difference maps with single-unit electrophysiology in a limited number of cases. Figure 17 shows data from a cell that lay in a region in V2 characterized by a similarity in orientation preference for luminance and subjective gratings (coded black in the orientation difference map). The cell preferred a luminance grating and a subjective grating of $45^{\circ}$ orientation, which was to be expected. Figure 18 shows examples from V1 in two different animals. The cell, shown on the left (Figure 18 A and B), is located in a dark gray orientation difference domain and its orientation preferences for luminance and subjective gratings differ by $45^{\circ}$. Similarly, a cell (Figure 18 C and D) whose orientation preferences for luminance and subjective gratings differ by $90^{\circ}$ is found to lie in a corresponding white orientation domain. Thus, there is a relatively good correspondence between the locations of domains in an orientation difference map and the responses of single cells in these domains to luminance and subjective gratings.

## DISCUSSION

*Comparison of orientation maps obtained with luminance and subjective gratings.*

The density of pinwheels for luminance and subjective orientation maps across both V1 and V2 were comparable. For the V2 maps of Figures 7 and 13, the luminance orientation maps had pinwheel densities of 1.1 pinwheels/$mm^2$ and 1.0 pinwheels/$mm^2$ respectively compared to 0.8 pinwheels/$mm^2$ and 0.9 pinwheels/$mm^2$ for the corresponding subjective orientation maps. Similarly, for the V1 maps of Figures 13 and 14, the pinwheel densities for luminance orientation maps were 1.6 pinwheels/$mm^2$ and 2.0 pinwheels/$mm^2$ respectively, compared to 1.9 pinwheels/$mm^2$ and 1.4 pinwheels/$mm^2$ for the corresponding subjective orientation maps[1]. It has been found that the pinwheel densities (Bonhoeffer and Grinvald '91, Bonhoeffer et al. '95) for luminance orientation maps are higher in V1 than V2. We confirm this finding (see above) and also find that subjective orientation maps in V1 as well show a higher pinwheel density than the subjective orientation maps in V2.

We have observed that pinwheels, which are regions of rapid orientation change, found in the orientation difference map are generally the result of a pinwheel present in one of the two maps (luminance or subjective) and a relatively constant orientation domain in the other. Hence, regions of rapid orientation change in one map coincide with regions of relatively constant orientation preference in the other.

*Orientation difference maps.*

The orientation difference map (angle subtraction map) is a map of the difference in

1. Our pinwheel density numbers for luminance orientation maps are in excellent agreement with the pinwheel densities reported by other investigators (Bonhoeffer and Grinvald '91 for V2; Bonhoeffer et al. '95 for V1).

orientation between luminance and subjective gratings. The subjective grating stimulus is so designed that it has both a luminance and a subjective component which are orthogonally oriented to one another. Thus a pixel's response to the subjective grating is a vector sum (maybe non-linear) of the response to the luminance-defined inducing lines and the response to the subjective edges. The degree of similarity in orientation preference between luminance and subjective gratings is a measure then of the strength of the response to the subjective edge relative to the strength of the response to the inducing lines. A pixel that responds to both the luminance and subjective components with roughly equal strength must have an orientation preference to the subjective grating (which is a combination of both the components) intermediate to that of pixels that respond exclusively to the subjective edges alone (orientation difference close to $0^{o}$) and pixels that respond to the inducing lines alone (orientation difference close to $90^{o}$). The difference in orientation preference (between luminance and subjective gratings) for a given pixel indicates the strength of that pixel's response to the subjective edges in the subjective grating, *relative* to the strength of its response to the inducing lines in the same stimulus.

A map of orientation difference provides a visual of the locations of regions of strong (and not-so-strong) response to subjective contours. The relationship between regions responding vigorously to the subjective edges (shown in black) to those that respond exclusively to the inducing lines (shown in white) and other regions of intermediate response (shown in different shades of gray) can be clearly seen; moreover, the similarities and differences between luminance orientation column organization and subjective orientation column organization can be readily discerned in an orientation difference map.

We have observed a slightly higher pinwheel density in the orientation difference maps of V1 than those of V2. This result corresponds well with the slightly higher pinwheel density found in cat V1 compared to V2 in response to luminance (1.9 pinwheels/$mm^2$ in V1, Bonhoeffer et al. '95; 1.2 pinwheels/$mm^2$ in V2, Bonheoffer and Grinvald '91) as well as subjective (see above) gratings. Due to the mutually exclusive locations of pinwheels between the luminance and subjective orientation maps, pinwheels in the orientation difference map are the result of pinwheels found in one map and not the other; this accounts for the overall higher pinwheel densities in the orientation difference maps in cat V1 and V2 (>2 pinwheels/$mm^2$) compared to the pinwheel densities for luminance and subjective orientation maps.

*The source of the optical signal.*

It has been shown that neuronal activity produces at least three characteristic types of intrinsic optical changes in brain tissue that affect the light intensity reflected from the active cortex. The first are light-scattering signals (Hill and Keynes '49, Cohen '73). These signals have multiple origins. A second type of intrinsic signal originates from changes in the absorption or flourescence of the transition states of intrinsic chromophores like hemoglobin, cytochromes or NADPH (Chance et al. '62, Jobsis et al.'77, LaManna et al.'85). The most important among these is hemoglobin which changes from oxyhemoglobin to hemoblogin (deoxygenated) in response to increased electrical activity (oximetry; Frostig et al. '90). A third type of intrinsic signal originates from changes in blood volume leading to changes in the overall light absorption by hemoglobin (Jobsis '77, Frostig et al. '90).

It has been shown recently that sensory stimulation of cortical columns initiates tissue hypoxia and vascular responses that occur within the first 3 seconds following stimulus onset and is highly localized to individual cortical columns (Malonek and Grinvald '96). However, the later phase of the vascular response is less localized, spreading over distances of 3 to 5 mms. In order to obtain a spatially localized and robust signal, we record optical response between 0-4 sec. following the onset of visual stimulation.

*Advantages of optical imaging.*

Optical imaging has proved invaluable in the study of subjective contours in cortex. Single-unit experiments show that cells in the same column share similar response to subjective contours (cf. Chapter 3). Using optical imaging, we have shown that these columns form clusters across the cortical surface, with columns in the same cluster having similar response to subjective contours, and columnar clusters of neurons that prefer adjacent subjective and luminance orientations neighboring one another, leading to a smooth and ordered representation of subjective orientations along the cortical surface. Optical imaging is ideal for obtaining mass statistics on a large number of cells. Using imaging and a well-defined subjective criterion for response to subjective contours, we have found that cells in V1 also respond to subjective contours, a finding we have later confirmed with single-unit recordings. However, proportionately fewer cells in V1 than in V2 respond to subjective contours; when sparse signals are summed over a large number of cells that are organized in columnar fashion, and averaged over a long time duration, the signal becomes better detectable with optical imaging. We have shown that optical imaging has been successful in pooling these signals into a demonstrable response of V1 to subjective stimuli.

*Limitations of optical imaging.*

While optical imaging affords several advantages over other conventional electrophysiological techniques, the gains comes with a price. There are several limitations of the technique.

It is important to note here that there is only an indirect correlation between the underlying electrical activity and the optical signal. The optical signal measures changes in blood flow (including blood oxygenation, blood volume changes and even light scatttering). Blood flow, in turn is an indicator of metabolic activity of the substrate responsible for the blood flow change. Metabolic activity is directly correlated with underlying electrical activity. 2-Deoxyglucose techniques exploit precisely this relationship between metabolic and electrical activity. Optical imaging has an advantage over 2DG since with 2DG, one can show only a limited number of stimuli for several hours after which the animal has to be sacrificed immediately. In contrast, one can show theoretically any number of stimuli (practically , time constraints prohibit more than 32, as a rule of thumb) in optical imaging and the technique does not require the animal to be sacrificed at the end of the experiment, hence has tremendous potential for chronic recordings whose advantages are obvious. Due to this indirect relationship between blood flow changes and electrical activity, it is not known whether there is a linear correlation between blood flow changes and electrical changes in the underlying substrate. Because of this, intrinsic signals are thus more useful at measuring relative changes in activity as opposed to absolute changes i.e. response of the same region to

two different stimuli, or difference in response between two spatial regions of the cortex to the same stimulus.

Since imaging measures changes in blood oxygenation and blood flow, the signal collected during imaging may very well be a combination of action potentials and subthreshold activity of neurons and may perhaps even be contaminated by electrical activity in the glia as well (Grinvald et al. '88). Moreover, since the signal takes time to build up and time to decay, temporal properties of the physiological response cannot be studied using this technique (Frostig et al. '90).

Finally, this technique also has limited spatial range along the depth dimension of the cortex (Malonek et al '90). It is generally believed that the optical signal averages the blood flow signal between 0-800 μm depth and so our findings using imaging are limited to the superficial layers (II,III) and perhaps a part of layer IV (Grinvald et al. '88, Frostig et al. '90).

## CONCLUSIONS

Cells in both areas V1 and V2 of cats are known to be orientation-selective and to cluster to form columns whose cells share the same orientation preference for luminance edges (Hubel and Wiesel '63,'68, Bonhoeffer and Grinvald '93). We have now shown that both areas contain neurons which also respond to the orientation of subjective edges, and that these neurons are clustered in discrete columns and organized into maps of subjective

orientation preference. The maps show a radial, pinwheel-like arrangement of orientation differences (between preferred subjective and luminance orientations), however a significantly larger region in V2 than in V1 responds to subjective orientations. The similarity of the luminance and subjective orientation maps in V2 indicate that the same cells respond to both types of stimuli, a fact borne out by the single-unit experiments (von der Heydt and Peterhans '89). Orientation maps seen in response to subjective contours are likely to be a critical first stage in analyzing the global disposition of edges that constitute object shapes. It has been shown earlier that orientation domains for luminance edges are radially arranged in a pinwheel-like fashion. Our finding that subjective orientation preference domains as well as domains for subjective signal strength are organized in a pinwheel-like fashion similar to that for (luminance) orientation maps argues strongly for the ubiquitousness of such an organization in cortex.

The presence of a significant response in V1 to subjective stimuli, as demonstrated in our optical imaging experiments, suggests that V1 and V2 work in tandem in the processing of these signals. In fact, V1 seems to be an important preprocessing stage of the subjective signal that then appears to be more widespread in V2. Since such weak signals are difficult to detect using single unit recording, that may be misinterpreted as an absence of response; our optical imaging studies have been successful in pooling these signals into a demonstrable response of area V1 to subjective stimuli.

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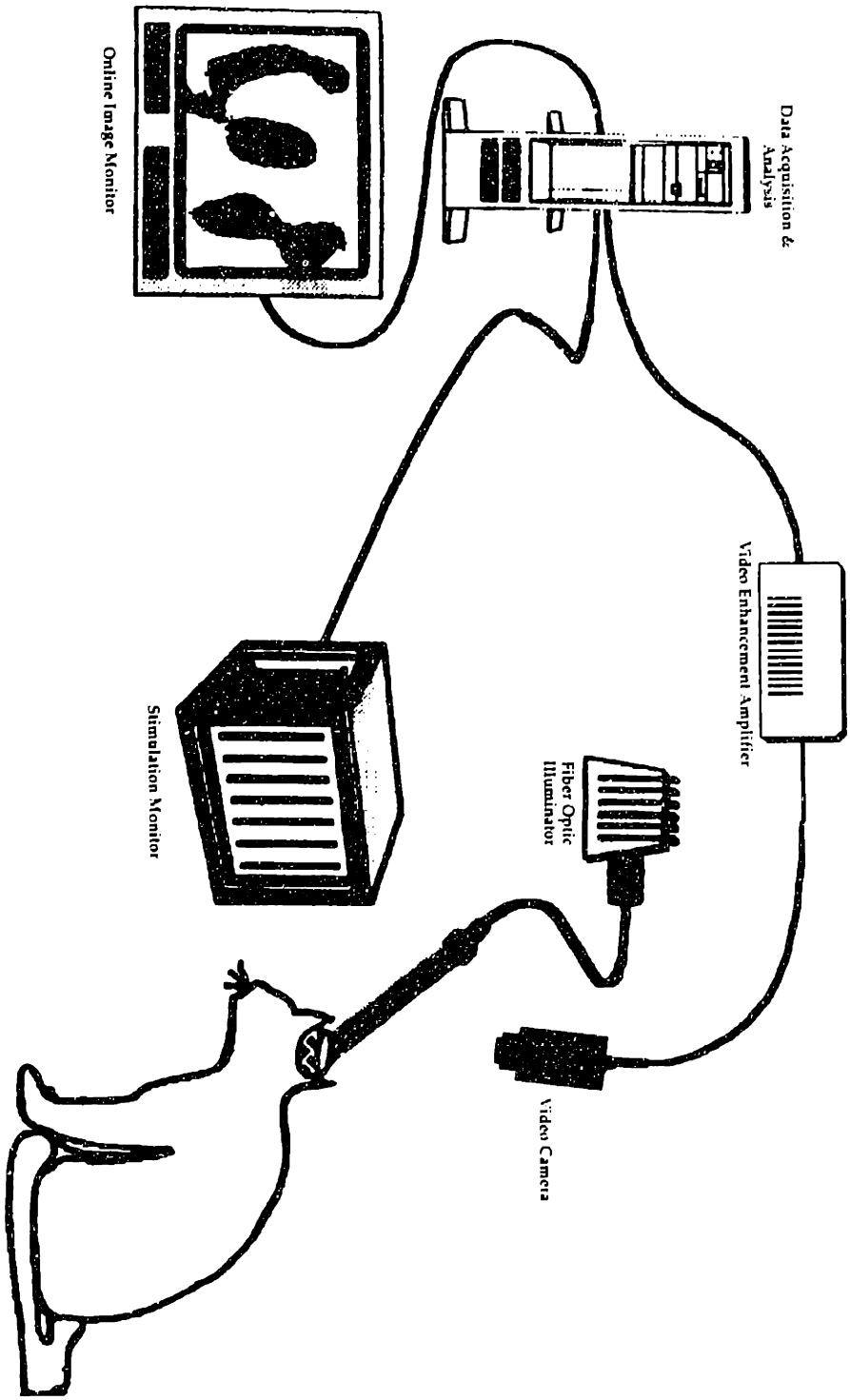

Online Image Monitor
Data Acquisition & Analysis
Video Enhancement Amplifier
Stimulation Monitor
Fiber Optic Illuminator
Video Camera

Figure 1. Adult cats (n = 9) were used in these experiments. Anesthesia was induced with ketamine (15 mg/kg, i.m.) and xylazine (1.5 mg/kg i.m.) and maintained with isofluorane (typically 0.5 - 1.5% in 70/30 $N_2O/O_2$) delivered through a tracheal cannula. Cats were paralyzed with an intravenous combination of gallamine triethiodide (3.6 mg/hr) and tubocurarine chloride (0.15 mg/hr) and artificially respired to maintain end-tidal $CO_2$ at ~4% at a partial pressure of 30 $\pm$ 3 mm Hg. The animal's EEG and heart-rate were continuously monitored to ensure adequate anesthesia. Craniotomy followed by durotomy was performed to expose visual cortex. For imaging area V2, we centered our chamber at A4 and recorded from an area that extended approximately from A3-A7 in the anteroposterior direction and between L0.5-L3.5 in the mediolateral direction. For imaging V1, the chamber was centered at P5 and a similar expanse of cortex was exposed. For imaging V1 and V2 simultaneously, the chamber was centered at A0 (Tusa et al., '78,'79). Techniques for intrinsic signal imaging were similar to those described by (Grinvald et al. '86) and used by us previously (Rao et al. '94). A stainless-steel recording chamber was attached to the skull surrounding the craniotomy, filled with silicone oil and then sealed with a quartz plate. A video camera (CCD-5024N Bishke, Japan, RS-170, >60 dB s/n) consisting of a 655 X 480 array of pixels equipped with a tandem-lens macroscope (Ratzlaff and Grinvald '91) was positioned over the cortex. This arrangement gave a magnification of 75 pixels/mm. Data were collected using an imaging system (Optical Imaging Inc.). The camera signal was amplified by a video enhancement amplifier; a baseline image was subtracted from each stimulus response image in analog form and then digitized by an 8-bit A/D converter (Matrox) installed on a 486-66 PC. Initially, a reference map of the blood vessel pattern at the surface of the cortex was obtained using light filtered at 550 nm $\pm$ 40 nm (Ealing). The camera was then focused down 300-500 μm below the surface of the cortex. Light from a 100W tungsten-

halogen light source driven by a DC power supply (Kepco) was passed through a 610 nm filter and used to illuminate the cortex during data collection. Frames were summed between 0.9-3.6 sec. after stimulus onset, corresponding to the time of maximum signal as determined by our previous experiments (Rao et al. '94). Data were analyzed using in-house programs written in C++ (Borland) and IDL.

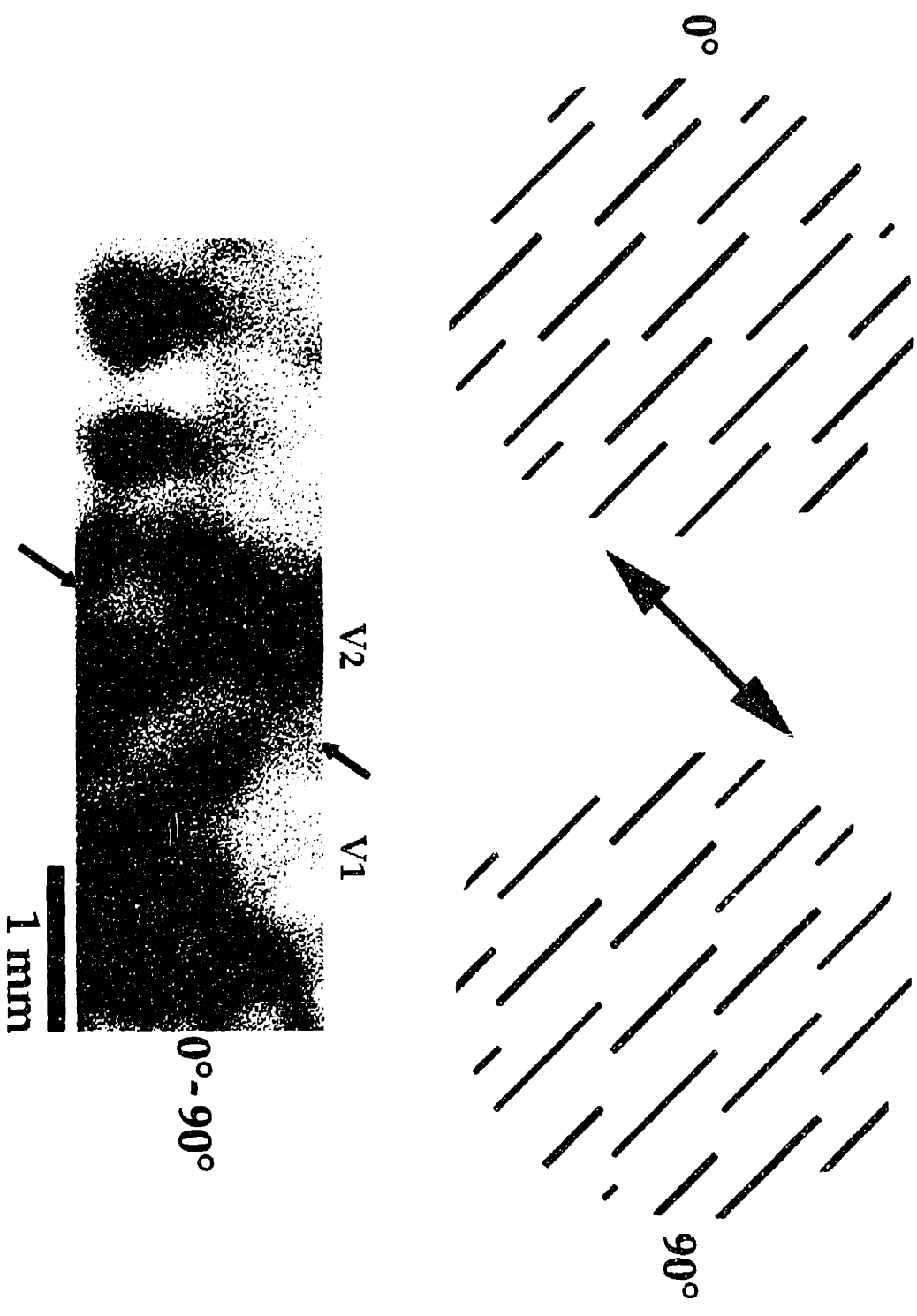

0°
90°
V2
V1
1 mm
0°-90°

Figure 2. Areas V1 and V2 of visual cortex contain clusters of neurons which respond preferentially to subjective orientations. Stimuli (top left and middle) with identical oblique inducing line orientation and identical directions of motion orthogonal to the inducing lines (arrows) but with orthogonal subjective edge orientation (marked $0^0$ and $90^0$), were presented in a randomly interleaved fashion. The optically imaged map (top right) was obtained by subtracting the response to the stimulus at $90^o$ from that at $0^o$. Dark patches show regions which prefer a $0^o$ subjective grating over a $90^o$ grating; vice-versa for light patches. The arrows show the V1/V2 border.

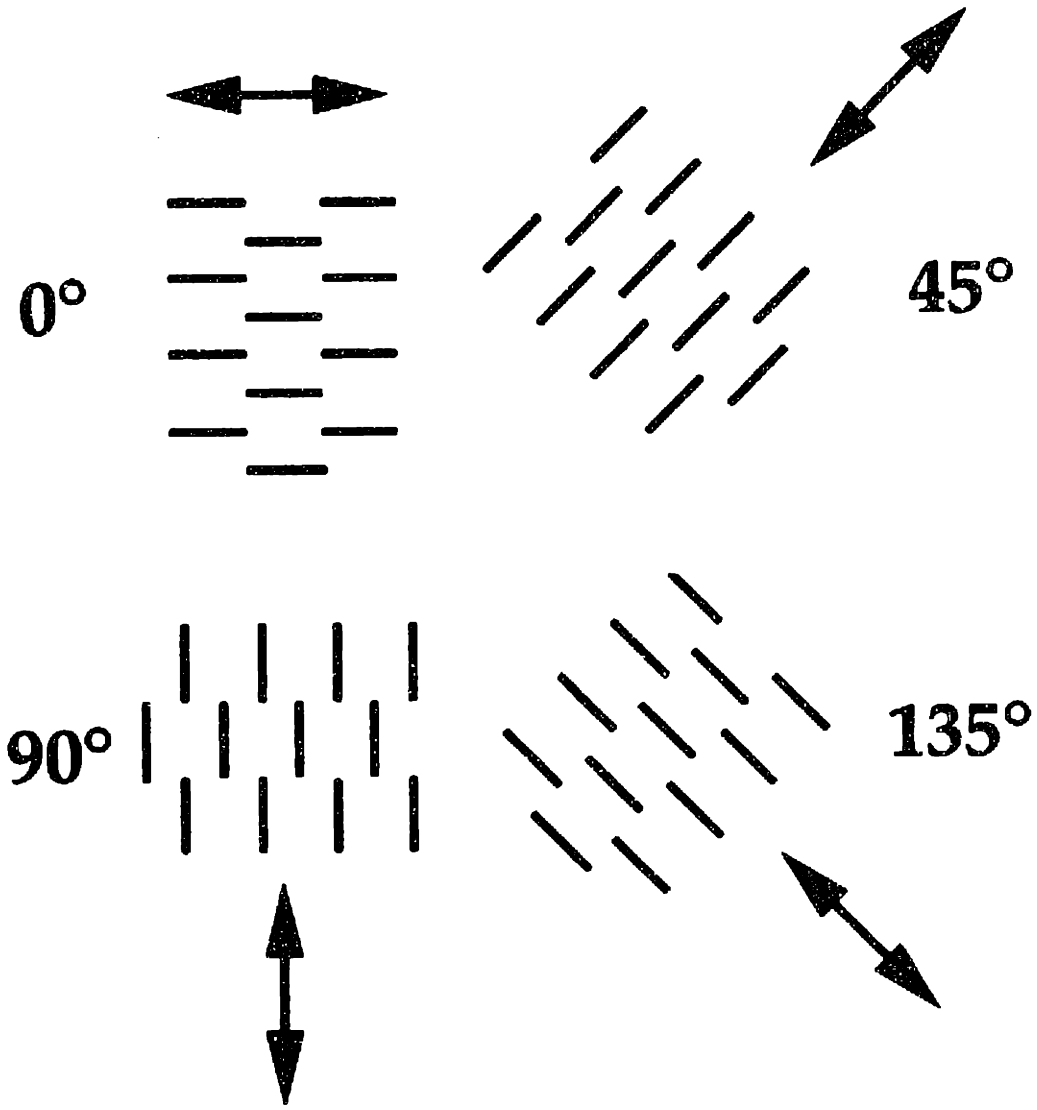

0°
45°
90°
135°

Figure 3. Subjective stimuli used in our experiments are shown. Subjective grating stimuli of four different orientations ($0^{o}$, $45^{o}$, $90^{o}$ and $135^{o}$) were randomly interleaved with square-wave luminance grating stimuli 80-100 times over a period of 4-6 hours on a 17 inch tangent screen placed 28.5 cms (or 57 cms) in front of the animal. Luminance defined inducing lines, 6-12 arcminutes (1 or 2 pixels) thick, forming the perceived edge were kept orthogonal to the subjective orientation for all subjective grating stimuli. Gratings were drifted normal to the subjective edge orientation and parallel to the orientation of the inducing lines in both directions separately. The spacing between the inducing lines (inducing lines spatial frequency) and spacing between the subjective edges (subjective contour spatial frequency) could be varied independently.

Stimulus
Response
Luminance gratings
0°
Subjective gratings
0°
Analysis
% pixels
Orientation difference
Stimulus
Response
90°
0°
% pixels
Orientation difference

Figure 4. Hypothetical responses to luminance and subjective gratings and a comparison of optical maps. Schematic response images for $0^{o}$ (vertical) and $90^{o}$ (horizontal) luminance gratings are shown at the top in green and red respectively. Schematic response images for a $0^{o}$ subjective grating (vertical subjective orientation, horizontal inducing lines), demonstrating two possible extremes of response are shown below. If cells in cortex respond almost exclusively to the subjective orientation and ignore the inducing lines, the same patches of cortex that prefer a $0^{o}$ luminance edge would also be activated by a $0^{o}$ subjective edge (left). A given pixel, then, would exhibit a preference for luminance and subjective gratings of the same orientation; constructing a histogram of the difference in orientation preference between luminance and subjective gratings (abscissa) vs. pixel count (ordinate) would show a peak at $0^{o}$ (bottom left). However, if cells in cortex prefer the orthogonal inducing lines and disregard the subjective orientation , the regions of cortex that respond to the $0^{o}$ luminance grating would not respond to a $0^{o}$ subjective edge; rather, the regions of activation would be mutually complementary (right). A given pixel would exhibit orientation preferences for luminance and subjective gratings stimuli which would differ by $90^{o}$ , and a histogram of the difference in orientation preference vs. pixel count would have a minimum at $0^{o}$ and increase to a maximum at $\pm 90^{o}$ (bottom right).

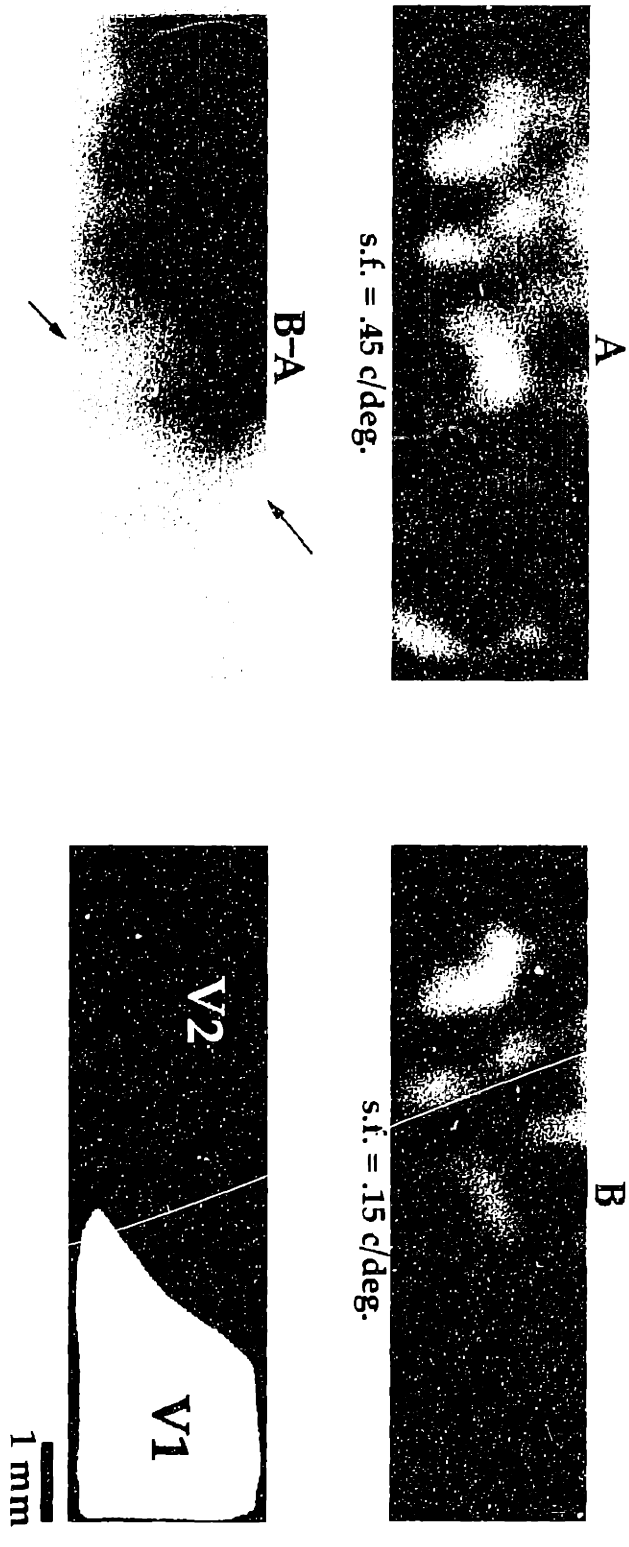

A
s.f. = .45 c/deg.
B-A
B
s.f. = .15 c/deg.
V2
V1
1 mm

Figure 5. Imaging of V1/V2 border. (A) Response of a 8.32 X 2.45 $mm^2$ area of cortex to a luminance grating of spatial frequency 0.5 cycles/deg. Posteromedial part of the image shows higher contrast with dark and light patches more clearly seen as compared to the anterolateral part of the image, indicating stronger orientation-specific response in putative V1. (B) Response of the same cortex to a luminance grating of spatial frequency 0.15 cycles/deg. Here, the posteromedial part of the image shows slightly lower contrast with dark and light patches not as clearly seen as compared to the anterolateral part of the image, indicating stronger orientation response in putative V2. Obtaining a differential map by subtracting response in B from the response in A, the anterolateral part of the image shows greater signal for the lower spatial frequency stimulus used in B. The arrows then give an approximate V1/V2 border with the resultant masks being shown at the bottom right. These masks will later be used to compare responses to subjective gratings in V1 and V2 areas (cf. Figure 13).

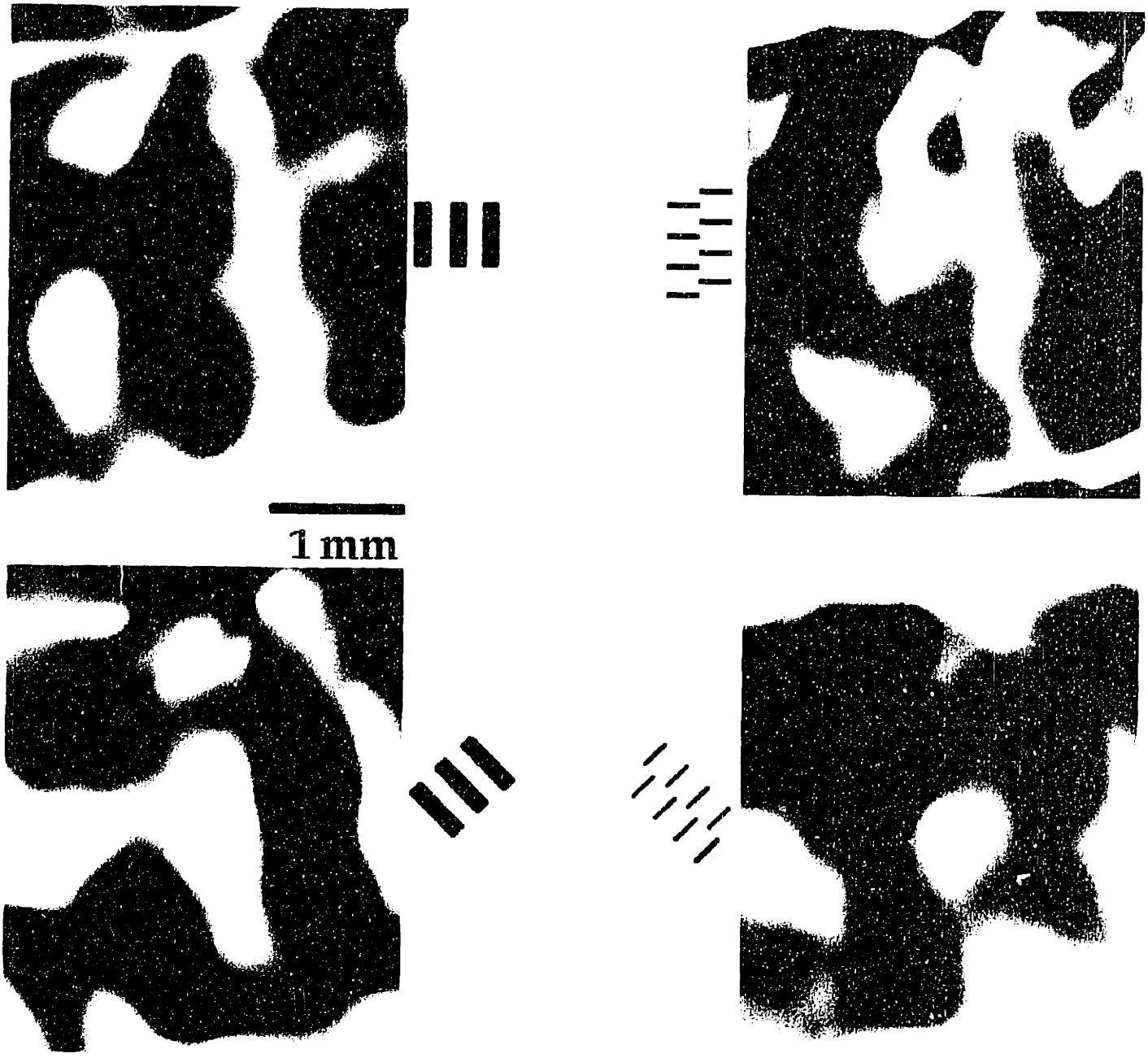

1 mm

Figure 6. V2 showed a strong subjective response. Differential maps for luminance (A) and subjective gratings (B) of a 3.6 X 2.9 $mm^2$ of cortical area V2 showed considerable overlap. Differential maps for $0^o$ - $90^o$ response were obtained by subtracting the raw single-condition map summed and averaged over all stimulus set trials for $90^o$ response from the raw single-condition map for response to $0^o$ gratings for the same trials (similarly for $45^o$ - $135^o$ differential map; cf. appendix for details). All stimulus conditions were presented in an interleaved fashion for 80-100 stimulus set trials to the animal for 4-6 hours time duration. The spatial frequency of luminance and subjective gratings (i.e. the subjective edges) were the same at 0.15 cycles/deg. The inducing lines were spaced at a frequency of 0.45 cycles/deg.

A
1 mm
B

Figure 7. Composite orientation-preference maps in V2 for (A) luminance and (B) subjective gratings. To obtain these composite maps, the stimulus orientation that elicited the maximal response from a given pixel was determined and this preferred orientation displayed in pseudo-color according to the key at right. Luminance and subjective gratings of identical orientation are coded in the same color (e.g., pixels responding best to a vertical subjective grating and a vertical luminance grating are both shown in blue). The density of pinwheels in Figure 7B is $0.8/mm^2$.

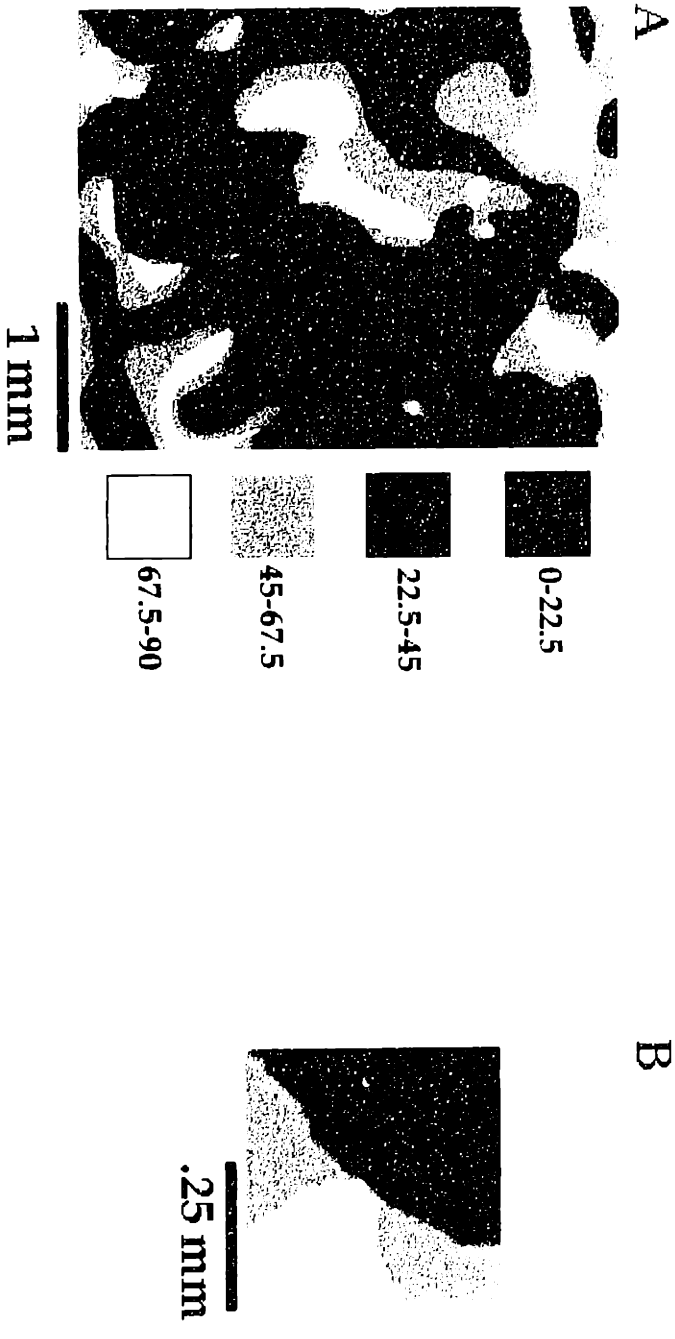

A
1 mm
0-22.5
22.5-45
45-67.5
67.5-90
B
.25 mm

Figure 8. (A)The map of orientation differences (comparing Figure 7A,B). For each pixel, the difference between its luminance and subjective orientation preferences is computed and coded in one of four shades of gray: 0 to $\pm 22.5^{o}$, black; $\pm 22.5$ to $\pm 45^{o}$, dark gray; $\pm 45^{o}$ to $\pm 67.5^{o}$, light gray; $\pm 67.5^{o}$ to $\pm 90^{o}$, white. (B) Magnified portion from (A), showing the radial arrangement of neurons in a pinwheel-like fashion. Regions of positive and negative orientation difference are coded in the same gray level, hence each gray level is represented twice around a pinwheel center.

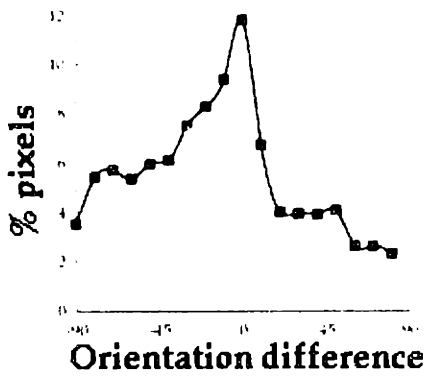

% pixels
Orientation difference

Figure 9. The pixel histogram quantifying the difference in orientation preference between luminance and subjective gratings derived from the maps in Figure 7A,B. The histogram shows a peak close to $0^{o}$ orientation difference, indicating a strong response in V2 to subjective orientations. 41% of pixels fell in the central $45^{o}$ ($0^{o}$ to $\pm 22.5^{o}$) orientation difference compared to 14% in the far $45^{o}$ ($\pm 67.5^{o}$ to $\pm 90^{o}$). This agrees well with the numbers provided by von der Heydt and Peterhans ('89) from monkey V2 recordings in which they found that 44% of the cells in V2 that they recorded from were classified as contour cells.

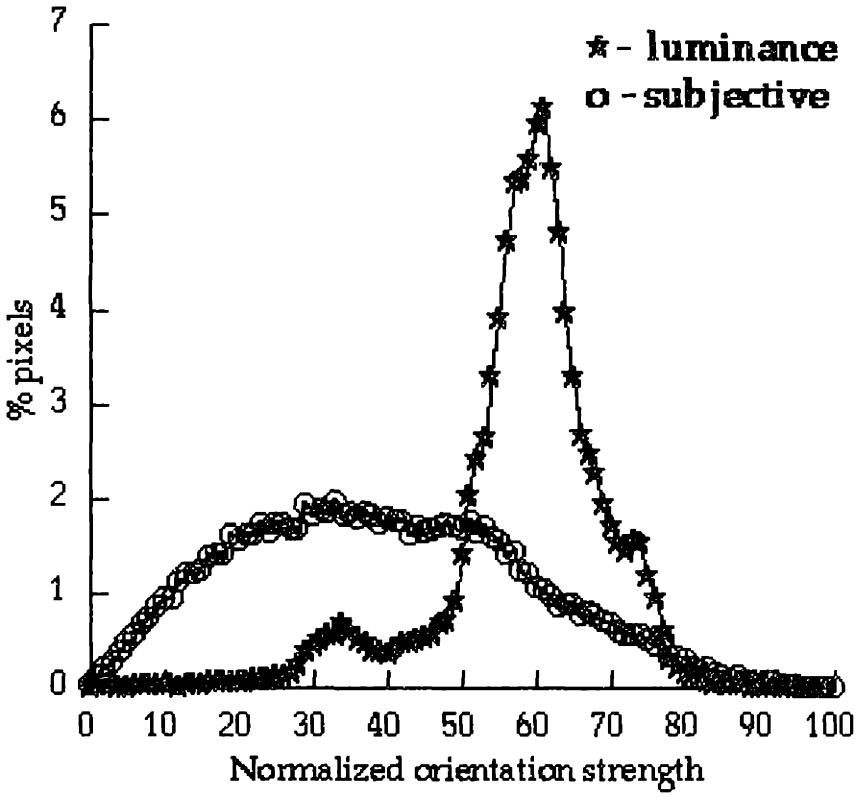
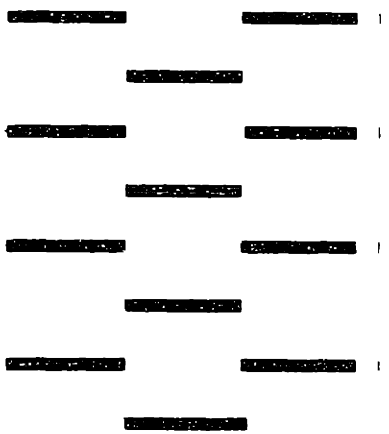
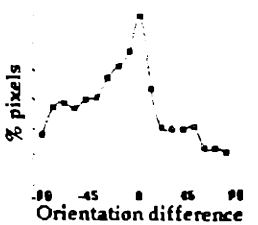

7
6
5
4
3
2
1
0
% pixels
0 10 20 30 40 50 60 70 80 90 100
Normalized orientation strength
* - luminance
o - subjective

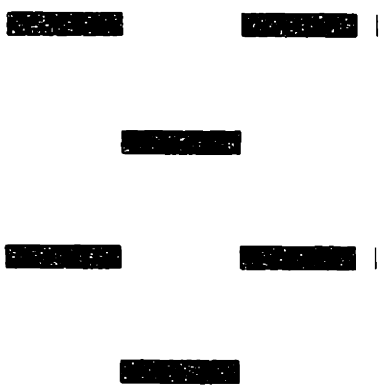
Figure 10. Normalized orientation strengths for luminance and subjective gratings across all pixels in imaged V2 are shown. Orientation strengths for subjective gratings was on average approximately three-fold lower than for luminance gratings. The signal for luminance gratings varied between $1.64 \times 10^{-5}$ and $1.10 \times 10^{-2}$ units with a median of $4.27 \times 10^{-3}$ and a mean of $4.39 \times 10^{-3}$ for luminance gratings; the range of orientation strengths for subjective gratings ranged from $1.18 \times 10^{-5}$ and $5.41 \times 10^{-3}$ units with a median of $1.32 \times 10^{-3}$ (31% of luminance median) and a mean of $1.41 \times 10^{-3}$ (32% of luminance mean) units. The maximum and minimum values across *both* maps were chosen and set at values 100 and 0 respectively and all pixel magnitudes for both maps were normalized to lie in this range. The range was divided into 100 bins of equal width.

inducing lines
s.f. = 0.45 c/deg.






inducing lines
s.f. = 0.225 c/deg.



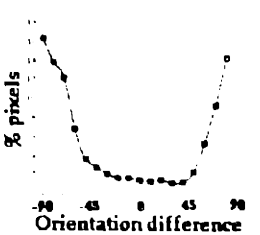
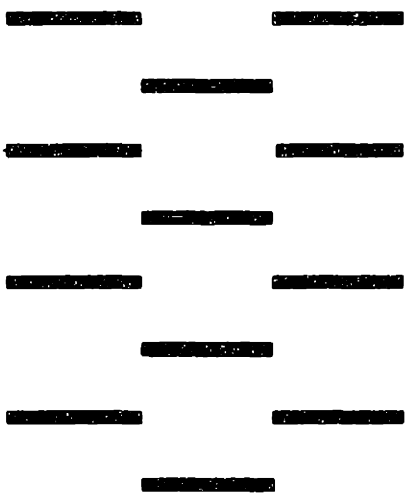
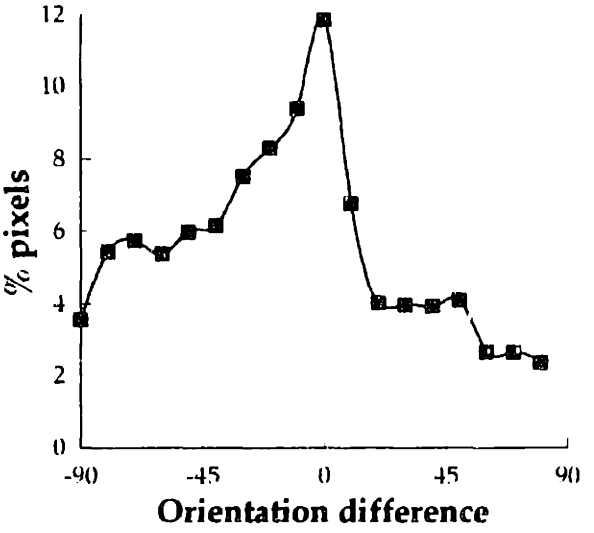


Figure 11. Effect of inducing line density on subjective orientation responses in V2. Inducing line spatial frequency, 0.225 cycles/deg; only 7% of pixels fell in the central 45° orientation difference, while 59% fell in the far 45°. The histograms in Figures 11 were significantly different ($p < 0.001$, $\chi^2$ test).

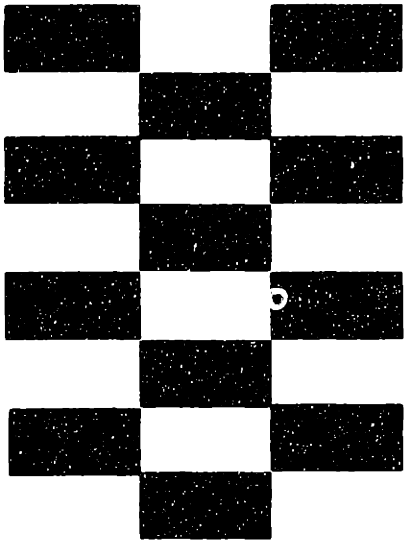
A



B


12
10
8
6
4
2
0
% pixels
-90
-45
0
45
90
Orientation difference

C



D

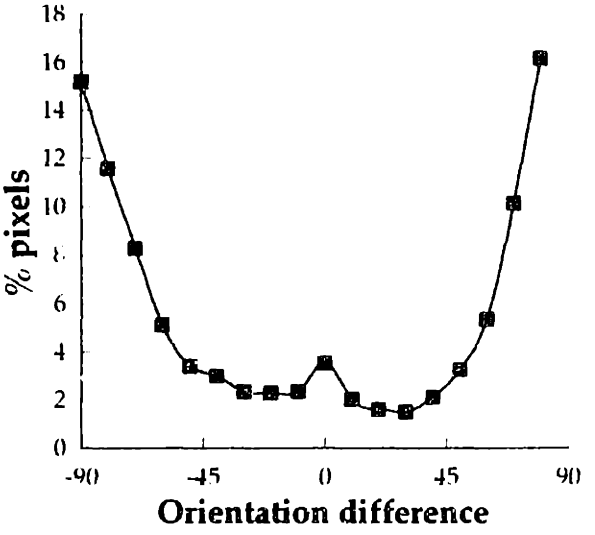
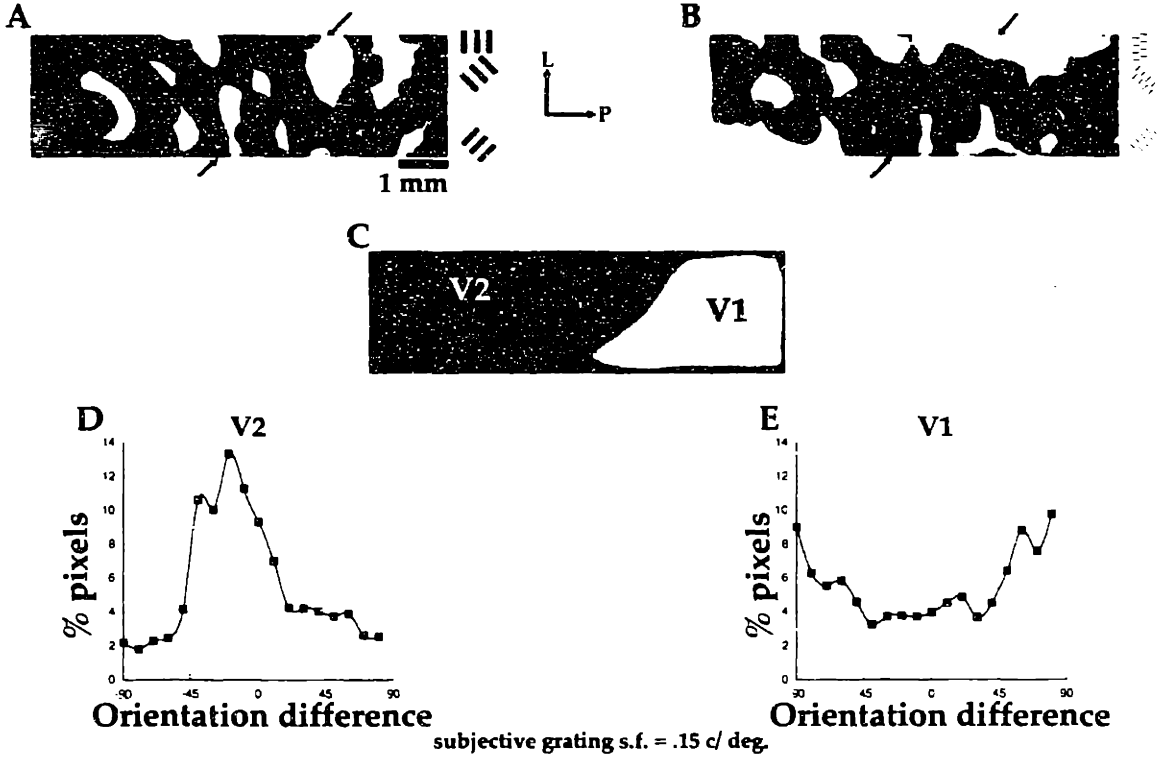

18
16
14
12
10
6
4
2
0
% pixels
-90
-45
0
45
90
Orientation difference

Figure 12. Responses in V2 to abutting square-wave gratings (rectangular checkerboard patterns). (A) A $0^{o}$ orientation subjective grating (0.15 cycles/deg. subjective spatial frequency, 0.45 cycles/deg. inducing bar spatial frequency). (B) The pixel histogram quantifying the difference in orientation preference between luminance and subjective gratings. (C) A $0^{o}$ orientation abutting square-wave grating (0.15 cycles/deg. "subjective" spatial frequency, 0.45 cycles/deg. inducing bar spatial frequency). The "subjective" edge is actually a physical contour running vertically across the figure. Stimuli of four different orientations ($0^{o}$, $45^{o}$, $90^{o}$ and $135^{o}$) were interleaved. (D) The pixel histogram quantifying the difference in orientation preference between luminance and abutting square-wave gratings recorded in the same animal.




subjective grating s.f. = .15 c/ deg.
inducing lines s.f. = .45 c/ deg.

Figure 13. Responses to subjective gratings in V1, and a comparison with responses in V2 imaged simultaneously. Composite orientation-preference maps in V2 for (A) luminance and subjective (B) gratings. Comparison of responses in V1 and V2 to the same subjective grating, imaged simultaneously (subjective edge spatial frequency, 0.15 cycles/deg.; inducing line spatial frequency, 0.45 cycles/deg.) (C) The V1/V2 border was defined with appropriate luminance gratings (see text and Figure 5); masked regions well inside V1 and V2 were used for computation of the pixel histograms comparing maps for luminance and subjective gratings (L, lateral; P, posterior). (D,E) Pixel histograms for V2 and V1; the two histograms were significantly different ($p < .001$, $\chi^2$ test) . V2: 41% of pixels fell in the central 45°orientation difference (0° to $\pm$22.5° ) and 9% in the far 45° ($\pm$67.5° to $\pm$90°). V1: 16% of pixels fell in the central 45° orientation difference (0° to $\pm$22.5° ) and 33% in the far 45° ($\pm$67.5° to $\pm$90°). However, 37% of the pixels fell within $\pm$45° orientation difference (0° to $\pm$22.5° ).

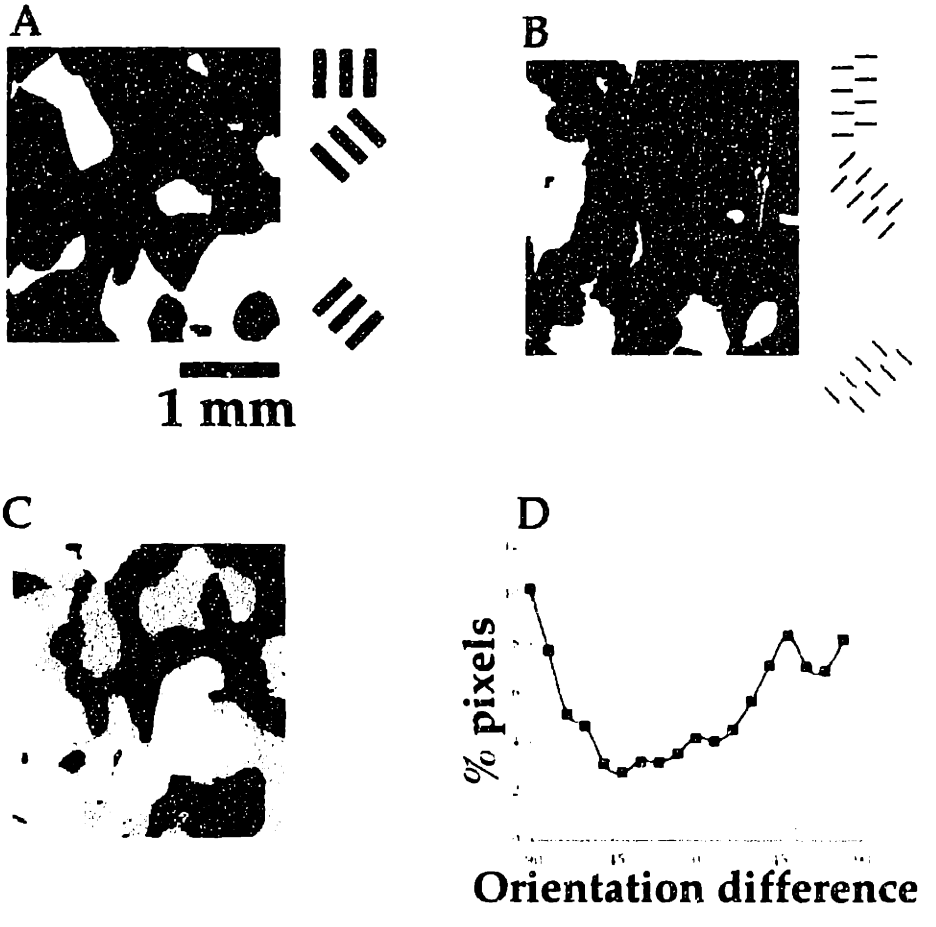

A
1 mm
B
C
D
% pixels
Orientation difference

Figure 14. Composite orientation preference maps from V1 are shown for (A) luminance and (B) subjective gratings. The density of pinwheels in B is $1.9/mm^2$. (C) Map of orientation differences (comparing A,B). (D) The pixel histogram, while peaking at $\pm 90^o$ orientation difference, had 38% of pixels within the central $\pm 45^o$ orientation difference, indicating the presence of cells in V1 that responded to the subjective edges in the stimulus. Stimulus parameters included a high spatial frequency of inducing lines (0.45 cycles/deg.) and subjective edges (0.5 cycles/deg.).

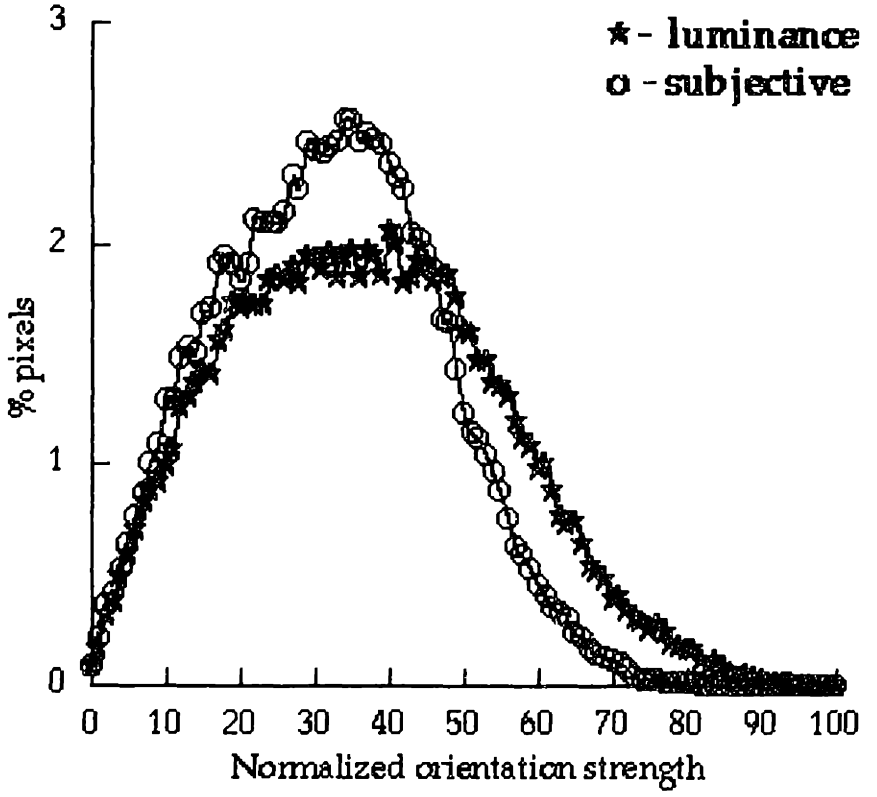

3
2
1
0
% pixels
★ - luminance
o - subjective
0
10
20
30
40
50
60
70
80
90
100
Normalized orientation strength

Figure 15. Normalized orientation strengths for luminance and subjective gratings across all pixels in the V1 map (Fig. 14) are shown. Orientation strengths for subjective gratings was on average nearly the same as for luminance gratings. The signal for luminance gratings varied between $7.03 \times 10^{-6}$ and $2.95 \times 10^{-3}$ units with a median of $1.08 \times 10^{-3}$ and a mean of $1.10 \times 10^{-3}$ units; orientation strengths for subjective gratings ranged between $7.14 \times 10^{-6}$ and $2.53 \times 10^{-3}$ units with a median of $0.97 \times 10^{-3}$ units (90% of luminance median) and a mean of $0.97 \times 10^{-3}$ units (88% of luminance mean).

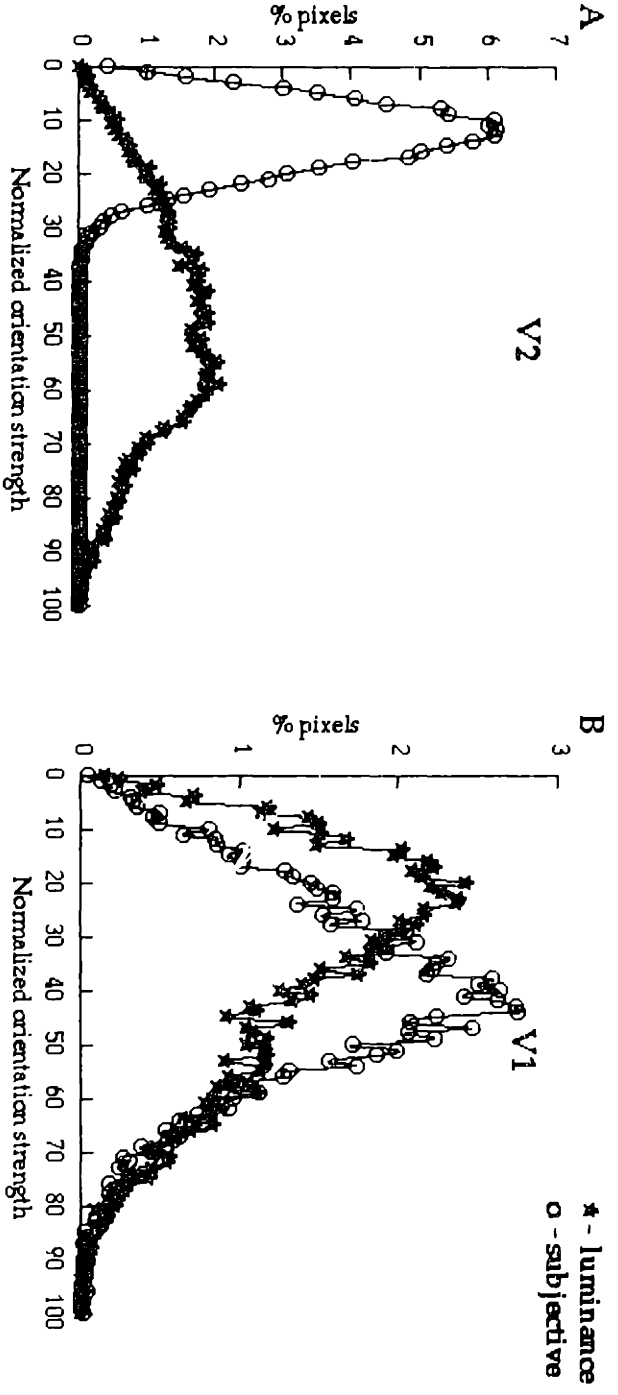
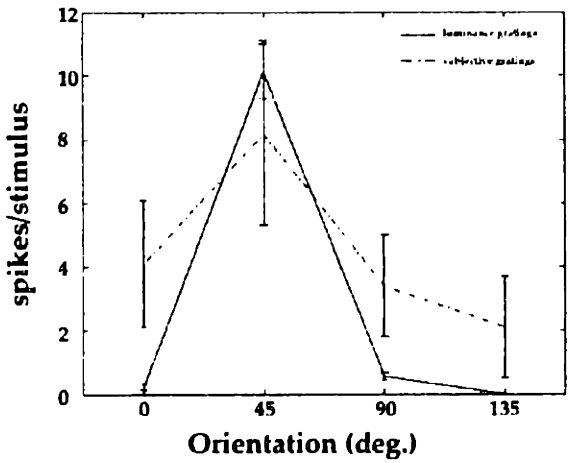

A
% pixels
V2
Normalized orientation strength
B
% pixels
V1
Normalized orientation strength
★ - luminance
o - subjective

Figure 16. Comparison of normalized orientation strengths for only those pixels in V2 (Fig. 8A) and V1 (Fig. 14C) that responded strongly to subjective edges (within $\pm 22.5^{o}$ orientation difference). The relatively fewer pixels in V1 that responded strongly to subjective edges had comparable orientation stengths for luminance and subjective gratings, whereas the orientation strengths for subjective gratings were, on avaerge, three-fold weaker than for luminance gratings for the proportionately more V2 pixels. V1: the mean orientation strength for subjective gratings ($1.00 \times 10^{-3}$ units) was slightly higher than the mean orientation strength for luminance gratings ($.87 \times 10^{-3}$ units); V2: the mean orientation strength for subjective gratings ($1.31 \times 10^{-3}$ units) was one-third of the mean orientation strength for luminance gratings ($4.56 \times 10^{-3}$ units).

A V2 cell




B V2 orientation difference map

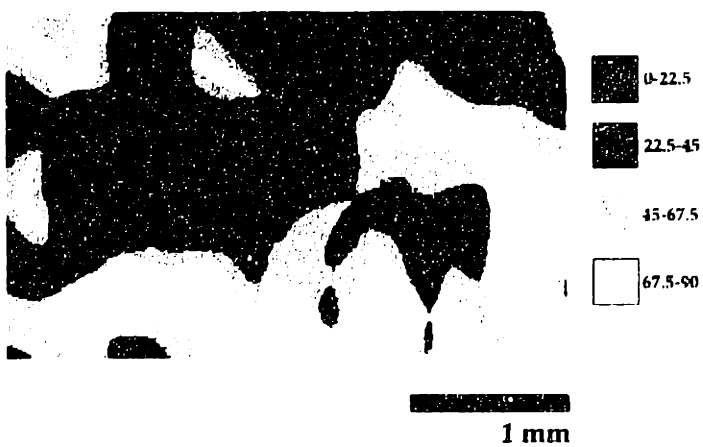
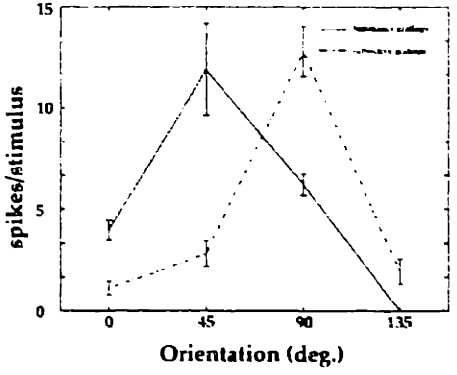
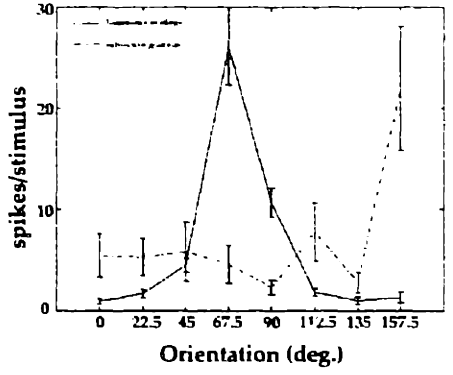


Figure 17. Comparison of optical maps and single-unit responses in V2. A. Orientation tuning curves for a luminance grating (continuous lines) and a subjective grating (broken lines) are shown. The cell prefers a luminance grating and a subjective grating of the same 45° orientation. B. The location of the cell in the optical orientation difference map is shown in red. The cell lies in a black orientation difference domain which is characterized by pixels having similar orientation preferences for luminance and subjective gratings ($< \pm 22.5°$).

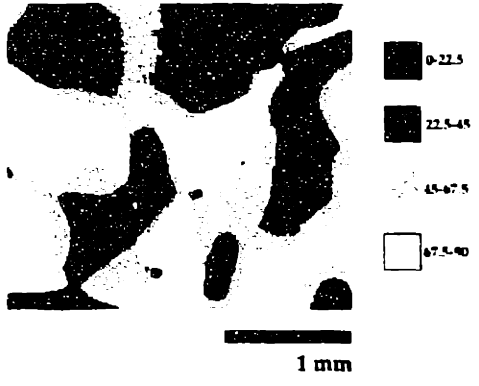
A V1 cell




C V1 cell




B V1 orientation difference map




D V1 orientation difference map

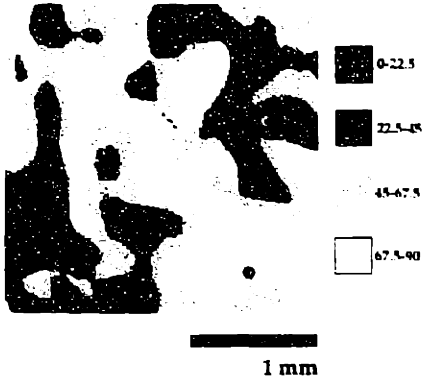


Figure 18. Comparison of optical maps and single-unit responses in V1. A. Orientation tuning curves of a cell in V1 for a luminance grating (continuous lines) and a subjective grating (broken lines) are shown. The cell prefers a luminance grating of 45° orientation and a subjective grating of 90° orientation. Thus, the difference in orientation preference between the two stimuli is -45°. B. The location of the cell in the optical orientation difference map is shown in red. The cell lies within a dark gray orientation difference domain but close to its border. This region contains pixels having orientation preferences for luminance and subjective gratings that differ by a value in the range ±22.5° --> ±45°. C. Orientation tuning curves of a cell in V1 of a different animal for a luminance grating (continuous lines) and a subjective grating (broken lines) are shown. The cell prefers a luminance grating of 67.5° orientation and a subjective grating of 157.5° orientation. Thus, the difference in orientation preference between the two stimuli is -90°. D. The location of the cell in the optical orientation difference map is shown in red. The cell lies in a region containing pixels having orientation preferences for luminance and subjective gratings that differ by a value in the range ±67.5° --> ±90°.

# Chapter 3

# Single unit responses in cortical areas V1 and V2 to subjective contours

# ABSTRACT

Single unit recordings in V1 and V2, employing the same stimuli as used for optical imaging, showed that individual neuron responses were consistent with the imaging results. Of all cells recorded in V2 (n = 26), half (13 cells) showed a response to subjective gratings with a preferred orientation within $\pm 45^{o}$ of the preferred orientation of luminance gratings. Unlike cells in V2, we did not find any cell in V1 that gave a strong response to subjective edges (n = 27), but we did find several cells (n = 9) whose subjective grating orientation preference was within $\pm 45^{o}$ of the preferred orientation for luminance gratings. Thus, our single-unit studies show that a large fraction of cells in V2 respond to subjective edges, whereas a smaller proportion of cells in V1 are partially responsive to subjective edges. Most neurons encountered in any given vertical penetration normal to the cortical surface (i.e. column) responded in a similar manner to subjective contours. Some cells that were earlier found to be driven by the inducing lines and not the subjective edges (n = 8) with conventional subjective gratings showed a clear orientation-specific response to a different kind of subjective grating stimulus (5 cells) in which the luminance component was kept the same across all stimuli in the set. This results shows that the response to subjective contours may, in fact, be even more widespread in V1 than obtained with conventional subjective gratings.

# INTRODUCTION

The imaging studies (cf. Chapter 2) have shown that neurons in superficial layers of areaV2 in cat cortex contains a number of cells that respond exclusively to subjective contours and these columns are organized into clustered domains for subjective orientation preference; V1 also contains cells that are clustered for subjective orientation preference but there are smaller regions that show a robust response to the subjective edges. The imaging technique makes an assumption that cells in the same column (same vertical penetration normal to the surface) have similar responses to the given stimuli. However, this assumption needs to be examined by single-unit recordings in the context of responses to subjective contours. Thus, it remains to be shown with single-unit extracellular recordings that a) some cells in V2 have a robust response to subjective contours, b) single cells in V1 display some response to subjective contours and that c) cells in the same column have similar response to subjective contours.

# GENERAL METHODS

Single-unit experiments were carried out in 9 cats. Prior to each experiment, appropriate contact lenses were fitted in order to focus the eyes on the monitor. Eye position was checked by projecting the location of the optic disk onto the monitor with a reversible opthalmoscope and eye focus was judged by focusing the image of the retinal vasculature onto the stimulus monitor. Single units were recorded with parylene

insulated tungsten microelectrodes (Fredrick Haer Corp., 1-2 Mohms impedance at 1 kHz). Responses were conventionally amplified, displayed and stored. After performing a craniotomy and durotomy, we lowered an electrode into the cortex normal to its surface by means of a microdrive (1 μm resolution). Agar (1.5% in saline) was then placed on the surface of the cortex to clamp down pulsations from the animal's heartbeat and respiration. Upon encountering electrical spiking activity, a single neuron was isolated by means of a window discriminator (Grass Instruments). The signal was amplified, filtered at 1-10 kHz, digitally windowed, and collected on an IBM-486 computer using a 200 MHz A/D board (software written by Louis J. Toth). We then plotted the cell's receptive field (using the minimum-field stimulation method) and approximate orientation preference (usually binocularly) by moving a hand-held bar in different directions. Other properties such as the cell's eye preference (contra/ipsi eye), classification (simple/complex), on/off subfields (simple cells only), end-stopping were judged as well. Stimuli used in our experiments were the same as those used for our imaging studies (cf. chapter 2). Luminance gratings of equally interspersed 4-8 orientations (22.5° apart for 8 orientations, 45° apart for 4 orientations) were interleaved with subjective gratings of the same number of orientations for 1-2 sec. (compare with our imaging experiments in which the stimulus was kept on for 3.6-4 sec.). Stimuli were generated by an IBM-compatible computer running STIM (K. Christian, Rockefeller Univ.), using a Sgt. Pepper+ graphics board with 4MB memory (Number Nine Corp.) at a resolution of 640 X 480 pixels. Stimuli were shown at a 30 Hz frame rate in a dual interlaced fashion (field rate 60 Hz) on a Princeton 17" monitor positioned either 28.5 / 57 cms (at 28.5 cms, 1cm = 2 deg. of visual angle; at 57 cms, 1cm = 1 deg. of visual angle)

from the animal's eyes. Individual frames for each stimulus were computed prior to the beginning of the experiment and shown under the timing of the optical imaging computer which controlled the spike acquisition program (which resided on another computer) as well. All visual stimuli were presented binocularly initially. In some cells, following determination of eye preference (usually the contralateral eye), we switched to monocular stimulation. In a select number of cells, we varied stimulus parameters (spatial frequency, temporal frequency, inducing line spacing), in order to investigate the cell's responsiveness to subjective gratings.

## RESULTS

*Responses of V2 neurons to subjective contours*

Recordings from V2 showed that a minority of neurons in V2 did respond to the subjective edges in the grating stimuli in an orientation-specific manner. Figure 1 shows the orientation tuning curves of a cell for luminance and subjective gratings. The cell had the same orientation preference for luminance and subjective gratings ($0^{o}$ vertical gratings) and had almost the same average response to the preferred subjective orientation as it did to the preferred luminance orientation; this cell was classified as a subjective contour cell. Figure 2 shows another cell encountered in the same penetration which was also a strong subjective contour cell, by our criterion, and had the same luminance as well as subjective orientation preference as did the cell in Figure 1.

Responsiveness to subjective edges, we found, was sensitive to the choice of stimulus parameters. If a higher spatial frequency subjective grating was shown, the cell became silent to the stimulus and did not respond to the subjective edges or the inducing lines. It is important to note that the cell did not change modes and respond like a luminance cell (cf. Subjective criterion). Also, we did not find a single luminance cell that switched modes and began responding to the subjective edges (and ignoring the inducing lines) under a different stimulus condition[1].

Figure 3 shows two cells obtained in yet another vertical penetration (160μm and 286 μm depth from the surface) which were both subjective contour cells and had the same subjective orientation preference. Figure 4 shows three cells in the same column that shared the same subjective orientation preference. Figure 5 shows two "luminance" cells, obtained in the same vertical penetration (colum) which responded predominantly to the inducing lines in the stimulus. Figure 6 shows cells from the same vertical penetration neither of which responded to subjective gratings of any orientation. These cells could not be driven either by the subjective edges or by the inducing lines and their response to subjective gratings of all orientations was not above the cells' spontaneous

1. However, we did not test the response of contour cells to a lower subjective spatial frequency (0.225 c/deg.) stimulus, a parameter we tested in our imaging experiments(cf. Chapter 2, figure 11). We predict that it is likely then for a contour cell to switch modes and respond strongly to the inducing lines.

activity (recorded while the the animal viewed a neutral gray intensity screen). Figure 7 shows a summary of penetrations (penetrations in which we recorded from 2 or more cells, and cells in the penetration (column) did not respond solely to the inducing lines i.e. the difference in orientation preference between luminance and subjective gratings was less than $90^{o}$[2]) across all animals and the subjective orientation preferences of these cells relative to each other.

We found that 27% of cells in V2 (n = 26, 7 cells) showed a strong response to subjective edges and were termed subjective contour cells (Figure 8A). 27% of cells recorded from in V2 did not respond at all to the stimulus - either to the subjective edges or the inducing lines. Thus, cells in V2 may be classified into three types : (a) cells that responded to the stimulus and showed at least some response to the subjective edges (13 cells, 50%), (b) cells that displayed weak, unoriented response to the subjective grating stimuli (7 cells, 27%), and (c) cells that responded strongly to the inducing lines (6 cells, 23%). Thus, it was relatively rare (about one out of four cells we recorded from) to find a V2 cell that gave responded vigorously to the subjective grating stimulus and was driven exclusively by the inducing lines in the stimulus. If a higher proportion of cells in V2 responded to the inducing lines, our imaging histograms would be bimodal with

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2. Since inducing lines are luminance edges, it should come as no surprise that cells responsive to the inducing lines i.e. luminance edges, in the subjective grating stimulus are organized in columnar fashion (Hubel and Wiesel '63,'74). If the difference in orientation preference between luminance and subjective gratings is $90^{o}$, it is because the cell responds exclusively to the inducing lines and ignores the subjective edges. Naturally, these cells are organized in columnar fashion. A column with cells responding to the inducing lines is termed a non-subjective column.

peaks at 0° (contour columns) and 90° (luminance) orientation difference. Figure 8B shows the histogram of a subset of V2 cells (Figure 8A) in which gratings at a finer orientation resolution (22.5°) were tried.

*Receptive field properties of V2 cells.*

Receptive field properties of a subset of V2 cells whose luminance and subjective orientation preferences differed by $\pm 45^{\circ}$ or less (10 cells) were studied in detail. Most of these cells (9 cells) were complex; one was a simple cell. Only one of the cells was end-stopped, the remainder (9 cells) were non end-stopped Of the cells that responded strongly to the subjective edges (orientation difference - 0°), four were complex and one cell was simple. All five cells were non end-stopped. Twelve cells whose locations were identified were encountered at a variety of depths (160 μm - 1300 μm); 6 cells were encountered in the superficial layers and 6 cells in the deep layers. The cells in V2 with similar preference for subjective and luminance orientations (7 cells) were encountered at a variety of depths (160 μm - 1300 μm); 5 cells were encountered in the superficial layers and 2 cells in the deep layers.

*Luminance and subjective tuning curves for a small fraction of V2 cells.*

We also found cells (n = 2) in V2 that showed a strong response to subjective stimuli but that had a flat response to luminance gratings (cells not included in the histogram in Figure 8). Figure 9 shows a cell that had a very sharp orientation tuning for subjective gratings but showed almost no response to luminance gratings. Thus, there may exist

cells in V2 that might respond exclusively to subjective grating stimuli and not to luminance grating stimuli[3].

*Why do contour cells ignore the inducing lines?*

Some V2 cells respond almost exclusively to the subjective edges and seem to ignore the inducing lines. This is surprising given that the inducing lines are luminance based contours. However, it should be noted that a cell responds in this way to subjective contours only in a narrow parameter range. The gratings are drifted in a direction parallel to the inducing lines and orthogonal to the subjective orientation. This might play some role in tilting the balance in favor of subjective edges. We recorded from 2 contour cells in V2 and changed the direction of motion of the gratings so they were parallel to the subjective edge orientation and orthogonal to the inducing line orientation (Figure 10). The responses of the cells changed dramatically. The cells, which earlier responded predominantly to the subjective edges and not to the inducing lines, now responded to the inducing lines instead (Figure 11). It has been shown in psychophysical experiments that prolonged fixation results in a steady drop in contour strength over trials which is not found when subjects are instructed to scan across the subjective contours and in other conditions requiring eye movements (Bradley and Pennella, '87). In a paralyzed animal (or in an awake animal which has to maintain steady fixation), there are no voluntary eye movements taking place and so the only relative motion between the stimulus and the eyes is provided by the stimulus. When

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3.We believe our ratio (2/28) is likely to be an underestimate since we usually isolated a cell based on our being able to elicit a strong response to bars and other luminance stimuli. Our failure at being able to do so would simply cause us to go down deeper into the cortex. We stumbled upon these cells by accident since subjective grating stimuli happened to be drifting on the stimulus monitor when we first encountered them.

subjective gratings are drifted in a direction parallel to the orientation of the subjective edges, the subjective edges appear stationary to a cell with a finite receptive field (cells in V2 we have recorded from have a receptive field width of about 6-12°) and the response caused by the subjective component then adapts out. At the same time, the inducing lines are drifting through the cell's receptive field with a near-optimal velocity which results in the cell responding to the inducing lines. The situation is almost reversed in the case when the grating is drifted orthogonal to the subjective edges and parallel to the inducing lines.

*Responses of V1 neurons to subjective contours*

Unlike V2 (see above), we did not find a single cell in V1 (n = 27) that responded exclusively to the subjective edges in the stimulus in an orientation-specific manner and ignored the inducing lines. Figure 12A shows a cell that did not respond to the subjective edges and responded to the inducing lines instead. As in the imaging experiments, we varied stimulus parameters and found that changing stimulus parameters did not change the cells' responsiveness to subjective grating stimuli dramatically (Figure 12B). The cell responded either poorly to the subjective edges (while responding strongly to the inducing lines) or did not respond to the stimulus at all. We also found cells that were driven at least partially by the subjective edges. Figure 13 shows a cell which responded strongly to the subjective edges and the inducing lines . Figure 14 shows a cell that also responded to a combination of inducing lines and subjective edges as shown by the 45° orientation difference.

Figure 15 shows a V1 cell whose orientation preferences for subjective and luminance

gratings differed by 45°, indicating a response driven both by the subjective edges as well as the inducing lines. Figure 16A shows a histogram of cell count vs. difference in orientation preference between luminance and subjective gratings. Thus, it is clear that cells in V1 do not respond as strongly to subjective contours as cells in V2, but some cells' responses are driven partly by subjective edges as evidenced by the intermediate orientation preferences found in several cells (9 cells, 32%). Cells in V1 almost all (25 cells, 93%) responded to the subjective stimulus: 59% (16 cells) responded exclusively to the inducing lines, 33% (9 cells) showed some response to the subjective edges, and 7% (2 cells) did not respond at all to subjective gratings of any orientation. Figure 16B shows the histogram of a subset of these V1 cells (Figure 16A) in which gratings at a finer orientation resolution (22.5°) were tried. Note the similarity of histogram shapes between our imaging and single-unit studies for both areas - V1 (Figure 16 and Chapter 2, Figures 13,14) and V2 (Figure 8 and Chapter 2, Figures 9,13).

Figure 17 shows a summary of penetrations made in V1 (penetrations in which we recorded from 2 or more cells, and cells in the penetration (column) did not respond solely to the inducing lines i.e. the difference in orientation preference between luminance and subjective gratings was less than 90°) across all animals and the subjective orientation preferences of these cells, relative to one another.

*Receptive field properties of V1 cells.*

Receptive field properties of a subset of V1 cells whose luminance and subjective orientation preferences differed by $\pm$45° or less were studied in detail. 5 cells were

complex; one was a simple cell. 2 cells were end-stopped, 6 cells were non end-stopped. Eight cells whose locations were identified were encountered at depths ranging between 300-1200 μm from the surface.

*Responses of luminance cells in V1 to iso-luminance subjective gratings.*

A small number of V1 cells, that had been classified as luminance cells based on their response to conventional subjective contours seemed to respond at least partly to the orientation of the subjective edges when a modified subjective grating was used (see Figure 18 for grating used, Figure 19 for recording). Stimuli used (cf. Figure 1, Chaper 2) in a few of our experiments had the same luminance component for both stimuli (hence termed iso-luminance subjective gratings) and hence any difference in response must be attributed to the subjective edges alone. Figure 20 shows one such cell's response to these subjective gratings that had the same luminance component across the stimulus set. The cell responded to the inducing lines in conventional subjective gratings (orthogonal inducing lines; data not shown), however, as the figure shows, it showed a clear orientation-specific response to a $0^{o}$ vertical subjective grating (vertical subjective edges, oblique incuding lines) of any direction. Figure 21 shows another luminance cell which responds to a $0^{o}$ vertical subjective grating (oblique inducing lines) with the subjective edges drifting left. Figure 22 shows another cell that responded best to a vertical $0^{o}$ subjective grating moving up and to the left. We recorded from several such luminance cells (i.e. cells that had earlier been classified as not responding to subjective edges at all) in V1 (n = 8) and found that more than half (5 cells) clearly preferred a

particular subjective orientation (and direction in some cells). These results show that V1 cells might respond even more robustly to other subjective contours within this class and the use of conventional subjective gratings (orthogonal inducing lines) may have caused fewer neurons to respond and with less strength to the subjective edge than otherwise capable of.

*Columnar arrangement of responses to subjective gratings.*

Figure 23 is the summary of penetrations made in both V1 and V2 combined. As can be seen, most cells in the same column had the same subjective grating orientation preference. Thus, cells in the same column of V1 and V2 shared the same response to subjective stimuli. A column either responded to the subjective edges in the stimulus, showed no response to subjective stimuli of any orientation, or responded to the inducing lines. Cells in the same subjective contour column shared the same subjective orientation preference. Cells in the same non-subjective column responded exclusively to the inducing lines. Cells in a non-responsive column all responded weakly to subjective grating stimuli of all orientations and could not be driven either by the subjective edges or by the inducing lines.

*Orientation tuning of luminance and contour cells.*

We computed the orientation tuning index for luminance (cells whose orientation preferences for luminance and subjective gratings differed by $90^{o}$) and contour cells (cells whose orientation preferences for luminance and subjective gratings was $\leq 22.5^{o}$) to luminance and subjective gratings. The mean orientation tuning across the ensemble

of contour cells (n = 12) for luminance gratings was two-fold higher (0.72) than the orientation tuning for subjective gratings (0.34), and the difference between the two was statistically significant (two-tailed t-test, $p < 0.001$). Figure 24 shows a cell-by-cell comparison of luminance and subjective orientation indices for contour cells. Most contour cells (11/12) had sharper orientation tuning for luminance than for subjective gratings. Thus, contour cells responded strongly to the subjective edges, however the responses to luminance gratings displayed sharper orientation selectivity as compared to the responses for subjective gratings. Similarly, for luminance cells (n = 12), the mean orientation tuning across the ensemble of cells for luminance gratings was higher (0.53) than the orientation tuning for subjective gratings (0.38), and the difference between the two was also statistically significant (two-tailed t-test, $p < 0.005$). As Figure 25 shows, the orientation indices of most cells (11/12) for subjective gratings was lower than the corresponding indices for luminance gratings. Thus, luminance cells were significantly more sharply orientation-tuned for luminance than for subjective gratings. Collectively, contour cells exhibited a sharper orientation-specific response for square-wave luminance gratings than luminance cells (mean orientation index = 0.72 for contour cells, .53 for luminance cells; Figure 26) and the difference in orientation selectivity between the two groups was statistically significant (two-tailed t-test, $p < 0.05$). Thus, contour cells seem to be more selective for bars and edges of a particular orientation than luminance cells.

## DISCUSSION

*V1 vs. V2: RF properties and its possible effects on differences in response to subjective contours.*

Hubel and Wiesel's initial findings of the presence of hypercomplex (also termed end-stopped) cells in area V2 and the absence of these cells in V1 (Hubel and Wiesel '65), and the presence of simple cells only in V1 have since been disproved. Several investigators (Gilbert, '77, Henry et al. ,'78, Kato et al., '78) have since shown that V2 also contains hypercomplex neurons. The proportions of simple and complex cells in V1 and V2 have also been found to be nearly the same (25% in V1 and 31% in V2, Ferster '81). Others have shown that neurons in V2 can be classified into two groups similar to the simple and complex types described in V1 (Dreher and Cottee '75, Ferster '81, Hammond and Andrews '78, Harvey '80, Orban and Callens '77, Tretter et al. '75) and all agree that the receptive field types are the same in V1 and V2. However, the proportions may differ between V1 and V2 (Stone et al. '79, Orban '84). Using hand-held (Orban '84) and quantitative techniques (Kato et al.'78), it was found that there were about twice as many end-stopped cells in V1 than in V2. Several authors have showed that there is, in fact, a continuum between end-stopped and end-free cells, with cells showing varying degrees of end-stopping (Bodis-Wollner et al. '76, Gilbert '77, Henry et al. '78); hence there are many cells in cortex which show some degree of end-stopping (40-50% subserving central vision in V1 according to one estimate, Kato et al. '78). Indeed, there are many sources for end-stopped input to V2 cells - both from V1 through corticocortical

projections and from V2 via intracortical connections. V1 cells may also receive end-stopped input from orthogonally oriented end-stopped cells in V1. End-stopped cells are believed to provide the input to cells that respond to subjective contours according to one of the models proposed for explaining response to subjective contours (von der Heydt and Peterhans '89, Peterhans and von der Heydt '89).

Most neurons in V1 and V2 (>90%) are orientation-selective, however the sharpness of orientation tuning differs between the cells in the two areas. As a population, cells in V1 have sharper orientation tuning (as measured by half-width of tuning at half-height) as compared to the population of cells in V2 (Hammond and Andrews '78, Rose and Blakemore '74, Henry et al. '73, Heggelund and Albus '78). Greater orientation selectivity of V1 cells for luminance bars and edges may account partly for the proportionately higher cells in V1, as compared to V2, that respond to the luminance-defined inducing lines in the subjective gratings.

The receptive fields in V2 tend to be larger than those in V1, and this difference increases with increasing visual-field eccentricity (Orban and Kennedy '82, Wilson and Sherman, '76). At an eccentricity of 10°, receptive fields of V1 cells typically are 1-3° across whereas fields of V2 cells are 3-5° across; at an eccentricity of 30-40°, receptive fields of V1 cells

typically are 3-4° across whereas fields of V2 cells are 8-10° across. The larger receptive fields of V2 cells allows for the cell to view a higher number of inducing lines of the subjective grating. It has been shown both psychophysically in cats (de Weerd et al. '90) and physiologically (von der Heydt and Peterhans '89) that the subjective contour percept/response improves with increasing number of inducing lines. Thus, the larger receptive fields in V2 may, in fact, play some role in the population of V2 cells showing a stronger response to subjective contours than V1 cells. Of course, this hypothesis implies that a smaller fraction of V2 cells encountered at low visual-field eccentricities should show a strong response to subjective contours than V2 cells at higher eccentricities, a prediction which can be tested experimentally. It should be noted that we have investigated V1 cells with higher spatial frequency inducing lines (1.0 cycles/deg.) but have not found any enhancement in the response to subjective contours as compared to the lower spatial frequency stimulus (0.45 cycles/deg.).

In addition, cells in V2 have lower spatial resolutions and lower optimal spatial frequencies than in V1 (Movshon et al. '78, Albus '80). Velocity tuning also differs among neurons in the two areas; in general, cells in V2 respond to higher stimulus velocities than cells in V1.

*Distinguishing properties of contour cells.*

Is it possible to classify contour cells based on other receptive field properties? If so, one might be able to predict what the cell's response to subjective contours will be simply by carefully charting out some key receptive field properties. Redies et al. ('86) claimed that all (and only) the standard complex cells that they recorded from (5 cells) responded to the phase shift in the subjective stimulus. Moreover, by the same criterion, none of the simple cells they recorded from responded to subjective contours. On the other hand, we find that only 17% (4 out of 23 cells) of complex cells we recorded from responded vigorously to subjective contours (contour cells, orientation difference = $0^o$). From our sample of simple cells (4 cells), one cell responded vigorously to subjective contours, and one cell showed a response to subjective orientations with a preference that was $45^o$ away from the optimal luminance orientation. Thus, a fraction of complex as well as simple cells respond to subjective contours. 16% (5 out of 31 cells) of non end-stopped cells responded to subjective contours. Thus, the assertion that only end-stopped cells can show a robust response to subjective contours is not borne out by the data. Finally, we did not find any correlation between a cell's laminar location and ability to respond to subjective contours since contour cells were found in both superficial as well as deep layers of the cortex.

We did find, however that contour cells were significantly more likely to have sharper orientation tuning than cells that did not respond to subjective contours (luminance cells; Figure 26). Of 8 cells that were strongly orientation-selective (0.8 orientation tuning index or higher), six were contour cells and only two were luminance cells. Of the cells that demonstrated poor orientation selectivity for luminance bars (0.5 orientation tuning index or lower), most cells (7/9) were luminance cells. Thus, a cell that demonstrates a sharp orientation tuning for luminance bars and edges is likely to respond strongly to subjective contours (contour cell), and a cell that demonstrates poor orientation tuning will more likely than not respond weakly or not at all to subjective contours (luminance cell). A more deterministic criterion which will pre-classify cells as being contour or luminance by calculating their orientation selectivity to luminance bars (an upper threshold above which a cell will certainly be a contour cell, a lower threshold below which a cell will certainly be a luminance cell) is required.

*Partial responses of V1 cells to subjective edges.*

A subjective grating contains both a luminance component formed by the inducing lines and a subjective component composed of regularly spaced subjective edges. A large number of cells in V1 prefer a subjective grating whose orientation preference is $\pm 45^{o}$ (or less) offset from the cell's orientation preference for luminance gratings. The $45^{o}$ orientation difference can be explained by a combination of responses to subjective and

luminance components. Consider a luminance orientation tuning curve and a pure subjective orientation tuning curve (no luminance variable) for a hypothetical cell which peak at the same orientation for both. Since the orientation preferences for both coincide, by definition, this hypothetical cell is a subjective contour cell. In a conventional subjective grating stimulus, the luminance and subjective components are mutually orthogonal and hence the tuning curves are offset by 90°. Since a conventional subjective grating contains both components, the cell's response to this stimulus can be considered to be a vector sum of responses to the two components, and thus a superposition of the two tuning curves. The resulting tuning curve will then have a peak at 45° orientation difference, indicating a response to both the luminance and subjective components of the subjective grating stimulus.

*Responses of luminance cells to subjective gratings.*

If a cell responds to the inducing lines in a conventional subjective grating with orthogonal inducing lines, as indicated by a 90° difference between its luminance and subjective orientation preferences, the cell is classified as a luminance cell - a cell that does not respond to the subjective edges. This does not necessarily imply that luminance cells do not convey any information at all about the presence of a subjective edge. A cell can provide information about the presence of a subjective edge in different ways depending on the strengths of the cell's responses to the luminance and subjective components of the stimulus relative to one another (cf. Chapter 2, discussion on

orientation difference maps). Any modulation in response owing to the presence of subjective edges contains some information about them. Signaling the orientation of the edge irrespective of whether the edge is luminance or subjective is one (very intuitive) way of informing other cells/areas of the brain about subjective contours. On the other hand, luminance cells do not show any orientation shift towards the orientation of the subjective edges, however their orientation selectivity for subjective gratings is significantly lower than for luminance gratings (Figure 25). If luminance edges are what luminance cells respond to regardless of the stimulus (whether luminance or subjective gratings), why then is there a higher degree of orientation selectivity for luminance gratings than for the luminance edges in subjective gratings? One may consider several possible reasons for this "detuning" observed in the luminance cells' response. Direction of motion may be a possibility since the luminance gratings are drifted perpendicular to the luminance edges whereas subjective gratings are drifted parallel to the luminance edges (inducing lines). We have seen the effects of direction on the response of contour cells and so this possibility cannot be eliminated. The overall luminance of a square-wave grating (50% duty cycle) is higher than that of luminance edges one pixel thick (<10% duty cycle) in a subjective grating stimulus, which may account for the sharper tuning for luminance gratings. However, the ratio of luminances of two square-wave gratings of any orientation is the same as the ratio of luminances of any two subjective

gratings (the ratio is one). So, there cannot be any *linear* effects due to the difference in overall luminance between square-wave luminance gratings and subjective gratings. A third possibilty may be the possibility of an orthogonal subjective edge which may suppress the response of the cell to its optimal luminance orientation. Recent studies in cat visual cortex (Kisvarday et al. '94, Kisvarday and Eysel '93) indicate that inhibitory connections may, in fact, connect not only iso-orientation domains but cross-orientation sites as well. Recent physiological studies (Knerim and van Essen '92, Lieke et al. '88, Grinvald et al. '94, Toth et al., in press) have shown that a when an optimally oriented area (bars or gratings) centered on the cell's receptive field is surrounded by a patch of orthogonal orientation, the cell's response is suppressed as compared to its response to the central optimally oriented patch alone. An orthogonally oriented subjective edge may also provide a suppressive effect on the cell's response. If this possibility is correct, a decrease in the cell's orientation selectivity when stimulated by a subjective grating can suggest the presence of another edge, possibly of orthogonal orientation; in the case of a subjective grating, the edge happens to be subjective.

Moreover, we have shown that luminance cells that earlier did not respond to the subjective edges of a conventional subjective grating did so and responded with a clear orientation preference when stimulated by an iso-luminance subjective grating cf.

Figures 20-22). Thus, responses of luminance cells to subjective gratings also carry information about subjective contours as do the rest of the cells in cortex; the amount of information and utitlity to other brain regions may vary from cell to cell.

*Similarities and differences between the extracellular signal and the optical signal.*

Several investigators have explored the relationship between the signal obtained with extracellular recording and the optical signal. Distributions of point spreads (PS = area of cat visual cortex activated by a minimal visual stimulus) measured with optical imaging which reflects both spiking and subthreshold activity, with those measured with extracellular electrodes, which reveal spiking activity alone were compared. The spiking PS represented only 5% of the area of activation, indicating that the remaining 95% was probably generated by subthreshold activation (Das and Gilbert '95). In another study (Toth et al. in press) done to explore the effects of surround stimuli on center activation, it was found that all but 6.8% of the activity in a central region of an intrinsic signal map is subthreshold in origin, and that subthreshold activity may therefore represent more than 1/2 of the maximum obtainable intrinsic signal activity. Thus, the optical signal is a mixture of both spiking neuronal activity and subthreshold activity of neurons from a much larger area. In V1 and in V2, the relative proportions of cells responding to subjective contours and pixels imaged that respond to subjective

contours are similar (cf. histograms in Chapters 2 and 3). Since it seems likely that optical activity sums both spiking and subthreshold activity, the data suggests that subthreshold responses to subjective contours may also be tuned in somewhat the same way as single-unit extracellular responses.

While the resolution of optical imaging across the cortical surface is excellent, the depth resolution is not nearly so good. The optical maps probably average the vascular activity in the cortex down to a depth of 600-900 μm (Malonek et al. '90) i.e. the supragranular layers. We have not systematically looked for differences in single-cell responses to subjective contours between superficial and deep layers; however we believe that our finding using single-unit recording, namely that responses to subjective contours are organized in columnar fashion, can only enhance the applicability of our imaging studies to infragranular layers.

## CONCLUSIONS

In conclusion, using stimuli identical to our imaging experiments, we found that the single-cell recording data were consistent with the imaging results. We found that some V2 neurons did indeed respond strongly to subjective contours. These cells responded

to subjective contours in a narrow parameter range and the direction of motion influenced the cells' response greatly. Fewer V1 cells respond to subjective contours compared to the cells in V2. We found that V1 cells, classified earlier as being luminance cells lacking a response to subjective contours showed instead a clear orientation-tuned response to subjective contours in which the luminance component of the stimuli could not differentially drive the cells' responses. Finally, cells in the same column of cortex (V1 and V2) showed similar response to subjective grating stimuli indicating columnar segregation of response to subjective contours.

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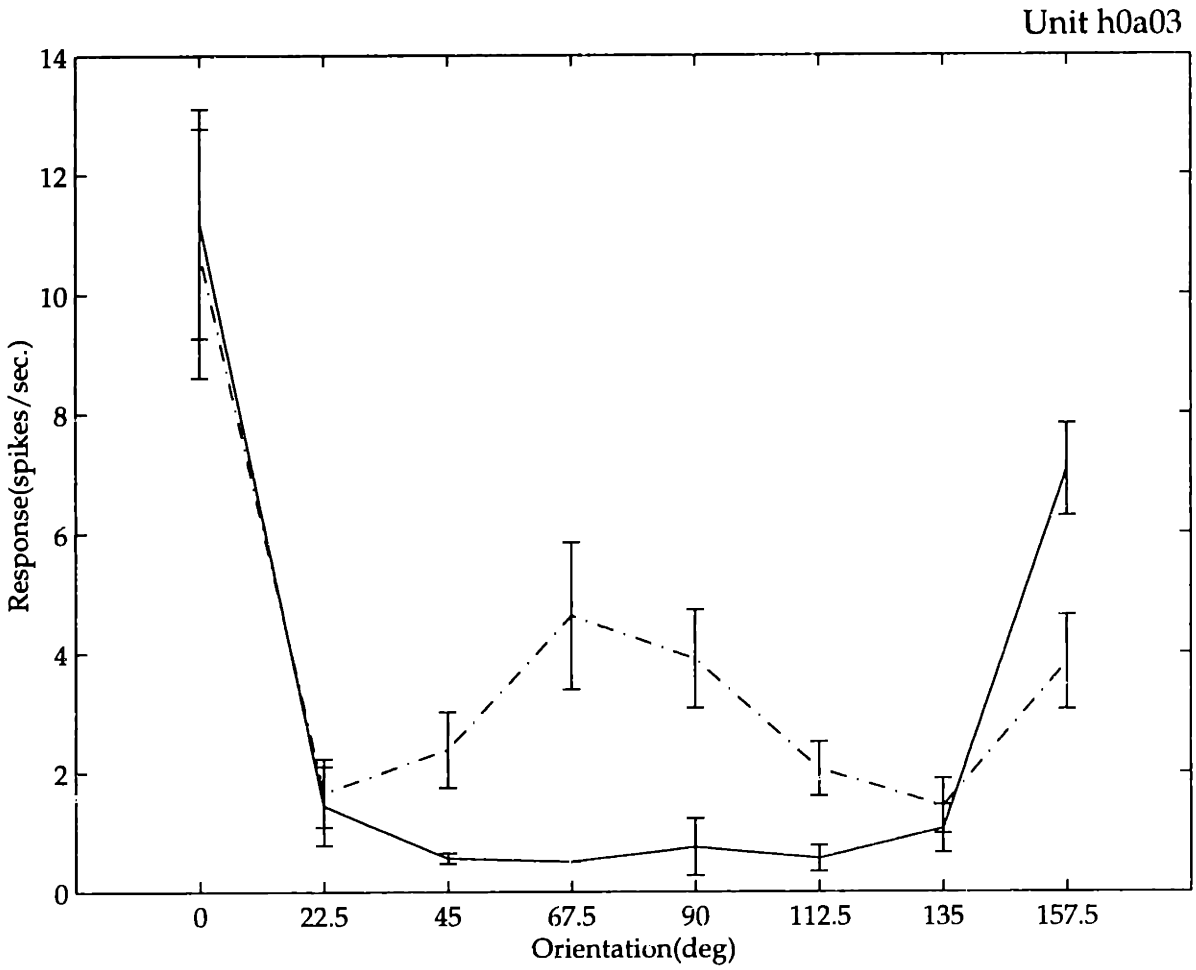

Unit h0a03
Response(spikes/sec.)
Orientation(deg)
0
2
4
6
8
10
12
14
0
22.5
45
67.5
90
112.5
135
157.5

Figure 1 A subjective contour cell (cf. subjective criterion, Chapter 3) in V2 obtained at 1288 μm depth below the cortical surface. The cell had a 12° X 10° receptive field at an eccentricity of 9° below the horizontal meridian, was complex and did not show any end-stopping. Luminance gratings (0.15 cycles/deg.) (continuous lines) and subjective gratings (0.15 cycles /deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency) (broken lines) were interleaved for a time duration of 2 sec./ stimulus for 8 stimulus trials. The responses were summed and averaged for each stimulus seperately. The neuron showed the same orientation preference for luminance and subjective gratings (0° vertical). The peak responses for luminance (11.19 spikes/stimulus) and subjective gratings (10.69 spikes/stimulus) were almost the same. The neuron shows some response to the orthogonal inducing lines as well, as indicated by the response at 90°.

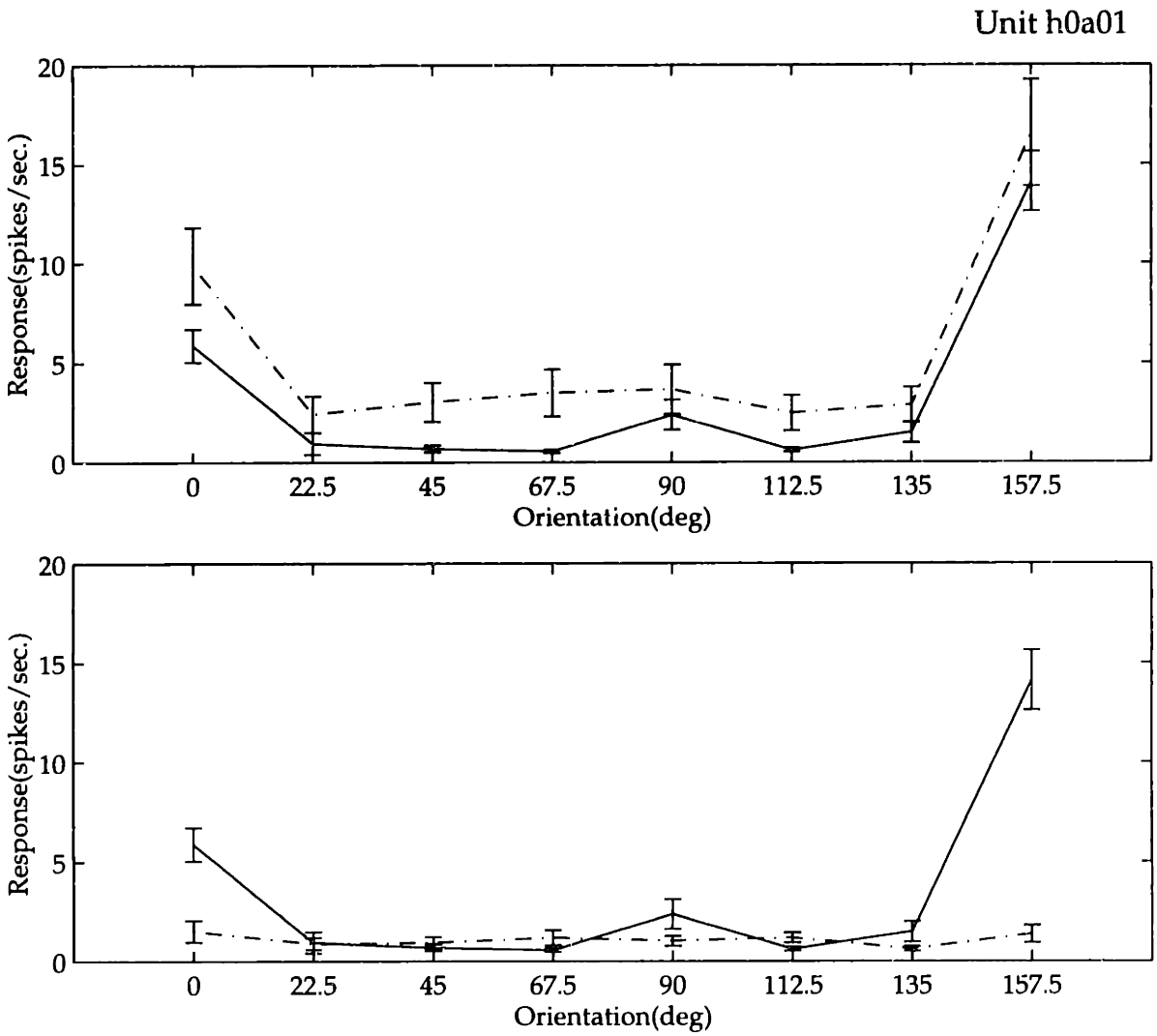
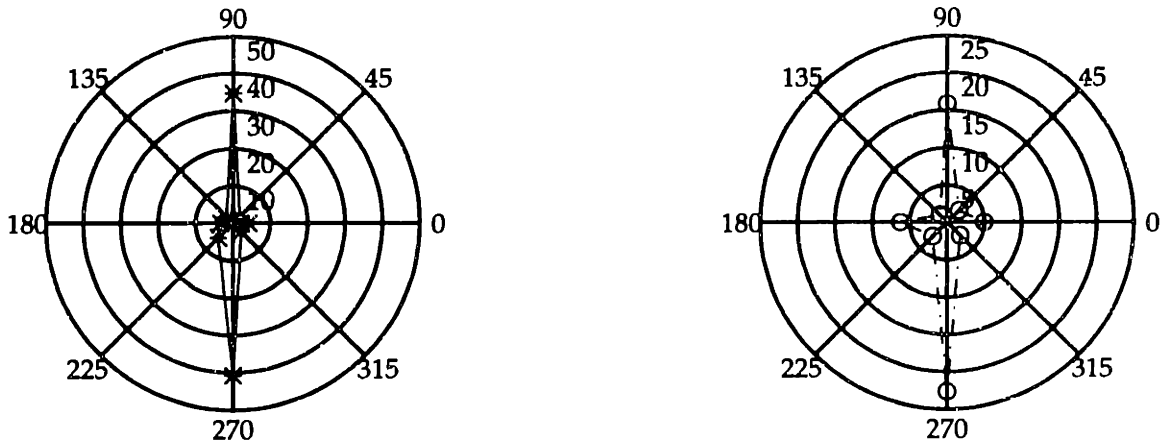

Unit h0a01
Response(spikes/sec.)
20
15
10
5
0
0
22.5
45
67.5
90
112.5
135
157.5
Orientation(deg)
Response(spikes/sec.)
20
15
10
5
0
0
22.5
45
67.5
90
112.5
135
157.5
Orientation(deg)

Figure 2 Another neuron encountered at 1153 μm depth in the *same* normal penetration as the cell in Figure 1. The cell was complex, did not show any end-inhibition and had a receptive field of similar size and location as the cell in Figure 2. Luminance gratings (0.15 cycles/deg., continuous lines) and subjective gratings (0.15 cycles /deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency, broken lines) were interleaved for a time duration of 2 sec./ stimulus for 8 stimulus trials. Luminance and subjective orientation preference were the same for this cell (157.5°), classifying it as a contour cell. Its orientation peaks for both stimuli differed from the orientation preferences for cell in Figure 1 for the same stimuli by only 22.5°. We found another cell in the same penetration whose subjective orientation preference (157.5°) was the same as for cell h0a03 in Figure 2.

B. The same neuron when presented with subjective gratings of higher subjective spatial frequency (0.5 cycles/deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency) (broken lines) gave a poor,weak, largely unoriented response to subjective gratings of all 8 orientations. The response to luminance gratings (2A, continuous lines) is shown for comparison.

A


Unit a0d01
90
135
45
180
0
225
315
270
50
40
30
20
10
25
20
15
10
5

B

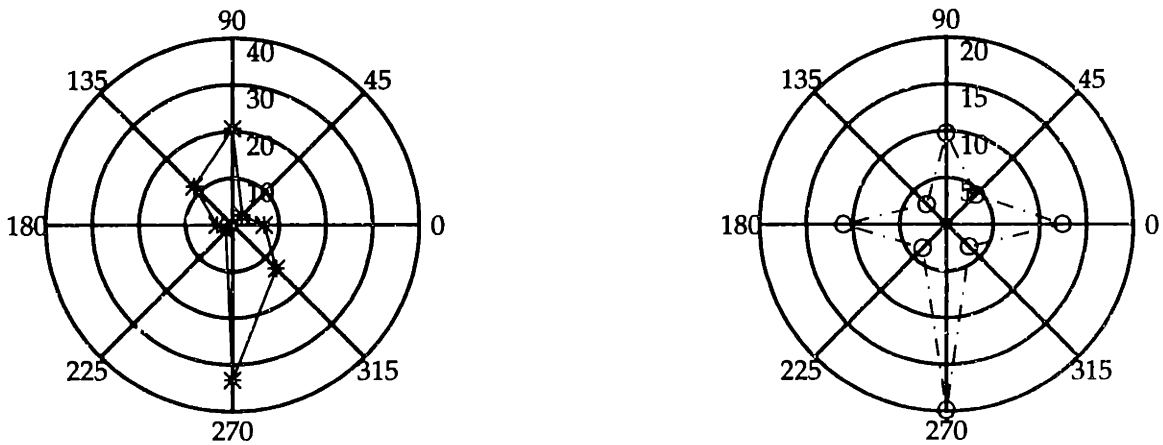

Unit a0d02
90
135
45
180
0
225
315
270
40
30
20
10
20
15
10
5

Figure 3 Subjective neurons from area V2

A. A V2 contour cell encountered at 160 μm depth that showed the same orientation preference for luminance and subjective gratings (90° horizontal). The responses are shown in a polar form where the angle from the horizontal gives the orientation angle and the distance from the origin gives the response magnitude (spikes/second). Peak response to subjective grating was about 40% of the response to the luminance grating.

B. Another V2 cell encountered at 286 μm depth in the same column that had identical orientation preferences for luminance and subjective gratings. However, this cell showed a strong response to the inducing lines as well.

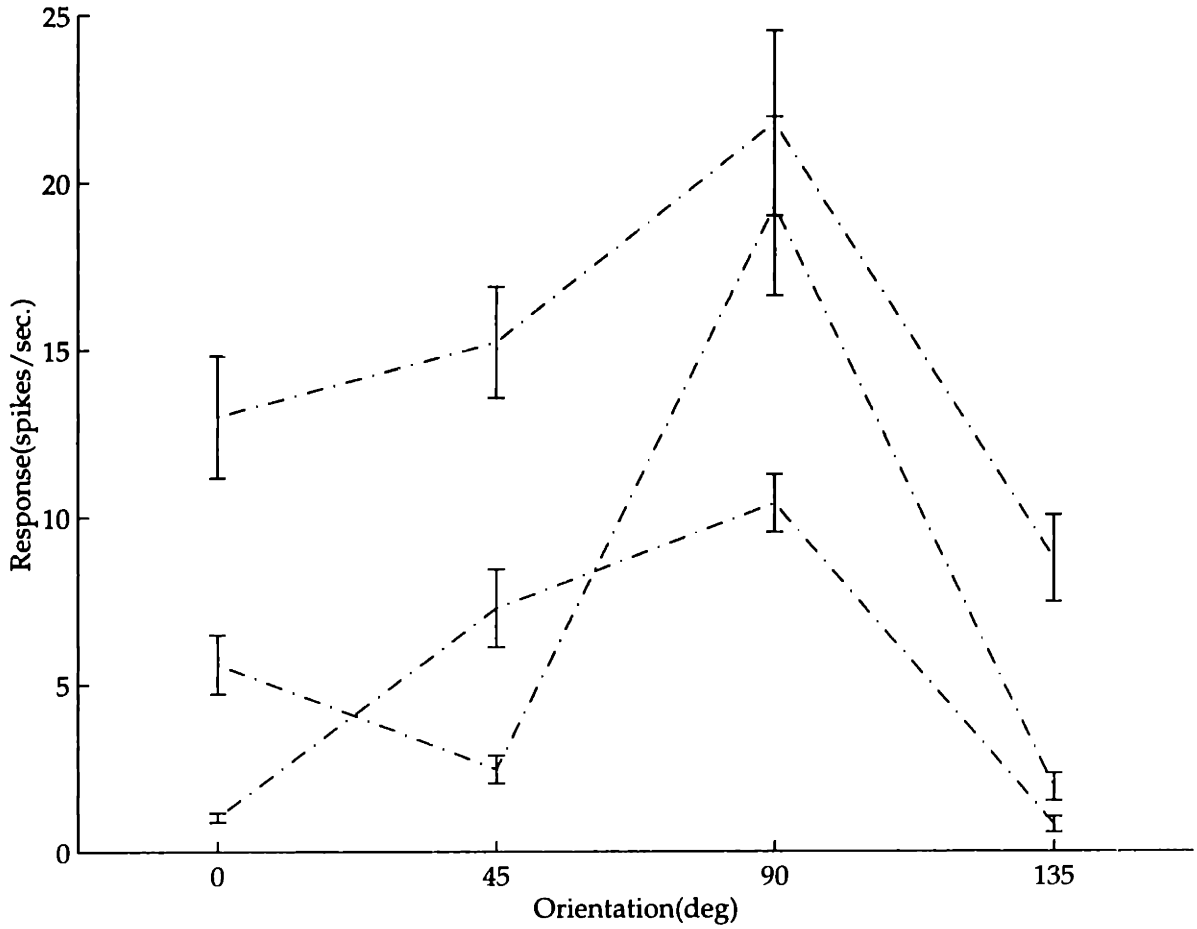

25
20
15
10
5
0
Response(spikes/sec.)
0
45
90
135
Orientation(deg)

Figure 4. V2 neurons in the same vertical penetration (column) share the same orientation preference for subjective gratings. All three neurons had the same orientation peak (90° horizontal subjective grating) and were obtained at depths 160 μm (cf. Figure 3A), 502 μm and 686 μm from the surface. We found a fourth neuron at depth 286μm that also responded best to 90° orientation (not shown for reasons of clarity; cf. Figure 3B, right for its subjective orientation tuning curve).

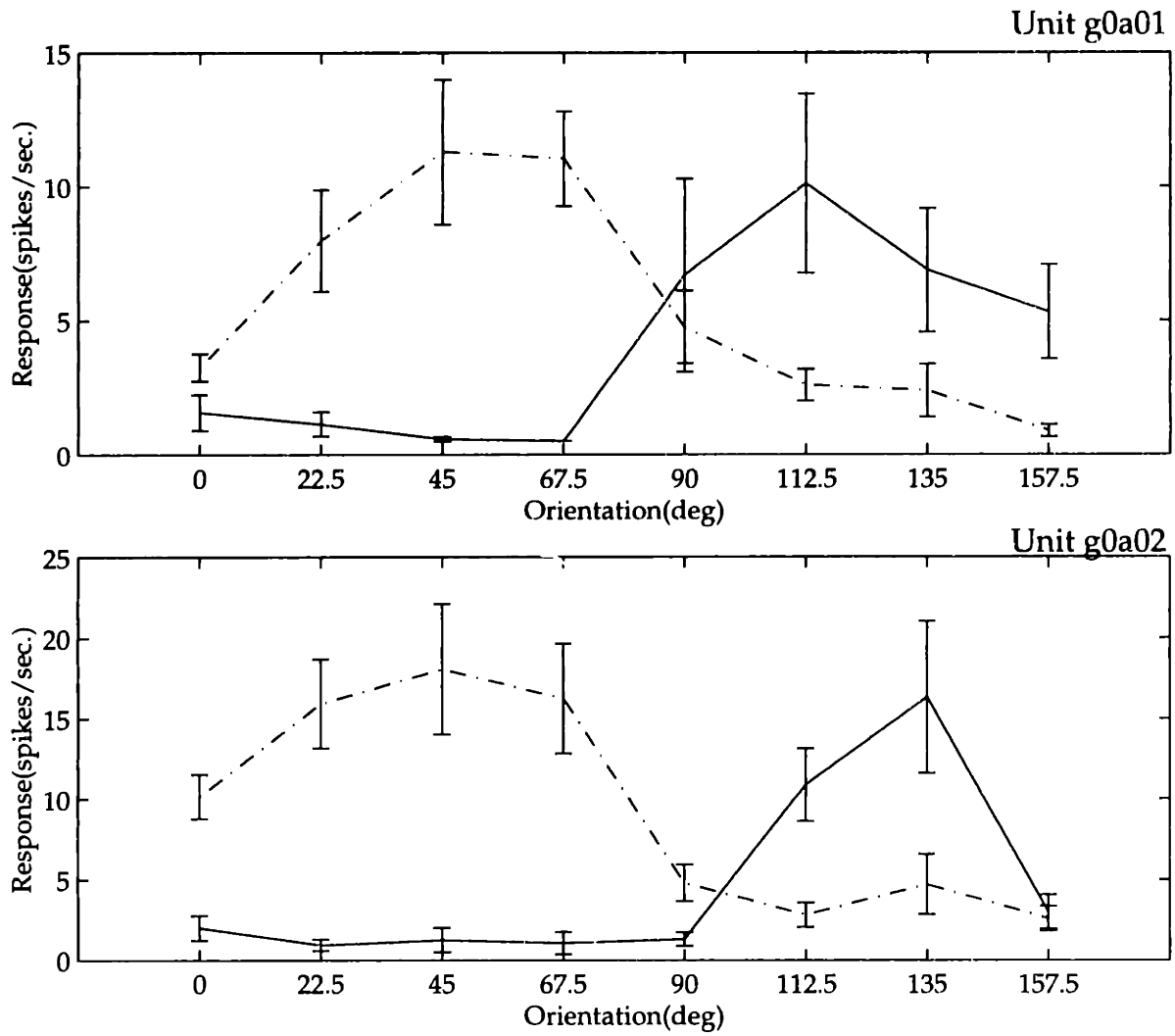
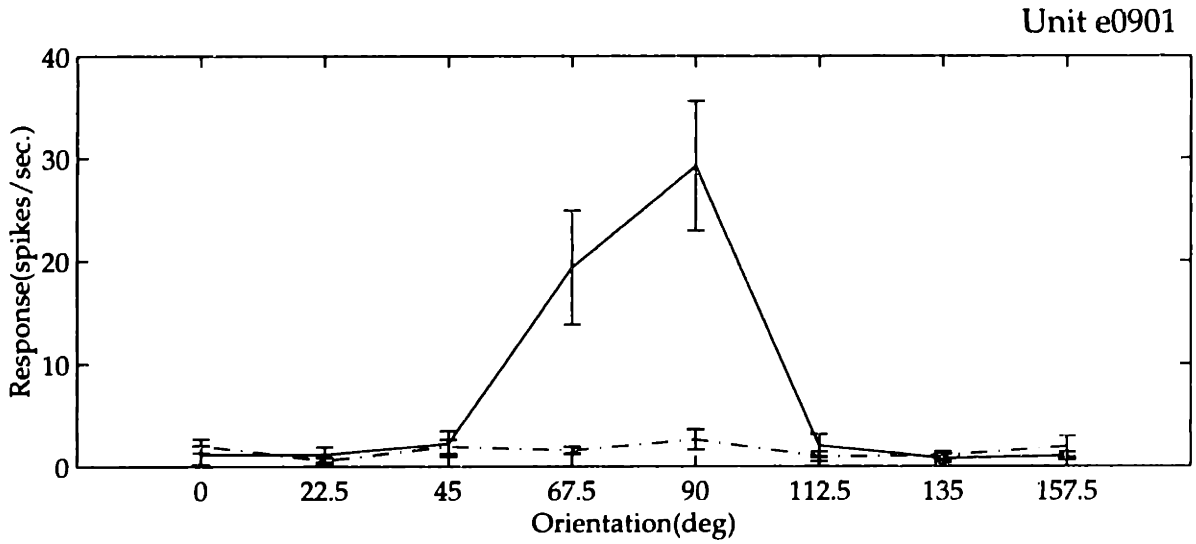

Unit g0a01
Response(spikes/sec.)
15
10
5
0
0
22.5
45
67.5
90
112.5
135
157.5
Orientation(deg)
Unit g0a02
Response(spikes/sec.)
25
20
15
10
5
0
0
22.5
45
67.5
90
112.5
135
157.5
Orientation(deg)

Figure 5. V2 neurons that responded predominantly to the inducing lines and ignored the subjective edge.

A. V2 neuron that showed orientation preference for a 112.5° luminance grating stimulus (luminance response shown in continuous lines) and a 45° subjective grating stimlus, (subjective response shown in broken lines) differing by 67.5°, showing a strong response to the inducing lines and a weak, if any, response to the subjective edge. Luminance gratings (0.15 cycles/deg.) and subjective gratings (0.15 cycles/deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency) were shown on the stimulus monitor.

B. Another V2 neuron belonging to the same column showed orientation preference for a 135° luminance grating stimulus and a 45° subjective grating stimlus, differing by 90°, showing a strong response to the inducing lines and ignoring the subjective edge altogether. Luminance gratings (0.15 cycles/deg., continous lines) and subjective gratings (0.15 cycles/deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency, broken lines) were shown here as well.


Unit e0901
Response(spikes/sec.)
40
30
20
10
0
0
22.5
45
67.5
90
112.5
135
157.5
Orientation(deg)

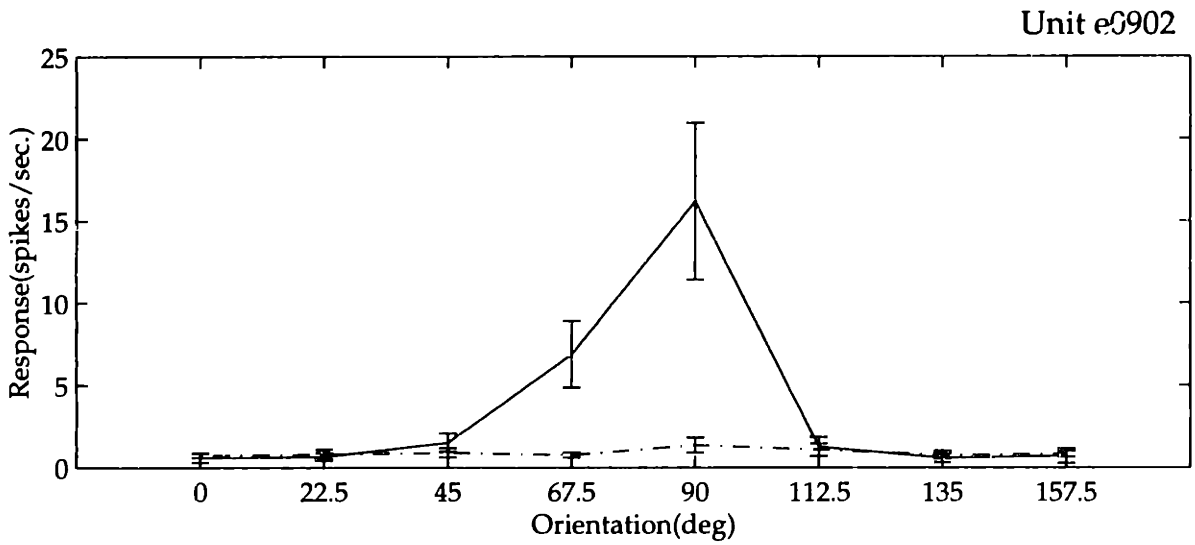

Unit e0902
Response(spikes/sec.)
25
20
15
10
5
0
0
22.5
45
67.5
90
112.5
135
157.5
Orientation(deg)

Figure 6. V2 neurons that did not respond to the subjective grating stimulus at all are shown. These neurons were silent to the presentation of subjective gratings stimuli of all orientations and were driven neither by the subjective edges or the inducing lines in the stimulus.

A. A V2 complex, non-end-stopped neuron encountered at a depth of 712 μm responded prefentially to 90° horizontal luminance grating and showed a weak, flat response to subjective gratings of all eight orientations. Luminance gratings (0.15 cycles/deg.) and subjective gratings (0.15 cycles /deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency) were shown on the stimulus monitor.

B. A V2 complex, non end-stopped neuron obtained at 807 μm depth also showed a flat response to subjective grating stimuli.

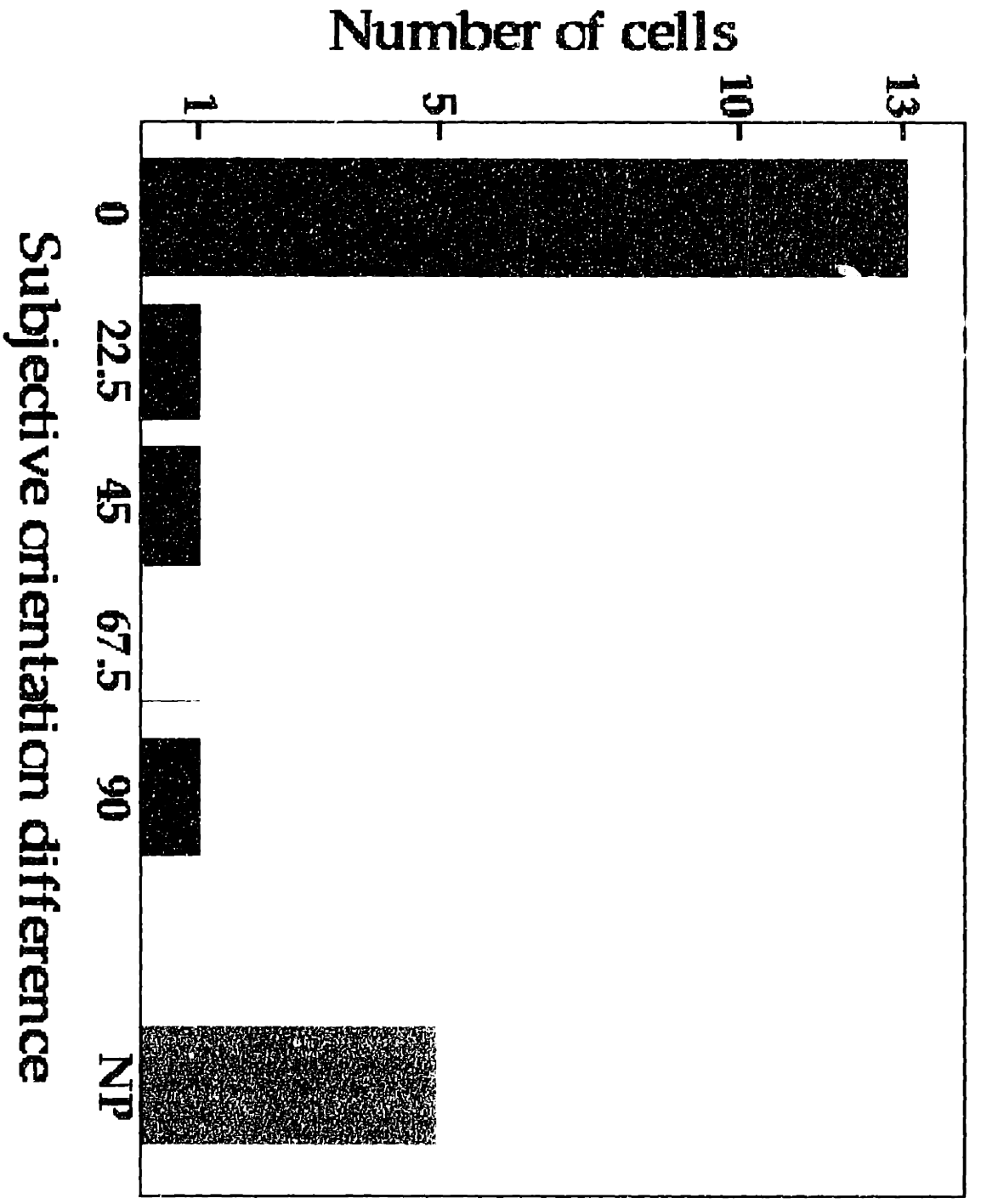

Number of cells
1
5
10
13
Subjective orientation difference
0
22.5
45
67.5
90
NP

Figure 7. Frequency histogram of subjective orientation preference of iso-columnar cells in V2. For each vertical penetration (column), the orientation preference of the column was determined by finding the subjective orientation preference of the majority of cells in the penetration. Then for each cell recorded within the column, the difference between its preferred subjective orientation and that of the column was obtained. This procedure was done anew for each separate penetration. Columns in which all the cells we found responded solely to the inducing lines in the subjective grating were discarded (columnar organization of luminance orientation preference). Only penetrations in which we recorded from 2 cells or more have been included in the histogram. A cell count of subjective orientation preference difference across all columns combined was maintained and plotted in figure. Of 21 cells we encountered in V2 (5 columns): 13 cells (62%) had the same orientation preference for subjective gratings as the rest of the cells in the column, 1 cell (5%) was within 22.5° of the preferred subjective orientation, 1 cell (5%) was within 45° of the preferred subjective orientation and 1 cell (5%) responded best to the orthogonal orientation of the subjective grating as the rest of the cells in the column. 5 cells (23%) had no subjective orientation preference.

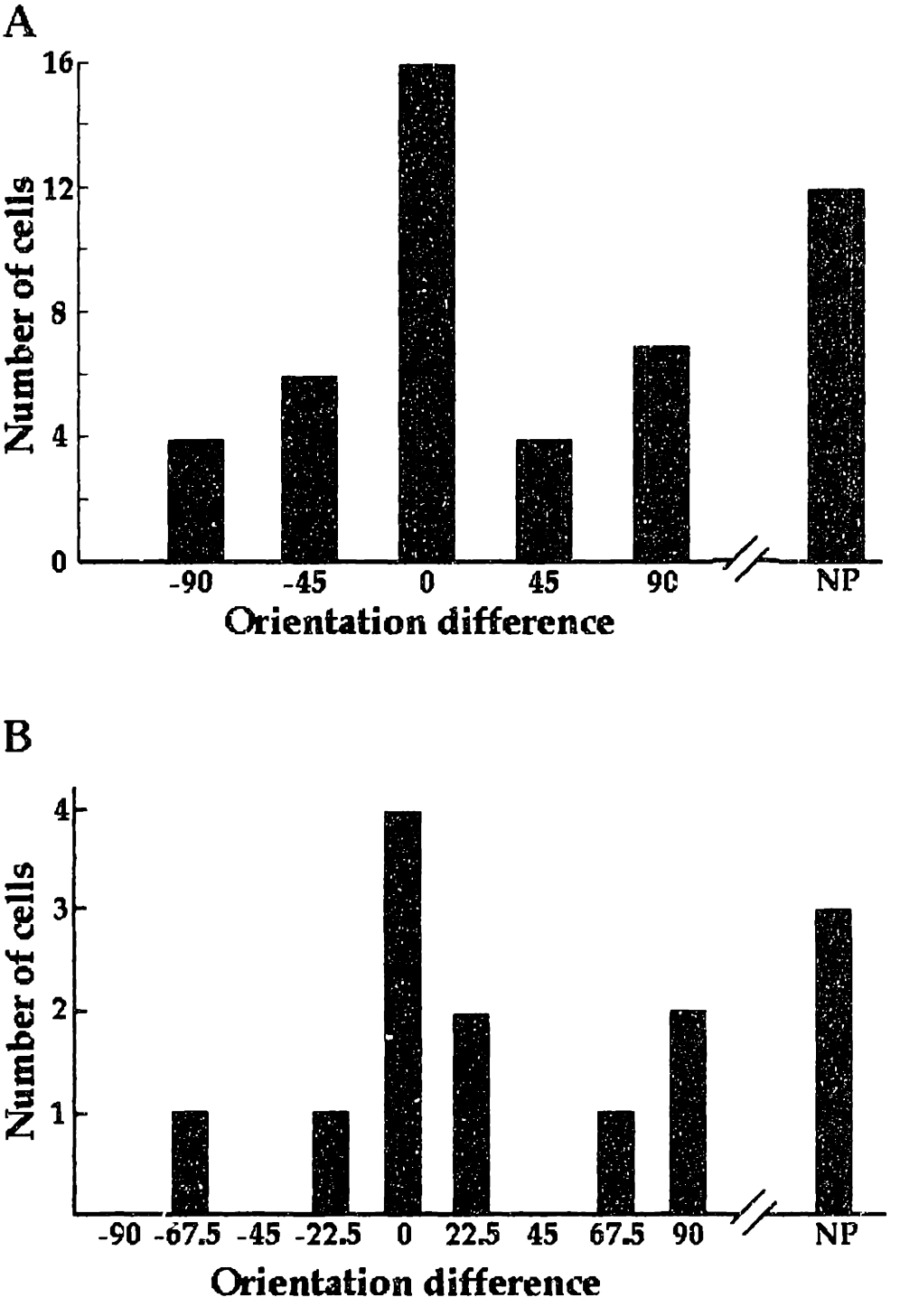

A
16
12
8
4
0
Number of cells
-90
-45
0
45
90
NP
Orientation difference
B
4
3
2
1
Number of cells
-90
-67.5
-45
-22.5
0
22.5
45
67.5
90
NP
Orientation difference

Figure 8.

A. Frequency histogram of the difference in orientation preference between luminance and subjective gratings of V2 neurons (n = 49). Neurons that had the same orientation preference for luminance and subjective gratings were binned into the 0° class (16 cells, 33%), neurons whose difference in orientation preference between luminance and subjective gratings differed by either 22.5° (8 orientations) or 45° were binned into the ±45° class (the sign was given by (preferred $orientation_{luminance}$ - preferred $orientation_{subjective}$)) (10 cells, 20%), and those neurons in which the difference between the two stimuli differed either by 67.5° (8 orientations) or 90° were binned into the 90° class (11 cells, 22%). Neurons that were silent to the subjective grating stimuli are shown in red (no subjective preference, 12 cells, 24%) and did not respond to the subjective edges or the inducing lines in an orientation-specific manner.

B. Frequency histogram of orientation preference difference for a subset of V2 neurons (n = 14) at a finer orientation resolution. These cells are a subset of the cells shown in A. Luminance and subjective gratings of eight orientations (22.5° apart) were used for the cells in this histogram.

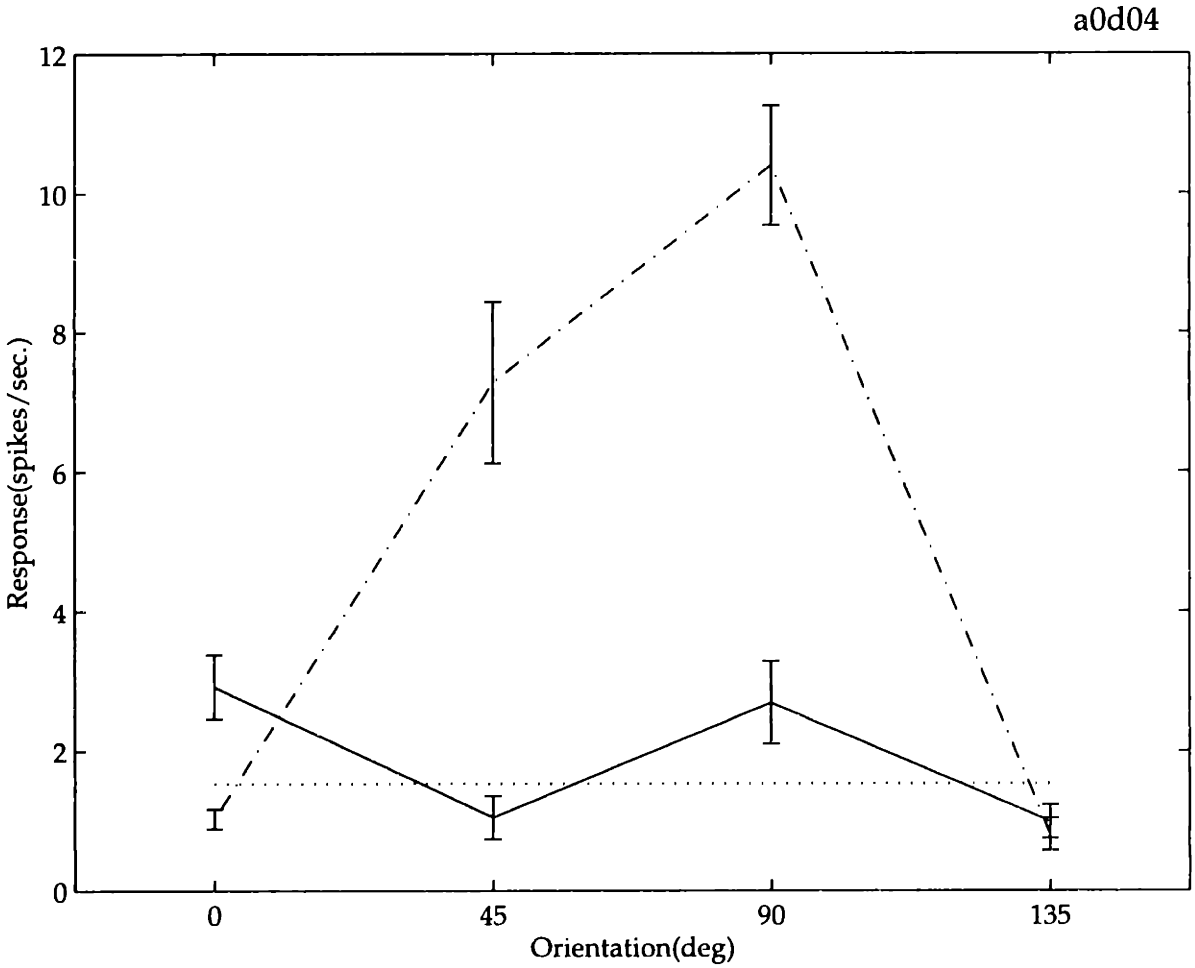

a0d04
12
10
8
6
4
2
0
Response(spikes/sec.)
0
45
90
135
Orientation(deg)

Figure 9. A V2 neuron that had sharp orientation tuning for subjective gratings (90° orientation preference) and poor tuning for luminance gratings. The spontaneous firing rate of the cell was 1.53 spikes/sec. We found neurons (2/28) that had sharp orientation tuning for subjective gratings and broader tuning for luminance gratings. Thus, there may exist neurons in V2 that respond exclusively to subjective grating stimuli.

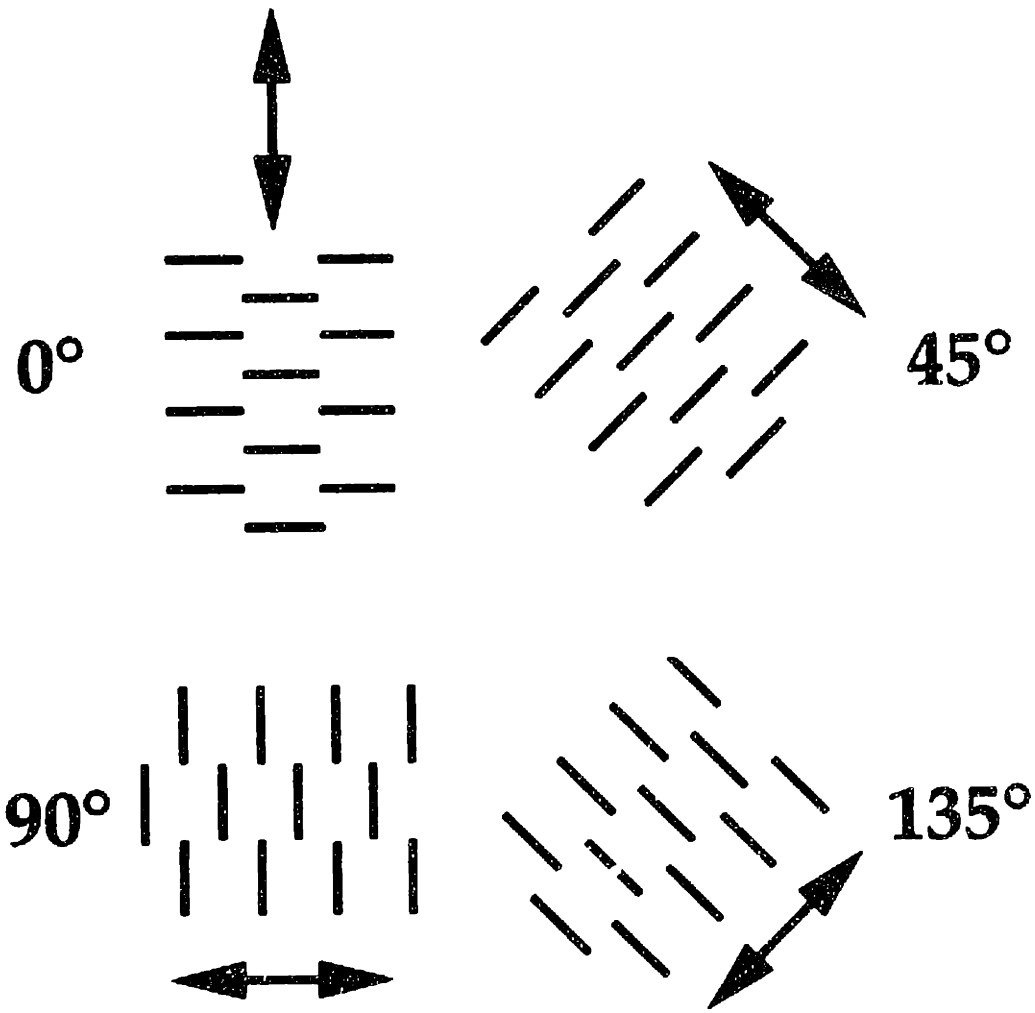

0°
45°
90°
135°

Figure 10. Subjective gratings in which the direction of motion is orthogonal to the inducing lines and parallel to the subjective edges.

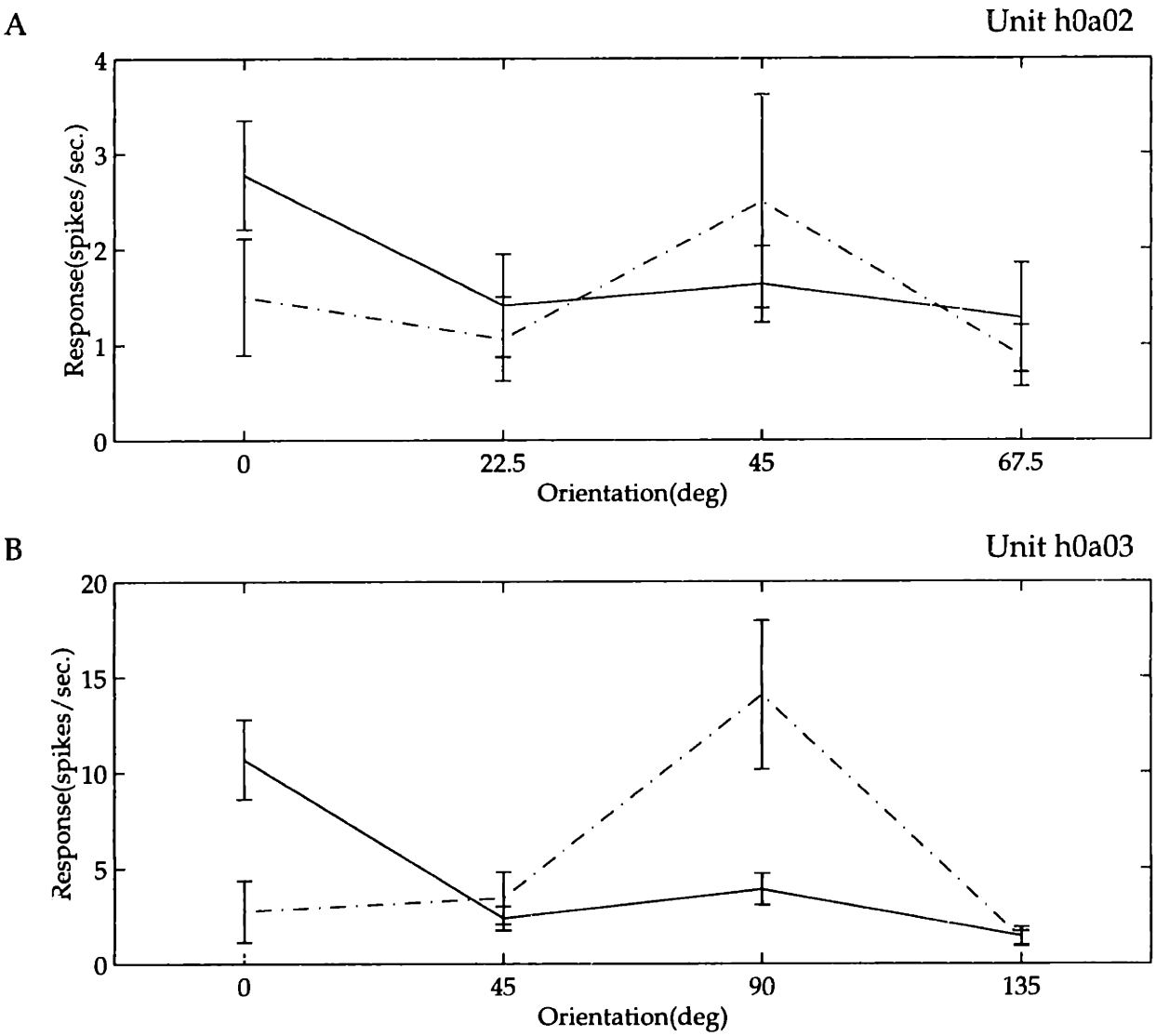

A
Unit h0a02
Response(spikes/sec.)
0
1
2
3
4
0
22.5
45
67.5
Orientation(deg)
B
Unit h0a03
Response(spikes/sec.)
0
5
10
15
20
0
45
90
135
Orientation(deg)

Figure 11. Responses of two contour cells to subjective gratings drifted either parallel to the inducing lines (continuous lines) or orthogonal to them (broken lines). Stimuli are shown in Chapter 2, Figure 2 and Figure 10 (above).

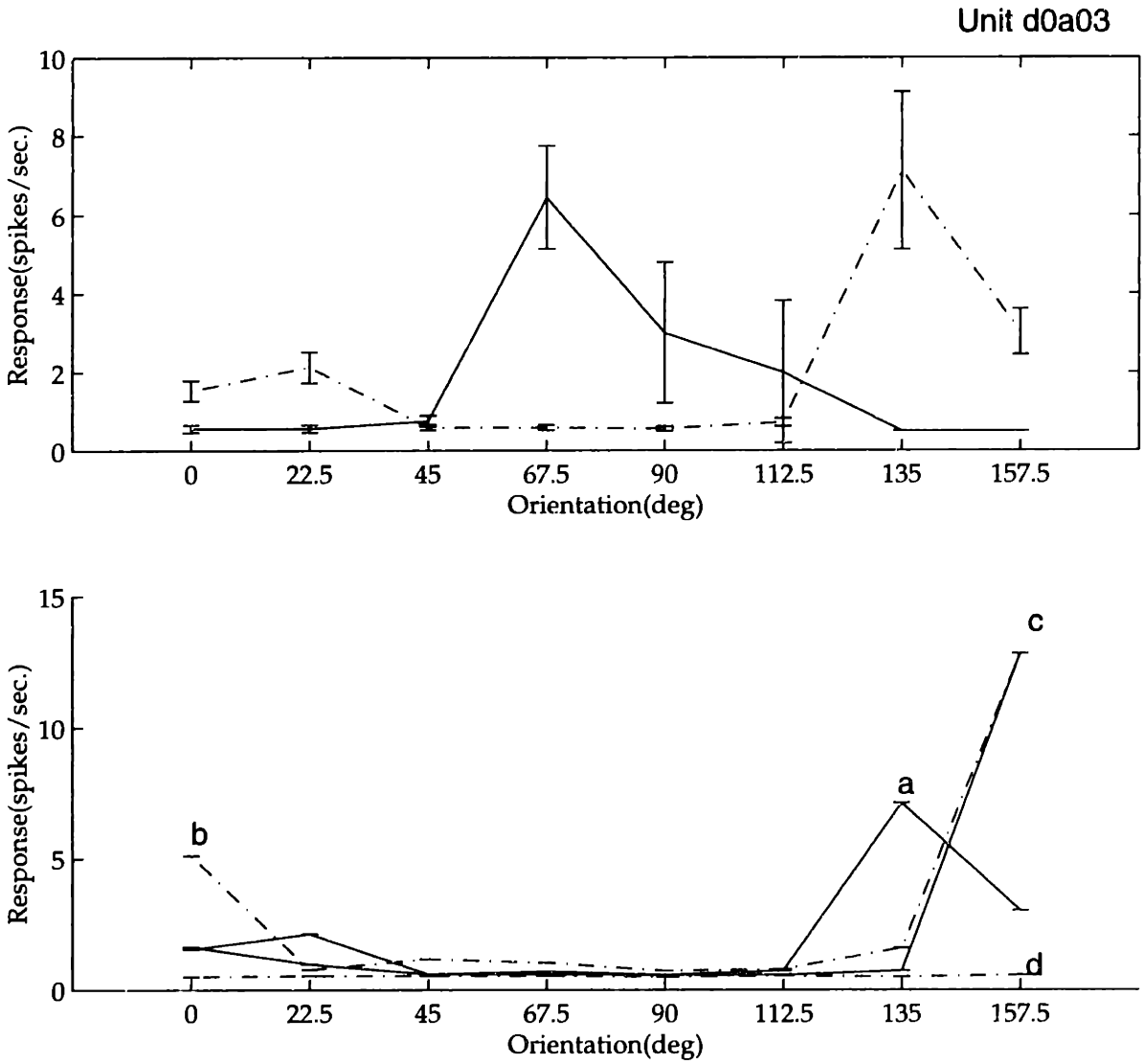

Unit d0a03
Response(spikes/sec.)
Orientation(deg)
0
22.5
45
67.5
90
112.5
135
157.5
a
b
c
d

Figure 12.

A. A complex, non end-stopped neuron recorded from area V1 that responded preferentially to a 67.5° luminance grating and a 135° subjective grating is shown. Thus, the neuron responded strongly to the inducing lines. Luminance gratings (0.5 cycles/ deg.) and subjective gratings (0.5 cycles /deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency) were shown on the stimulus monitor.

B. The neuron did not change subjective orientation preference with change in stimulus parameters. The following four sets of stimulus parameters were tried a) subjective spatial frequency - 0.5 c/deg., inducing lines spatial frequency 0.45 c/deg., b) subjective spatial frequency - 0.5 c/deg., inducing lines spatial frequency 1.5 c/deg.,c) subjective spatial frequency - 1.0 c/deg., inducing lines spatial frequency 1.5 c/deg., d) subjective spatial frequency - 0.25 c/deg., inducing lines spatial frequency 1.5 c/deg. - none of which changed the subjective response of the cell. The cell either retained the same subjective orientation preference or remained silent for the stimulus set. The cell never changed modes to become a "contour" cell.

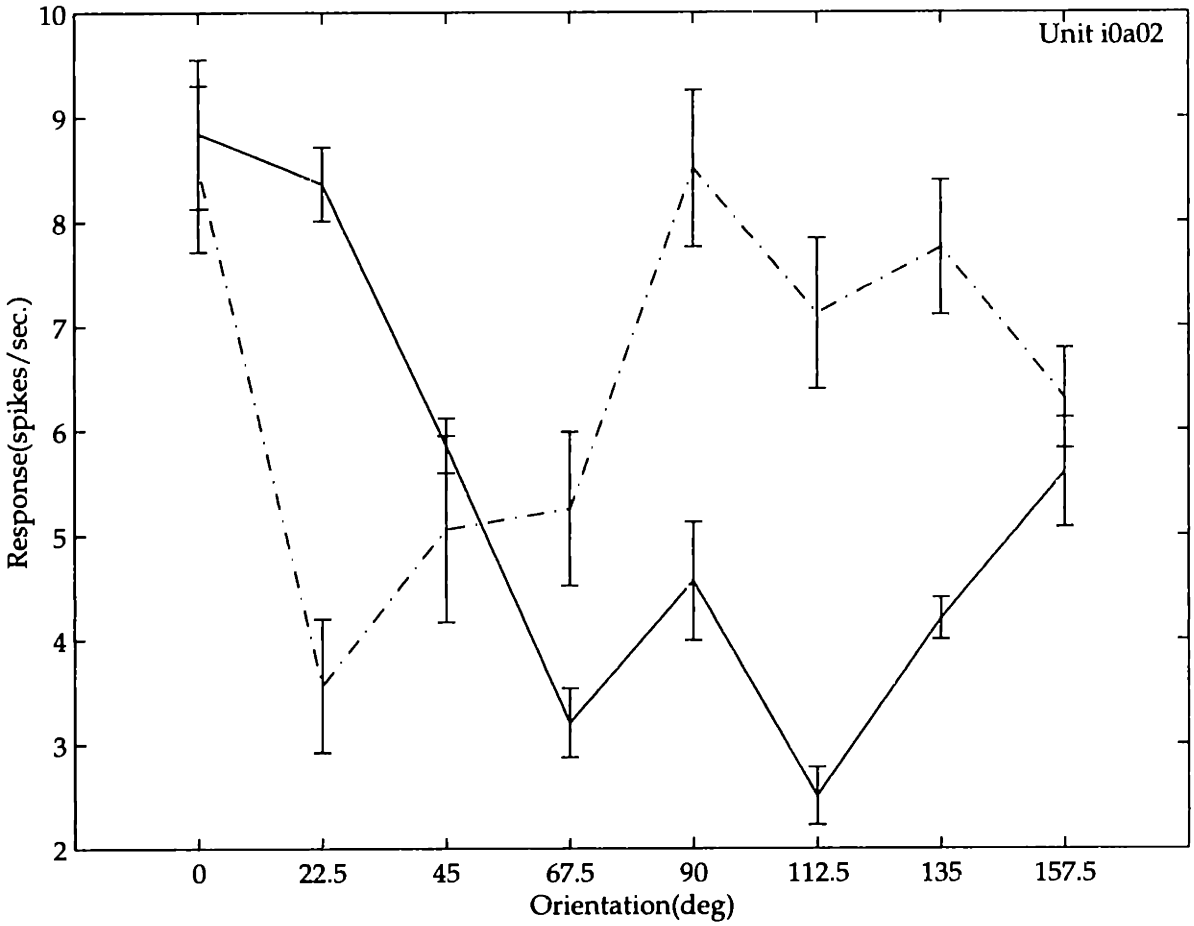

Unit i0a02
Response(spikes/sec.)
Orientation(deg)
10
9
8
7
6
5
4
3
2
0
22.5
45
67.5
90
112.5
135
157.5

Figure 13. A complex, non end-stopped V1 cell encountered in the deep layers that responded both to the subjective edges and the inducing lines of the same orientation with equal strength. The cell preferred a luminance grating of $0^{o}$ orientation. The orientation tuning curve for subjective gratings had two peaks - at $0^{o}$ and $90^{o}$ orientations. The displayed tuning curves for luminance and subjective gratings are normalized to their respective peak values. Luminance gratings (0.5 cycles/deg.) and subjective gratings (0.5 cycles /deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency) were shown on the stimulus monitor. The cell had a tuning peak at $112.5^{o}$ for a subjective grating of .15 cycles/deg. subjective frequency (not shown).

Unit a0c04

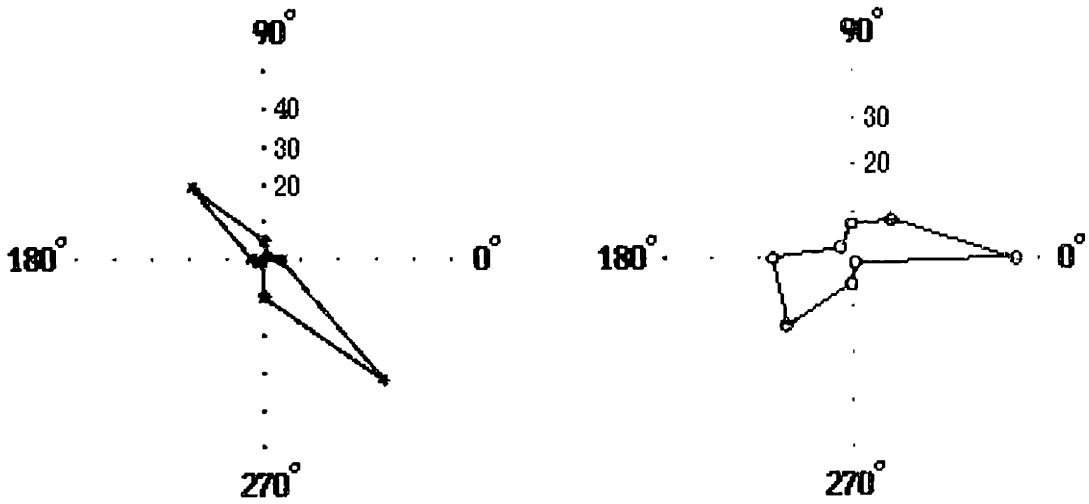
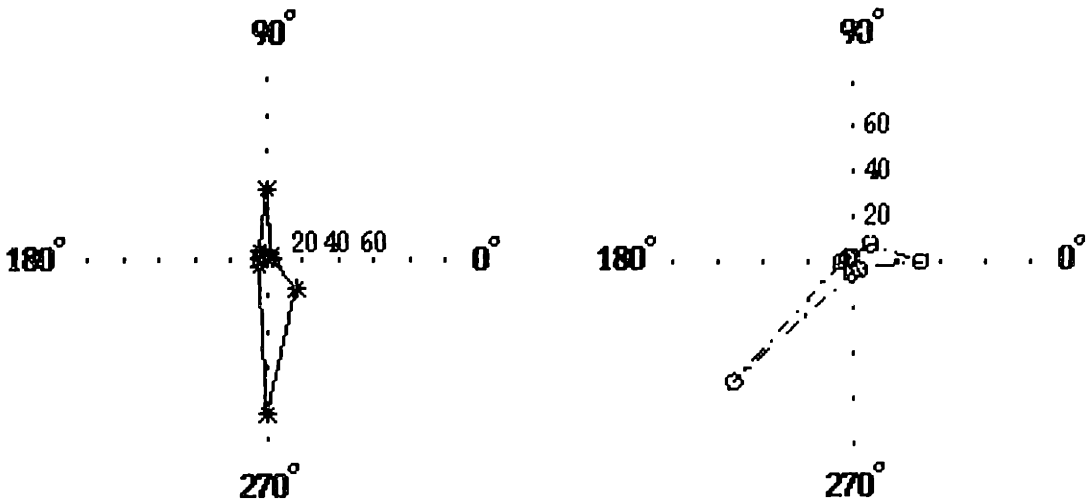

90°
40
30
20
180°
0°
270°
Luminance gratings
90°
30
20
180°
0°
270°
Subjective gratings

Figure 14. An end-stopped V1 cell that responded to a combination of the subjective edges and the inducing lines in the subjective grating. The cell preferred a luminance grating of 315° direction and subjective grating of 0° direction. Luminance gratings (0.5 cycles/deg.) and subjective gratings (0.5 cycles/deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency) were shown on the stimulus monitor. Thus, the cell preferred a subjective grating that was 45° off from the cell's preferred luminance grating orientation.

Unit a0c02




Luminance gratings

Subjective gratings

Figure 15. Another complex, end-stopped V1 cell that also responded to a combination of the subjective edges and the inducing lines in the subjective grating. The cell preferred a luminance grating of 270° direction and subjective grating of 225° direction. Luminance gratings (0.5 cycles/deg.) and subjective gratings (0.5 cycles/deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency) were shown on the stimulus monitor. Thus, the cell preferred a subjective grating whose orientation was 45° off from the cell's preferred luminance grating orientation.

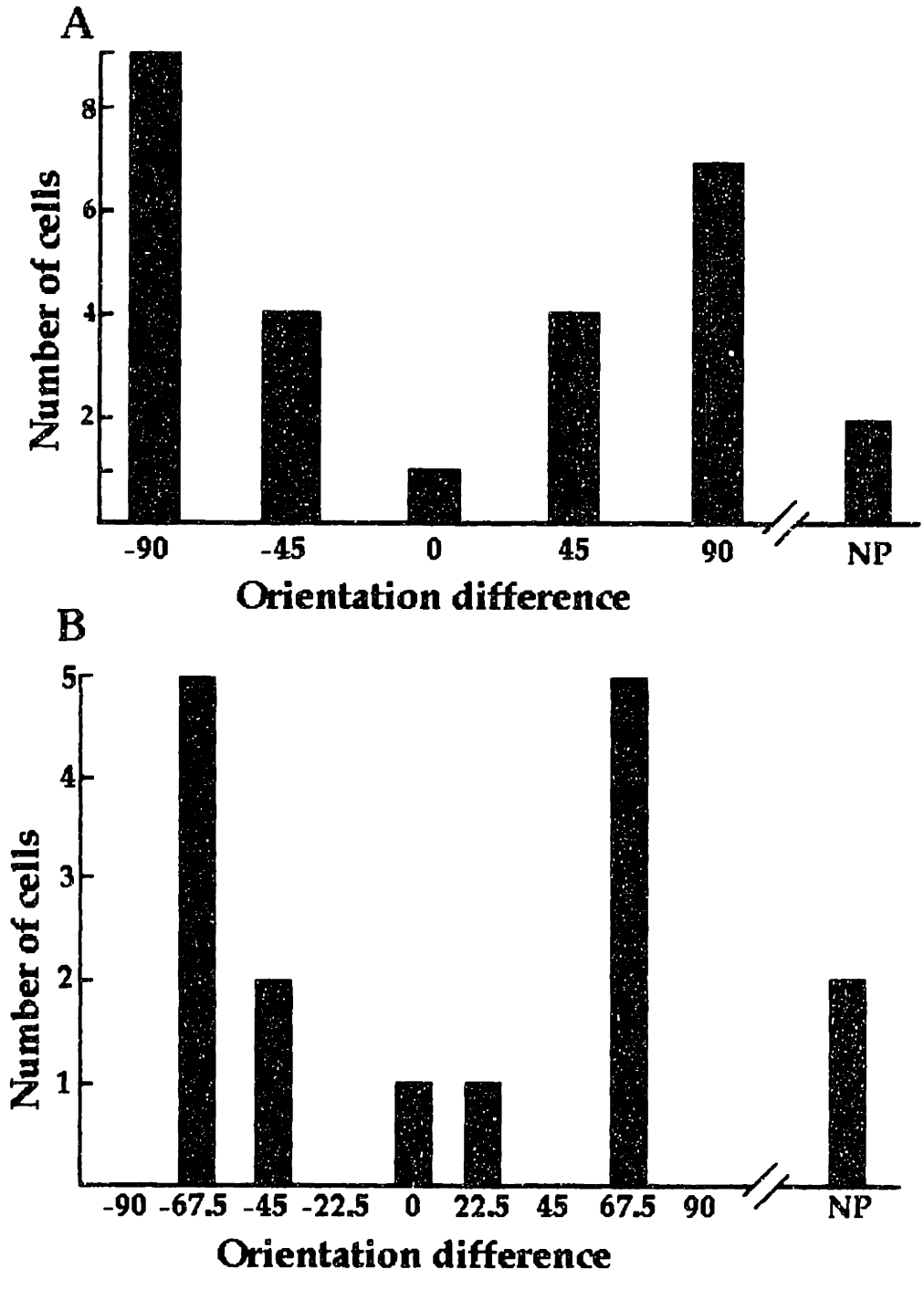

A
Number of cells
8
6
4
2
-90
-45
0
45
90
NP
Orientation difference
B
Number of cells
5
4
3
2
1
-90
-67.5
-45
-22.5
0
22.5
45
67.5
90
NP
Orientation difference

Figure 16.

A. Frequency histogram of the difference in orientation preference between luminance and subjective gratings of V1 neurons (n = 27). Neurons that had the same orientation preference for luminance and subjective gratings were binned into the 0° class (1 cell, 4%), neurons whose difference in orientation preference between luminance and subjective gratings differed by either 22.5° (8 orientations) or 45° were binned into the ±45° class [the sign was given by (preferred $orientation_{luminance}$ - preferred $orientation_{subjective}$)] (n = 9, 33%), and those neurons in which the difference between the two stimuli differed either by 67.5° (8 orientations) or 90° were binned into the 90° class (n = 16, 59%). Neurons that were silent to the subjective grating stimuli are shown in red (NP = no subjective preference) (n = 2, 7%) and did not respond to the subjective edges or the inducing lines in an orientation-specific manner.

B. Frequency histogram of orientation preference difference for V1 neurons (n = 15) at a finer orientation resolution. The cells are a subset of the cells shown in A. Luminance and subjective gratings of eight orientations (22.5° apart) were used for the cells in this histogram.

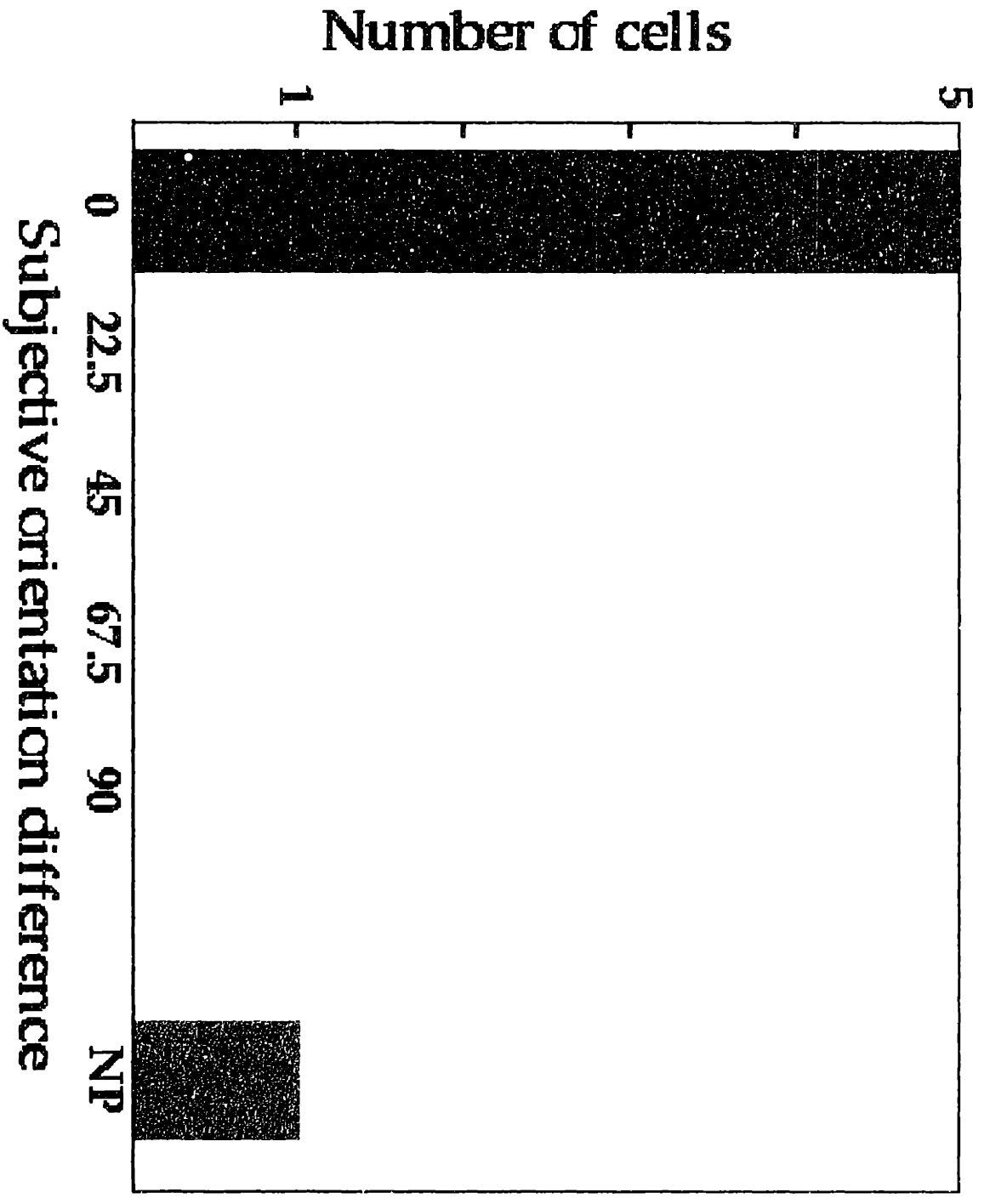

Number of cells
1
5
Subjective orientation difference
0
22.5
45
67.5
90
NP

Figure 17. Frequency histogram of subjective orientation preference of iso-columnar cells in V1. For each vertical penetration (column), the orientation preference of the column was determined by finding the subjective orientation preference of the majority of cells in the penetration. Then for each cell recorded within the column, the difference between its preferred subjective orientation and that of the column was obtained. This procedure was done anew for each separate penetration. Columns in which all the cells we found responded solely to the inducing lines in the subjective grating were discarded (columnar organization of luminance orientation preference). Only penetrations in which we recorded from 2 cells or more have been included in the histogram. A cell count of subjective orientation preference difference across all columns combined was maintained and plotted in figure. Of 6 cells we recorded from in V1 (2 columns), 5 cells had the same orientation preference for subjective gratings, 1 cell did not show any subjective orientation preference.

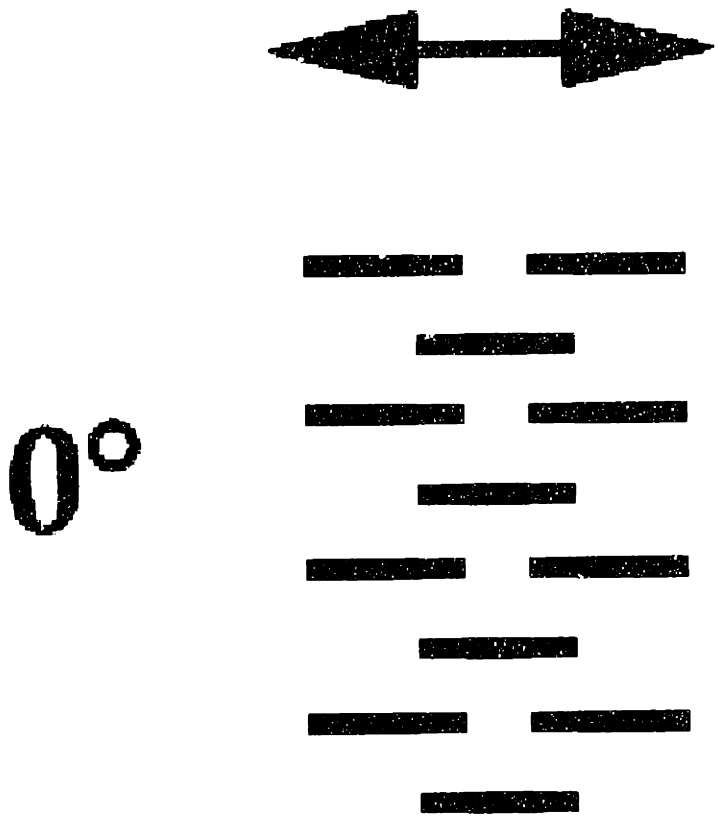

0°

Figure 18. A modified subjective grating used for eliciting a stronger response to subjective contours in previously classified luminance cells. The inducing lines overlap in spatial extent, however there is no luminance gradient across the vertical edge. This is so because the individual inducing line segments in the portion containing twice as many line segments, each has half the luminance of the inducing line segments in the other region. We call this stimulus a "scotch-tape" grating.

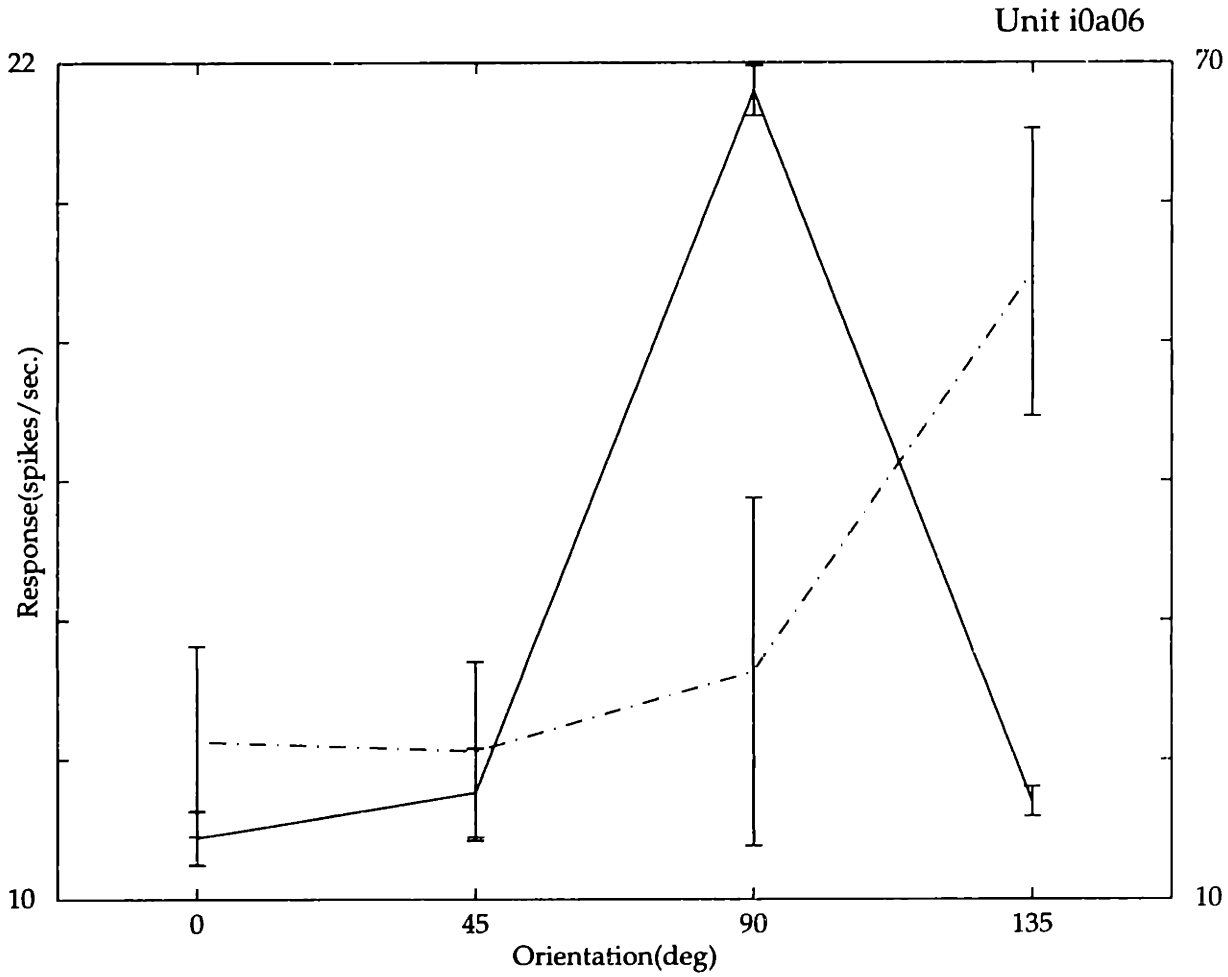

Unit i0a06
22
10
70
10
Response(spikes/sec.)
0
45
90
135
Orientation(deg)

Figure 19. We recorded from V1 cells (6 cells) previously classified as being unresponsive to subjective contours (luminance cells). Most failed to respond to the modified scotch tape subjective grating (cf. Figure 1), however one cell did show a clear response composed of both the luminance and subjective components. Luminance grating response is shown in continuous lines, scotch-tape grating response is shown in broken lines. The vertcial scale on the left shows the response to luminance gratings, the scale on the right gives the response to scotch-tape gratings. The orientation preferences differ by 45°. The cell's subjective grating orientation preference was 90° off (not shown).

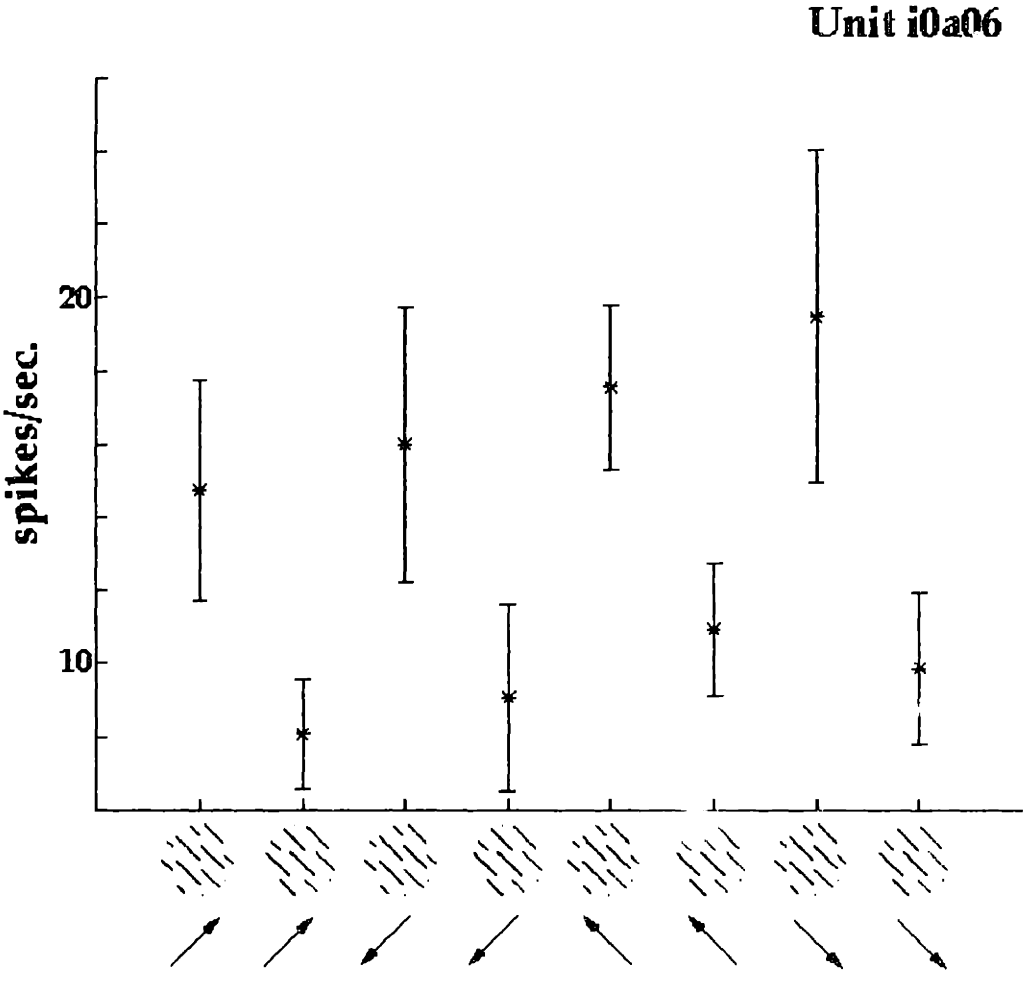

Unit i0a06
spikes/sec.
20
10

Figure 20. We recorded the response of V1 luminance cells (8 cells) to subjective gratings that had identical inducing line orientation, identical direction of motion, and mutually orthogonal subjective orientations (iso-luminance subjective gratings, orientations: $0^o$ and $90^o$; cf. Chapter 2, Figure 2). 5/8 cells showed a clear subjective orientation preference (some in a particular direction). One such cell's response is shown that responded best to a vertical $0^o$ subjective grating of any direction (orthogonal or parallel to the inducing lines). This cell also responded best to a horizontal $90^o$ luminance grating. The average spontaneous activity has been subtracted from all responses.

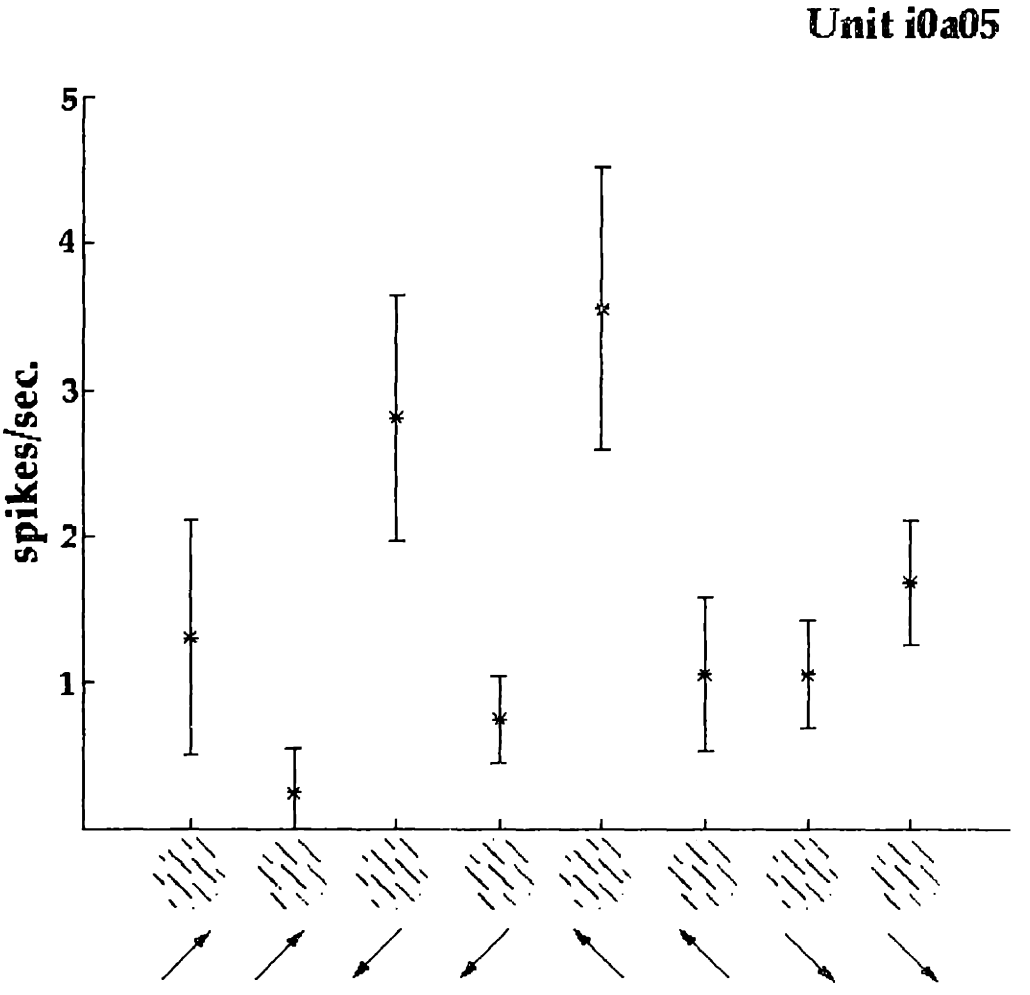

Unit i0a05
spikes/sec.
5
4
3
2
1

Figure 21. A V1 luminance cell that responded best to $0^{o}$ subjective grating with subjective edges moving left. The average spontaneous activity has been subtracted from all responses.

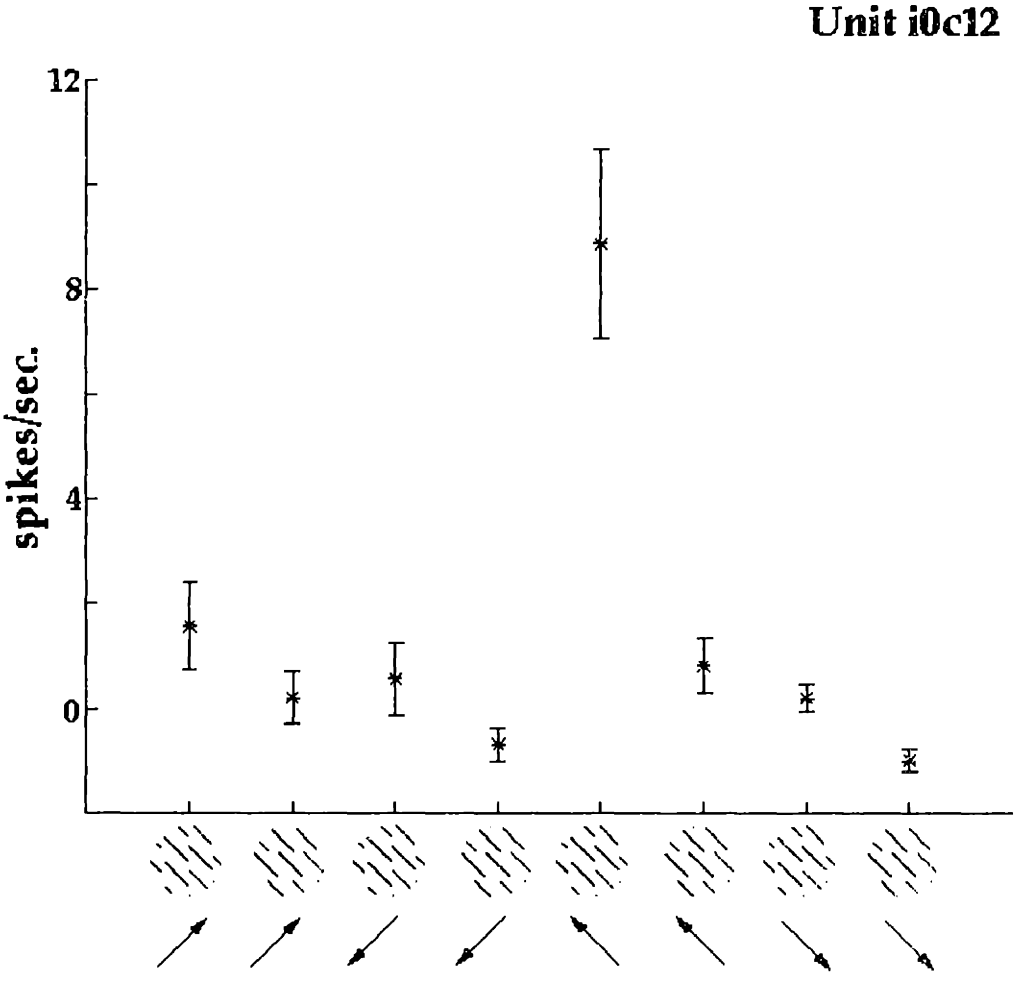

Unit i0c12
12
8
4
0
spikes/sec.

Figure 22. A V1 luminance cell that responded best to a vertical $0^{o}$ subjective grating moving up and to the left. The cell's orientation and direction-specific response can be explained partly by a response to the vertical $0^{o}$ subjective edge and partly a response to the oblique inducing lines drifting parallel to their orientation (compare responses to stimuli 3 and 4 as well in the figure). The average spontaneous activity has been subtracted from all responses.

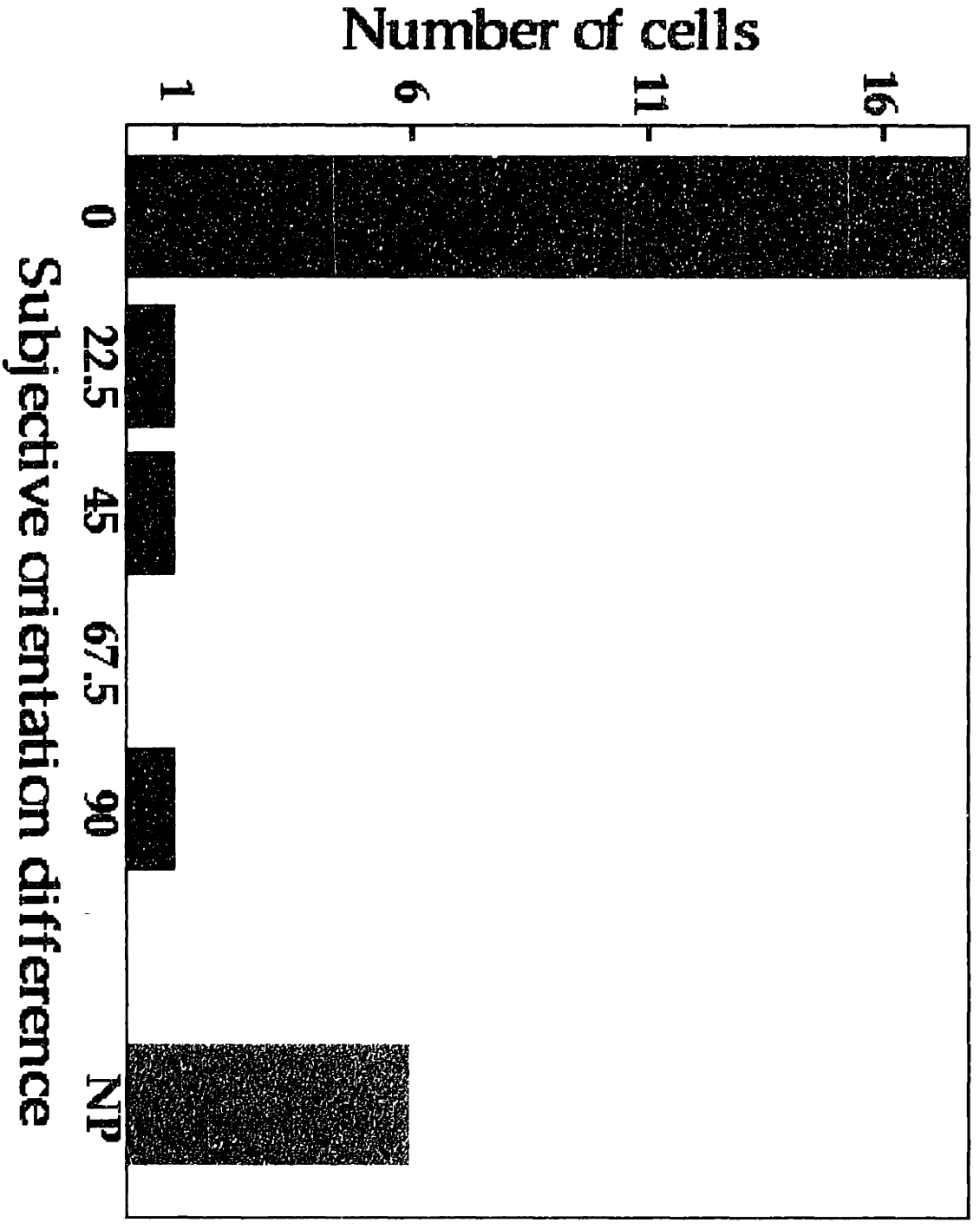

Number of cells
1
6
11
16
Subjective orientation difference
0
22.5
45
67.5
90
NP

Figure 23. Frequency histogram of subjective orientation preference of iso-columnar cells in V1 and V2 combined. Of 27 cells we encountered in V1 and V2 (7 columns): 18 cells (66%) had the same orientation preference for subjective gratings as the rest of the cells in the column, 1 cell (4%) were within 22.5° of the preferred subjective orientation, 1 cell (4%) were within 45° of the preferred subjective orientation and 1 cell (4%) responded best to the orthogonal orientation of the subjective grating as the rest of the cells in the column. 6 cells (22%) showed no subjective orientation preference. This is a combined histogram of the distributions shown in Figures 7 and 17.

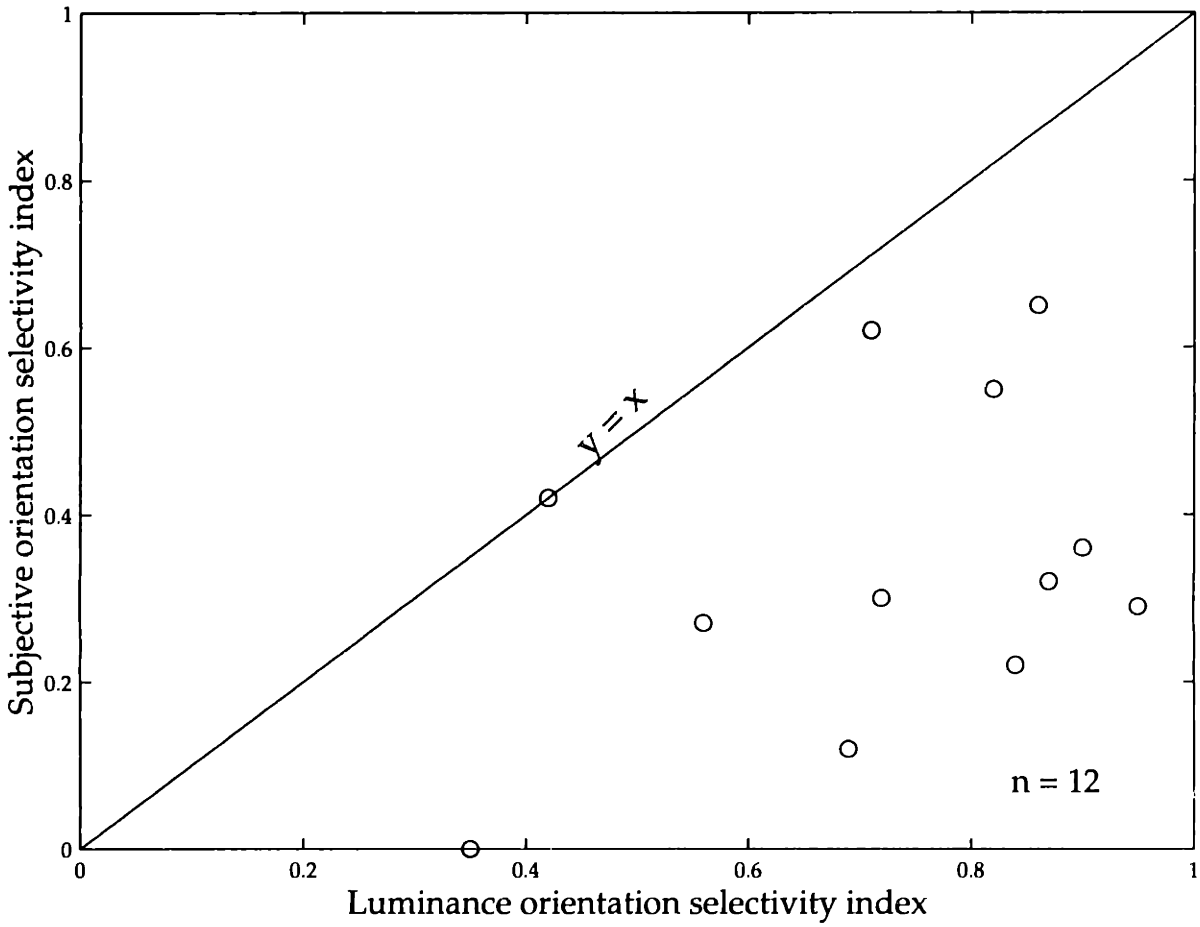

Subjective orientation selectivity index
Luminance orientation selectivity index
y = x
n = 12
0
0.2
0.4
0.6
0.8
1

Figure 24. A comparison of orientation tunings between luminance and subjective gratings for contour cells in V1 and V2 (n = 12). The orientation selectivity index for each stimulus was calculated by using the following formula :

$$(response_{optimal} - response_{ortho.}) / (response_{optimal} + response_{ortho.}),$$

The formula yields a number in the range [0,1] with higher values signifying sharper orientation tuning. For each cell, the orientation selectivity index for luminance and subjective gratings is plotted. $y = x$ is the line at which the orientation indices for both gratings is equal; above the line the subjective orientation index has a higher value than the luminance orientation index and vice-versa for the region below the line. Most cells have sharper orientation selectivity for luminance gratings (mean = 0.72) than for subjective gratings (mean = 0.34) as indicated by the fact that most points (11/12 cells) fall below the line. The difference between the two indices is statistically significant (two-tailed t-test, $p < 0.001$). The correlation between the orientation indices for the two stimuli is negligible ($r = 0.38$). One cell had a subjective orientation selectivity index of zero since it responded best to two orthogonal orientations (the orientation of the subjective edges and the orthogonal orientation of the inducing lines) and with equal strength to both (cf. Figure 13).

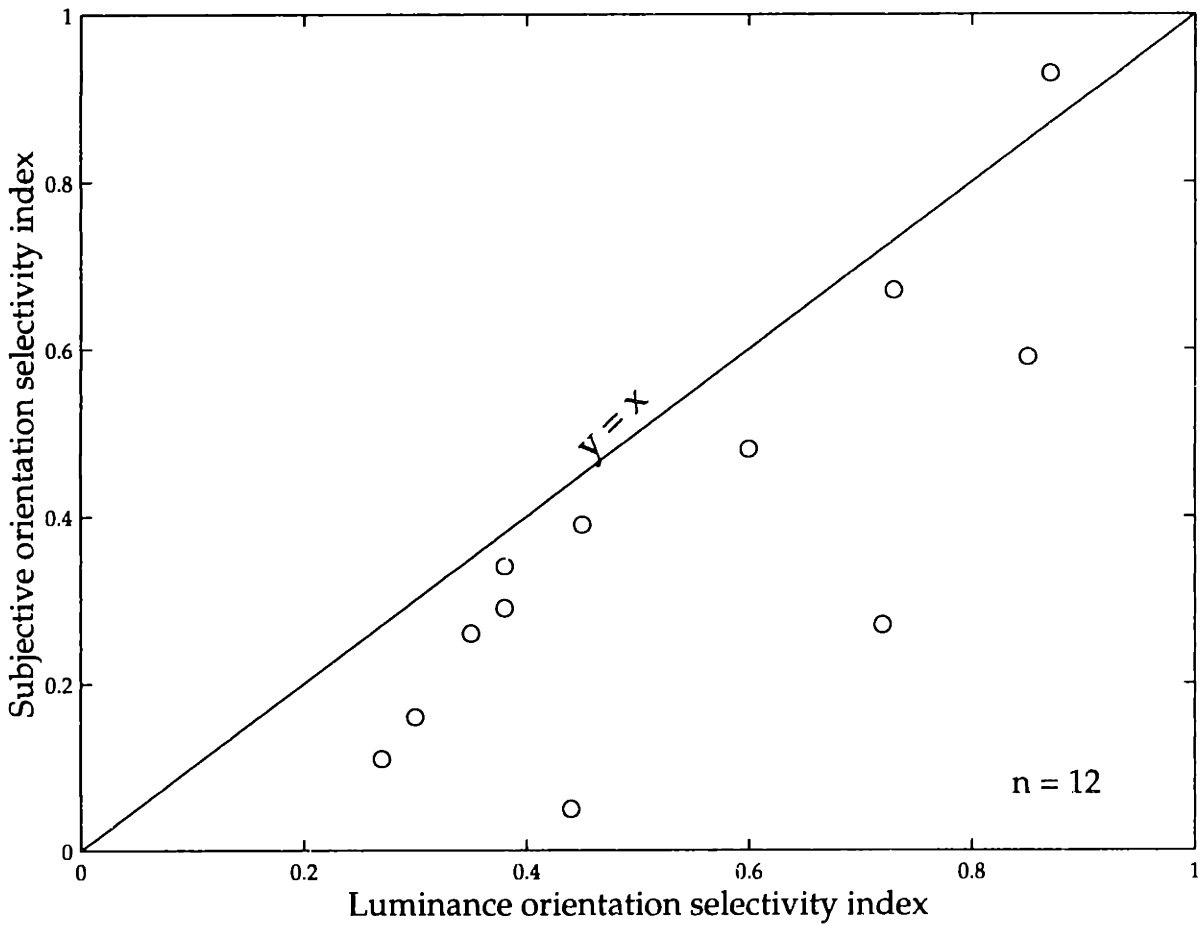

Subjective orientation selectivity index
Luminance orientation selectivity index
y = x
n = 12
0
0.2
0.4
0.6
0.8
1

Figure 25. A comparison of orientation tunings between luminance and subjective gratings for luminance cells in V1 and V2 (n = 12). The orientation selectivity index for each stimulus was calculated by using the following formula :

$$(response_{optimal} - response_{ortho.}) / (response_{optimal} + response_{ortho.}),$$

The formula yields a number in the range [0,1] with higher values signifying sharper orientation tuning. For each cell, the orientation selectivity index for luminance and subjective gratings is plotted. $y = x$ is the line at which the orientation indices for both gratings is equal; above the line the subjective orientation index has a higher value than the luminance orientation index and vice-versa for the region below the line. Most cells have sharper orientation selectivity for luminance gratings (mean = 0.53) than for subjective gratings (mean = 0.38) as indicated by the fact that most points (11/12 cells) fall below the line. The difference between the two indices is statistically significant (two-tailed t-test, $p < 0.005$). Since luminance cells by definition, respond to the luminance edges (inducing lines) in the subjective grating, a very high correlation between the orientation indices for the luminance and subjective gratings is to be expected ($r = 0.81$).

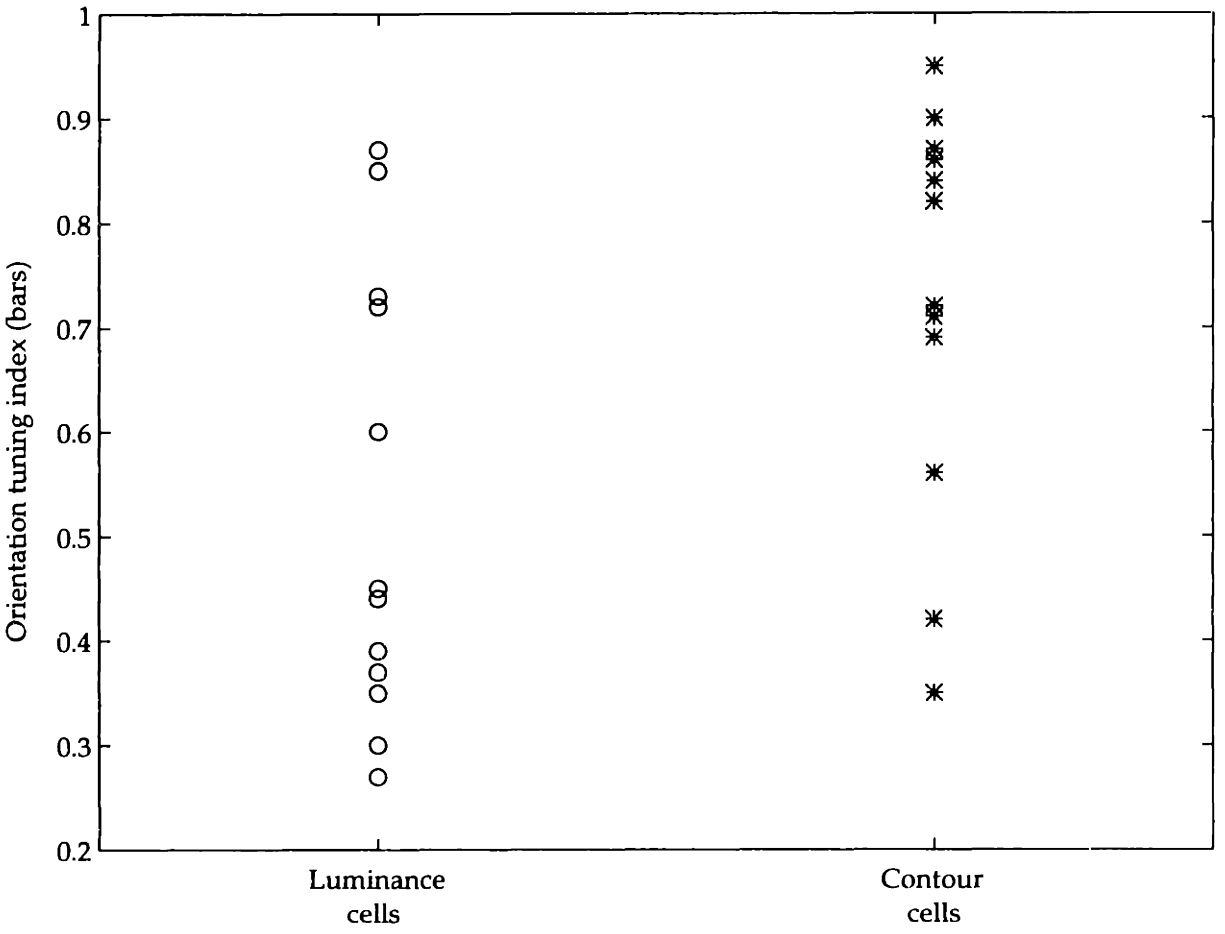

Orientation tuning index (bars)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
Luminance cells
Contour cells

Figure 26. A comparison of orientation tunings for luminance gratings between luminance and contour cells in V1 and V2. The orientation selectivity index is computed as described earlier in Figures 23,24. Contour cells have sharper orientation tuning as indicated by higher orientation index values than luminance cells. The difference between the two groups of cells is statistically significant (two-tailed t-test, $p < 0.05$).

# Chapter 4

# Mechanisms and models

# INTRODUCTION

Using imaging and single-unit recording we have shown that cells in both V1 and V2 respond to subjective contours. These cells are organized in columnar fashion for response to subjective contours and bear a complex relationship with the functional organization for luminance contours. Furthermore, we have done some experiments to specifically examine models that attempt to explain response to subjective contours. Using single-unit recording and optical imaging, we have recorded from V1 and V2 in cats and observed their response to specific visual stimuli designed for this purpose.

Some cells in V2 that shared the same orientation preference for luminance and end-stopped subjective gratings (contour cells) preferred a grating composed of a grid of dots (one pixel in size) of a *different* orientation (same spatial frequencies as used in the subjective grating). Other cells that shared the same orientation preference for subjective gratings and a grating composed of dots had sharper orientation selectivity for subjective grating. These results show that a simple mechanism based on response to end terminations alone cannot account for the response to subjective contours. More sophisticated mechanisms must hence be responsible for the response to this complex stimulus.

We have found that cells in V2 that respond strongly to end-stopped subjective contours respond even more vigorously to overlapped gratings of the same orientation. V1 also responds more vigorously to overlapped gratings than to subjective gratings. Using

abutting square-wave gratings (rectangular checkerboard patterns), we have observed that V2, a substantial portion of which responds to subjective edges in the subjective gratings, responds instead to the inducing bars of this new stimulus. These data suggest that the neural explanations for response to the class of end-stopped subjective contours may need revision.

## NEURAL SUBSTRATE FOR RESPONSE TO END-STOPPED SUBJECTIVE CONTOUR

This study tested one class of illusory stimuli - end-stopped subjective contours. Several mechanisms have been proposed to explain the cortical responses. The simplest mechanism proposed is that the response to the illusory borders is simply a response to the line terminations in the stimulus. The illusory stimulus can be conceived of as a row of line terminations along a certain orientation. The line terminations are thus organized in a certain way and they line up along the orientation of the subjective edges. When the subjective grating is drifted perpendicular to the orientation of the subjective edges, the line terminations all appear first in the cell's receptive field. This encroachment of line ends into a cell's receptive field may be what activates the cell. Y cells from the LGN project to V2 in cats. Cells in the Y-cell pathway are known to have a transient response to stimuli and they cease responding to stimuli within a few seconds (Cleland et al. '71, Hoffman et al. '72). Thus the cells in V2 may be responding transiently to the line ends in the stimulus which could account for the response to the illusory border. In the case

of a contour cell (a cell that responds preferentially to the same orientation for both luminance and subjective gratings), the alignment of these line ends along the cell's optimal luminance orientation may then account for the cell favoring a subjective grating of the same orientation as its preferred luminance orientation.

The mechanism states that the response to the illusory borders is explained by the response to the dots or line terminations and hence the response of a cell in cortex to subjective gratings must follow the response to a grating composed of dots in three different ways. First, the orientation preferences of the cell to a subjective grating stimulus and a grating composed of dots should be the same. Second, the cells should show a sharper orientation tuning for the dots than for a subjective grating. Third, the magnitude of a cell's response to a subjective grating of its preferred luminance orientation must be less than or equal to the response of the cell to a grating composed of dots of the same orientation.

Even in its most restricted form, all the above must hold true for contour cells at the very least. If a cell responds to subjective contours (contour cell; a cell that prefers a subjective grating of the cell's optimal *luminance* orientation), it is because of the presence of the line terminations in the stimulus and the response to a stimulus reduced to these line ends (dots) alone can account for most, if not all, the cell's response to the subjective grating. If a cell responds best to a subjective grating and a luminance grating of the same orientations (a contour cell), it must prefer a grating composed of dots of the same orientation as well. According to this hypothesis, not only do the inducing lines not

contribute to the cell's response to the subjective edges in the stimulus, these orthogonal luminance edges may in fact, suppress the response to the line terminations. Hence, not only must the orientation preferences for subjective gratings and dots coincide, the response to the optimally oriented subjective grating must be less than or equal to the response to the dots stimulus of the same orientation. Finally, because of this suppression that may arise due to the presence of the orthogonal edges, the cell must be more broadly tuned for subjective gratings than for a grating composed of a grid of dots.

We have examined the hypothesis experimentally by recording from single-units and comparing the cell's responses to subjective gratings and a grating composed of dots which are the same size, luminance and are the exact same number (i.e. same spatial frequency) as the line terminations in the subjective grating stimulus. We compared the responses to these two stimuli for the subclass of cells that respond best to a luminance grating and a subjective grating of the same orientations (contour cells). Figure 1 shows a cell whose orientation preferences for luminance and subjective gratings were the same and the cell preferred a dots stimulus of a different orientation and direction. Figure 2 shows another cell that shows the same effect. Both these stimuli were interleaved over 8-16 stimulus presentations. Thus, the cells preferred the same orientations for luminance and subjective gratings but responded best to a dots stimulus of a *different* orientation. This is in direct disagreement with the model (first point above). Cells were just as likely to have the same orientation preference for both the subjective grating and the dots stimulus (3/9 cells) as not (3 cells). Figure 3 summarizes the population data for all of the V2 cells.

Next, we compared the orientation tunings and response magnitudes for the cells that shared the same orientation preferences for luminance gratings, subjective gratings and the dots stimulus. Figures 4 and 5 show two such cells (these cells are contour cells by definition). The magnitude of the cells' response to their respective preferred subjective orientations was higher for the subjective grating than for the dots stimulus. Not only that, both cells showed a sharper orientation tuning for subjective gratings than for dots. The model would predict that the magnitude of the response be higher for the dots stimulus than for the subjective grating and the orientation tuning for the subjective grating be broader than for the dots stimulus. Our data does not support either of these claims. We have compared the orientation tunings for both the stimuli for all the contour cells that fit this criterion i.e. did not prefer subjective gratings and dots stimuli of different orientations[1]. The orientation tunings were significantly sharper for subjective gratings than for dots across the sub-population (two-tailed t test, $p < 0.05$) (Figure 6).

In fact, over the entire population of cells recorded from ($n = 23$), we found that the orientation preferences for subjective gratings and for gratings composed of a grid of dots were the same for only a fraction of cells (6 cells, 27%). Thus, a cell's response to a subjective grating cannot necessarily be predicted by the response to the dots stimulus.

The reductionist model of trying to explain the response to subjective contours based on line terminations alone does not appear to hold true in light of the data shown above. In

1. This set contains cells that had the same orientation preference for dots and subjective gratings and cells that showed poor orientation tuning for the dots (orientation selectivity index < 0.10).

a substantial number of cells either the response to the subjective grating of the optimal orientation or the sharpness of orientation tuning or even the orientation preference to subjective gratings did not follow the responses elicited by the dots stimuli. The dots stimulus thus has little predictive value for assessing a cell's response to subjective gratings. Hence, more complex and sophisticated mechanisms must be responsible in order to process this complex stimulus in early visual cortex. The next section describes the two most popular models to explain early cortical response to subjective contours.

*Recap of models*

There has been a flurry of models to explain the response to a somewhat broader class of subjective contours, of which two have gained considerable popularity due to their neurobiological plausibility and predictive power. The first model proposed by Peterhans and her colleagues (Peterhans et al. '86) is based on end-stopped receptive fields converging on a cell in V2. These fields are lined up in a row with their orientations approximately perpendicular to it. The spatial arrangement of these fields accounts for the sensitivity to subjective contours. Inducing lines activate the excitatory sub-regions of the end-stopped input cells and fall short of encroaching upon the inhibitory end-zones and so there is no suppresion of response. These activated cells then project to a subjective contour cell that is thus activated by a stimulus with abutting thin lines (subjective contour).

The second model (Grossberg and Mingolla '85) relies on two key processes - end-cutting and collinearity. A line segment of a given orientation causes orientation

detectors of that particular orientation to be activated, and its end (line having a finite width) causes cells preferring other orientations to be activated. This is end-cutting - the process by which line ends cause activation of edge detectors in cortex. This weak activation is then strengthened if there are other detectors, also of the same orientation and aligned along the cell's orientation axis. This process is called collinearity. With abutting inducing lines of a particular orientation, cells preferring other orientations are also activated by the inducing line ends, other line ends that lie along the subjective edge mutually reinforce this weak activation leading to a more robust response to the subjective edge.

*Experimental tests for subjective contour response.*

*The end-stopped model.*

We designed specific stimuli: Gratings whose inducing line ends were made to infringe into the end-zones of neighboring inducers (partially overlapped end-zones; overlapped gratings; Figure 7). If end-zones are spatially aligned (as a result, the receptive field centers are slightly displaced) hypothesized in the end-stopped model, the inducing lines (lines have same thickness and length and the same number of line ends across each edge as in subjective gratings) forming the overlapped gratings encroach upon the end-zones and inhibit the contour cell's response to its optimal orientation (recall: contour cells have same subjective and luminance orientation preference). Thus, the response of the contour cell to the overlapped grating should be less than its response to the subjective grating of the same optimal orientation. In single-unit recordings from V2 cells (2 cells), that had been classified earlier as being contour cells, we found that the

response to overlapped gratings was stronger than the response to the subjective grating of the same preferred orientation (Figures 8,9). All cells recorded from had the same overlapped and subjective orientation preferences, in accordance with their bar preference. The overlapped gratings do indeed encroach upon the putative end-zones, but the increase in response (compared to the response to the subjective gratings) due to the presence of an additional luminance component in the overlapped gratings may mask the decrease in response that may have been caused by the activation of the inhibitory end-zones by the overlapped grating. This possibility is difficult to eliminate. Another possibility is that the receptive field centers of the input cells are in fact, aligned and so the end-zones are not (Dayan, P., personal communication). As a result, overlapped gratings are able to better elicit a response than subjective gratings (since the inducing line now encroaches upon the inhibitory end-zone).

In order to address this issue, we have designed a new stimulus - a "scotch-tape" subjective grating (cf. Chapter 3, Figure 18). This stimulus has intermeshed inducing lines, however the stimulus does not have a luminance gradient. This stimulus needs to be tried on subjective contour cells. If the cell responds more or the same to the scotch-tape grating than a subjective grating of the cell's preferred orientation, the end-stopped model's key assumption of end-stopped input cells would need to be examined further. Alternately, a square-wave grating stimulus with the same luminance gradient values as the overlapped grating could be shown and the contour cell's response to this stimulus subtracted from the same cell's response to the overlapped grating of the same (preferred) orientation. This should supposedly cancel out the effect of the luminance component on the increase in the contour cell's response to its preferred orientation. If the subtracted response to the overlapped grating is the same or is higher than the

response to the subjective grating, this might call for, at the very least, a new interpretation of the end-stopping model.

*The Grossberg-Mingc!la model.*

In the Grossberg-Mingolla model, thickness of inducing lines plays a central role in order for collinearity to have an effect. If the inducing lines are sufficiently thick, the cells preferring the same orientation as the line ends are activated, however the activation does not propagate (Grossberg and Mingolla '85a,'85b) and the percept does not form. Thus, if one were to vary the thickness of the inducing lines of the subjective grating, with increasing line thickness, the number of cells in V2 responding to the subjective edge should decrease. A greater proportion of cells would then be activated by the orientation of the inducing bar and the subjective orientation would influence the cells less. If one were to record from V2 with subjective gratings (inducing lines 1 pixel thick), the pixel histogram for orientation difference should peak at $0^{o}$ indicating the presence of a substantial fraction of cells responding vigorously to the subjective edges and signaling a border independent of whether it is luminance-defined or not (i.e. subjective). However, if at the other extreme, one were to make the inducing lines thick enough that the spacing between the abutting lines is reduced to zero (hence the term abutting square-wave gratings or rectangular checkerboard patterns), the cells stop responding to the subjective edges and respond instead to the inducing bar orientation. In such a case, the histogram should peak at close to $90^{o}$ orientation difference indicating a lack of response to the "subjective" edges orthogonal to the inducing bars and parallel to the inducing bar ends. We find exactly that in imaging experiments on abutting square-wave gratings (checkerboard patterns) in V2. We have found that using thick inducing bars, cells in V2 which earlier responded to subjective edges now responded to

the inducing bars in the stimulus (cf. Chapter 2, Figure 12)[3].

We have not been able to test Grossberg and Mingolla's claim of end-cutting experimentally. One way of testing this claim is the following: isolate a cell and obtain its orientation tuning curve. When an orthogonally oriented bar, which is longer than the cell's receptive field, is flashed so that one of its ends lies within the cell's receptive field, the cell should show a statistically greater response as compared to when the ends of the bar are made to lie outside the cell's receptive field. Varying the orientation of the line and keeping the orientation of the line end constant should still not change the enhancment in response when the line's end are made to lie within the receptive field (as compared to the case when the line's ends lie outside the cell's receptive field). The difference in response should be enhanced when other lines are flashed so the line ends are aligned along the orientation of the line ends. This would be a test for collinearity. Also, the response should be enhanced more when the line ends are aligned and not otherwise. This would be the strictest possible test for collinearity. Evidence for collinearity-dependent mechanisms have recently come from psychophysical and physiological studies by (Kapadia et al. '95). When placed within a noisy background, the response of a substantial portion of complex cells (42%) in monkey striate cortex to their optimally oriented bar declines. Much of the inhibition was eliminated as surround elements were rotated to become collinear with the target, and, in some instances,

3. The result is not unsurprising in light of the work of de Valois (de Valois et al. '79). Square checkerboard patterns have no energy whatsoever at the edges of the checkerboard and the fundamental Fourier components are oriented $45^0$ away from the edges. Cells in both cat and monkey striate cortex respond to the orientation of the Fourier fundamental. In case of a rectangular checkerboard of aspect ratio 0.33/1 as what we have used (inducing line spatial frequency = 0.45 c/deg; "subjective" spatial frequency = 0.15 c/deg.), the Fourier fundamentals are oriented very close to the orientation of the long edges (the inducing line orientation; $\sim 10^0$ difference between the inducing bar orientation and the orientation of the Fourier fundamentals). Hence, the cells respond to the Fourier fundamentals. Our result that V2 cells also behave as V1 cells do is somewhat new though.

increased beyond the response to the central bar stimulus.

Our data is consistent with the Grossberg-Mingolla model, however more rigorous tests need to be designed and tested on cortical cells in order to constrain the model. The two key mechanisms of end-cutting and collinearity must be found to exist in cortex before the model can be accepted as something more than a phenomenological model and only then can it help answer the more general question of object delineation in real-world scenes.

## IMPLICATIONS OF THE DATA

*Complexity of early cortical processing.*

We have shown that early visual cortex (V1 and V2) of cats responds to subjective contours. It is generally believed that low-level cortex, such as V1 and V2, perform low-level visual functions. However, complex stimuli, such as subjective contours, also elicit a response from single cells in these areas, bringing into question the original, somewhat artificial distinction between low and high level cortices. Over and above that, cells in V1 and V2 cluster to form columnar domains for subjective orientation preference, in maps that bears a systematic relationship to orientation maps for luminance edges. The existence of an organizational architecture for the representation of a complex stimulus in early visual cortex, shown for the first time in our study of subjective contours, calls into question the role believed to be played by low-level cortex and this work, in conjunction with the single-unit work of others (Lamme '95, Zipser et al. '94, von der

Heydt and Peterhans '89) may cause us to appreciate better the complexity of early cortical processing.

Our work on anesthetized animals also begs the question regarding the role of attentional processes and behavioral state in visual perception. While attention may aid in eliciting a yet stronger response to subjective contours in V1 and V2, it is by no means necessary to evoke a response in the first place.

*Comparisons between cat and monkey.*

We have found that a demonstrable number of neurons in V2 respond to subjective contours, and some do so while ignoring the orientation of the inducing lines; cells in cat V1 also show some response to subjective contours but the number of neurons that do so are significantly fewer than in cat V2. von der Heydt and Peterhans (von der Heydt and Peterhans '89) have shown in awake monkey that cells in V2 respond to subjective contours, whereas cells in monkey V1 do not. There are important differences between cat and monkey functional neuroanatomy that may account for the differences in our findings. In cat, V2 is considered to be very much like V1 in many ways and V1 and V2 are generally considered to be parallel visual areas in this species. Both V1 and V2 receive strong projections from the LGN, and the basic receptive field organization of neurons is very similar in the two areas. Removal of inputs from V1 in cat has little effect on the major receptive field properties of V2 (Donaldson and Nash '75, Dreher and Cottee '75, Sherk '78), which suggests that the major response properties of neurons in V2 are derived in parallel from dLGN inputs. It is well-known that in cat, X cells from

the retina project to V1 via the LGN and the Y cell pathway projects to V1 and V2 in the cat (Garey and Powell '67, Sherman and Spear '82). Whereas, in monkey, LGN projects almost exclusively to area V1 and area V1, in turn, projects to V2. In contrast to cat lesion experiments, cooling of monkey V1 silences the responses of V2 (Schiller and Malpeli '77). Furthermore, it is not until areas 17,18 and 19 are all damaged in cat that one sees the same visual impairments typical of monkeys with damage to V1 (Pasik and Pasik '71, Weiskrantz '72, Spear '79, Miller et al. '80). Despite important differences between cat and monkey neuroanatomy in the LGN projections to V2 and the behavioral role of V2 in both species, there is a remarkable convergence in the physiology; both monkey and cat V2 show a strong response to subjective contours. Roughly similar numbers of cells (30-40%) in cat and monkey V2 exhibit a robust response to subjective contours. One may speculate then that it is the similarities between cat and monkey that yield similar responses in V2 of both these species. Thus, the relationship between intracortical connections in V2 and corticocortical projections from V1 to V2 and orientation column organization (whether iso- or ortho-orientation domains preferentially connect) must be investigated (a surprisingly heretofore largely ignored topic; cf. Gilbert and Wiesel '89 for study of corticocortical connectivity in cats though) in both cat and monkey and compared between the two species. Such studies may shed some light on the mechanisms underlying the responsiveness of V2 to subjective contours.

A smaller, but significant, proportion of cells in V1 show a strong response to subjective contours; many more show a partial response to subjective contours, and a large fraction

of cells in V1 show a clear orientation-specific response when an iso-luminance subjective grating is used. In fact, similar LGN projections to V1 have been observed in cat and monkey. Moreover, an iso-orientation long-range lateral intracortical connectivity pattern (Gilbert and Wiesel '89, T'so et al. '86, Malach et al '93) has been shown to exist in both cat and monkey V1. We strongly suspect that a thorough and careful study of response to subjective contours in monkey V1 might yield a similar response to what we have found in cat V1. The study conducted by von der Heydt and Peterhans had some clear shortcomings. The criterion used to define a response to subjective contours was not given. The summary data for the V1 ensemble was never shown in their work and thus the reader did not have a chance to judge for himelf/ herself. Since the subjective gratings they used had varying luminance and subjective components across the stimulus set (as do we for the majority of our experiments), it is important to take a close look at the summary data since a clear orientation preference shift away from the orientation of the inducing lines may likely be attributed to the orientation of the subjective edges which are also present in the subjective grating stimulus they used.

Moreover, they tried only one kind of end-stopped subjective contour stimulus. Based on our cat findings, perhaps an iso-luminance subjective contour stimulus could have yielded clear orientation responses in at least some of the cells in monkey V1 that they did not find to be responsive with the conventional subjective stimulus. However, these experiments need to be done in monkeys to prove the point one way or another.

*Localization of function to a single cortical area.*

While V2 showed a significant response to subjective contours, V1 also showed some response. V2 is thus, by no means, the first brain region to respond to subjective contours. In fact, V1 may very well be an important preprocessing stage of the subjective signal that then appears to be more widespread in V2. While the response is significantly greater (proportionately more neurons) in V2 than in V1, the perceptual signal may not arise out of the blue from nowhere in V2 [4]. This illustrates an important principle of brain processing. A measurable response to a particular stimulus does not arise *de novo* in a certain area. The responses must build up over several stages of processing (it is not necessary for these stages to be hierarchical). Direction selectivity is a ubiquitous and defining property of cells in MT (Albright '84), but is found at least at the level of V1 (Schiller et al. '76, Marcar et al. '92, Snowden et al. '92), a principal source of input to MT (Girard et al. '92, Rodman et al. '92). In fact, in some species, direction selective cells have been observed in the retina. V1 cells are strongly orientation tuned, however orientation selectivity is found, though of weaker strength, in cells in the lateral geniculate nucleus, a relay station (if one may) between the retina and V1 (Levick and Thibos, '82, Vidyasagar and Urbas,'82, Soodak et al. '87, Shou and Leventhal, '89). It may thus be naive to assign a distinct function to a given area; a given area may subserve several visual tasks and a particular stimulus may elicit a response in several areas, though maybe differing in strength and/or cell proportions.

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4. There is a possibility that Y cells which provide geniculate input to V2 in cats may be partly responsible for the response to subjective contours in V2. Nonetheless, this again argues for subjective contour response as not being an emergent property of V2 cells.

# FUTURE DIRECTIONS

*A different stimulus may elicit a more vigorous response to subjective contours.*

The stimulus used in the studies is generally considered a weak form of subjective contours in terms of the strength of the psychophysical percept (B. Anderson, personal communication). A better stimulus may be designed which elicits a stronger percept, and hopefully thereby, perhaps a more robust response in V1. A stimulus with abutting inducing lines of various random orientations was considered since it was known to evoke a more vigorous percept in humans. A subjective stimulus of this type has luminance energy over all orientations, hence it becomes difficult to attribute intermediate orientation preferences to subjective edges or to the presence of luminance-defined inducing lines of multiple orientations. Less robust, nonetheless important, responses to subjective contours are thus not interpretable. A small number of V1 cells, that had been classified as luminance cells based on their response to conventional subjective contours, showed some response to the orientation of the subjective edges when a modified subjective grating was used (cf. Chapter 3, Figure 18 for grating used, Figure 19 for cell). This shows that V1 cells might respond even more robustly to other subjective contours within this class. The challenge of designing other appropriate subjective stimuli that could address this issue more completely remains open.

Also, the stimulus used for most of our experiments (orthogonal inducing lines) had a luminance component whose orientation varied along with the subjective edge

orientation. Hence, the luminance and subjective components of the cells' response competed with one another. The presence of a luminance component whose orientation varies concomitantly with the orientation of the subjective edges (orthogonal to one another) over the subjective grating stimulus set may mask the response due to the subjective edges alone and thus weaken the effect. It is thus better to design a stimulus which either does not have a luminance component or if it does so, is of the same amplitude and orientation across the entire stimulus set. Stimuli used (cf. Figure 1, Chaper 2; iso-luminance subjective gratings) in a few of our experiments had the same luminance component for both stimuli and hence any difference in response could thus be attributed to the subjective edges alone. Luminance cells in V1 responded in an orientation-specific manner to these subjective gratings.

*Does V1 influence the response of V2 cells to subjective contours?*

Does V1 play a role in the strong, more commonly seen response to subjective contours in V2? V1 sends a dense projection to V2 and so by silencing the projections from V1 to V2 and recording from V2, one would predict that the response to subjective contours should be washed away or be considerably attenuated, at the very least (of course, the response to luminance gratings should remain nearly the same and orientation maps for luminance gratings should still be seen). Such an experiment will be a litmus test for the claim that V2 cells build on sparse responses seen in V1.

*Top-down influences on V1 and V2 response.*

Does feedback from higher cortical areas lead to a response to subjective contours in V2?

In order to address this question, one would have to cool a large part of cortex (higher visual areas and association areas) except V2 and look for a response before cooling, during cooling (if feedback, response should wash out, otherwise stay unchanged) and post-cooling (response should recover). This experiment is relatively hard since one would have to ensure that the higher cortical areas are indeed inactive during cooling (by recording), and a large region of the cortex would have to be cooled and temperature maintained over several hours of imaging. The converse experiment of lesioning V1 and V2 has already been done in cats. Lesions in V1 and V2 destroy cats' ability to discriminate the orientation of subjective contours (de Weerd et al '93). This experiment provides evidence that V1 and V2 must be integral to subjective contour processing in the brain. The pathway(s) that lead to subjective contour perception in the brain must run through V1 and V2 and responses of V1 and V2 neurons are not just modulated by subjective contours; these neurons play an active role in subjective contour processing.

*Role of other areas in processing subjective contours.*

Are other areas involved in the processing of subjective contours? If so which areas might be involved and how are the responses of the cells in these areas modulated? Certainly, other areas must be involved in subjective contour processing. Lesions made in areas to which V1 and V2 project (but not in V1 and V2) also lead to a deficit in orientation discrimnability of cats to subjective contours (de Weerd et al. '93). So which areas might be involved? A possible way to address this question is to have a subject (cat or human) actively view subjective contours and record from the subject's brain with fMRI. This should give a rough idea of the areas that are activated by subjective

contours, after which conventional techniques of single-unit recording can be applied in these areas to investigate this issue in greater spatial and temporal detail.

Lastly, the responses to other classes of subjective contours (Kanizsa stimuli) must be investigated. Do the same cells/ same areas respond to the different subjective stimuli and are the underlying neural mechanisms the same?

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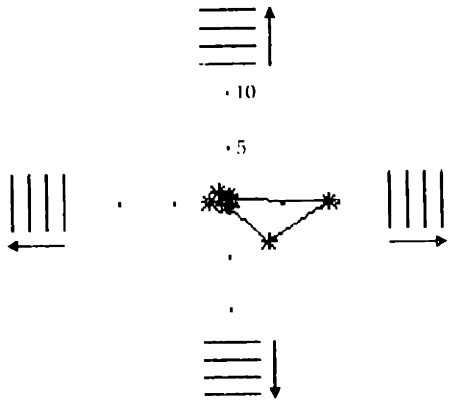
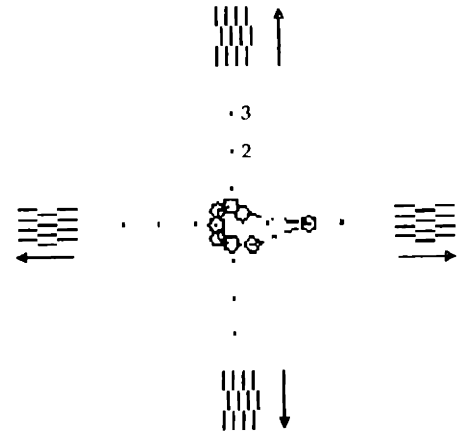
**Unit k0c08**



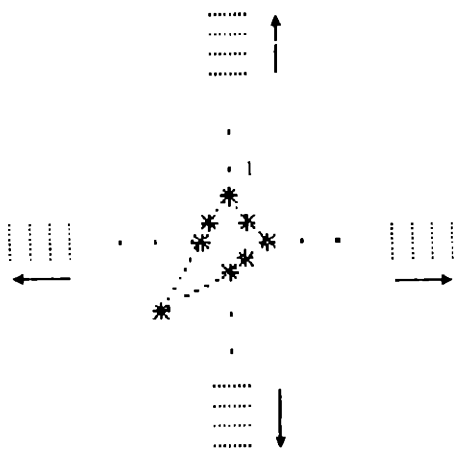
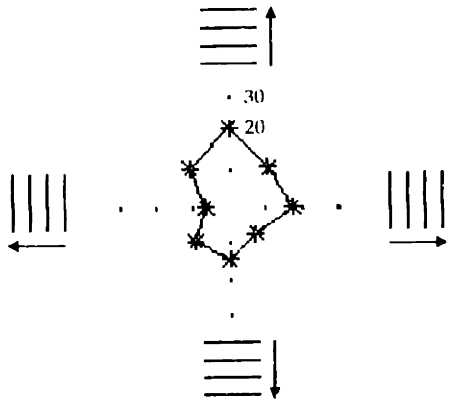
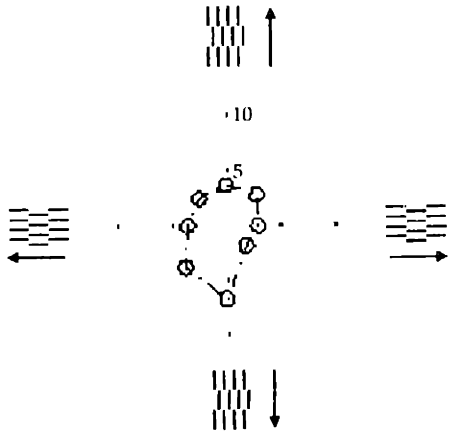



Figure 1. A subjective contour cell (cf. subjective criterion, Chapter 3) in V2 obtained at 650 μm depth below the cortical surface. Luminance gratings (0.15 cycles/deg.) (continuous lines) were shown (12 trials, 3 sec./stimulus presentation). Subjective gratings (0.15 cycles /deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency) (broken lines) and gratings composed of dots (same parameters as subjective grating) were interleaved for a time duration of 3 sec./ stimulus for 12 stimulus trials. The responses were summed and averaged for each stimulus seperately. The responses are shown in a polar form where the angle from the horizontal gives the direction of motion and the distance from the origin gives the response magnitude (spikes/ second). The cell showed the same orientation and direction preference for luminance and subjective gratings ($0^{o}$ vertical moving to the right) but preferred a dot stimulus of of different orientation and direction ($225^{o}$ diagonal, moving down and to the left).

**Unit j0f17**



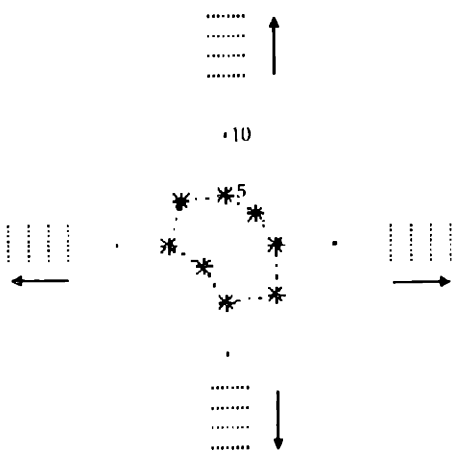



Figure 2. Another subjective contour cell (cf. subjective criterion, Chapter 3) in V2 obtained at 651μm depth below the cortical surface. Luminance gratings (0.15 cycles/ deg.) (continuous lines), subjective gratings (0.15 cycles /deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency) (broken lines) and gratings composed of dots (same parameters as subjective grating) were interleaved for a time duration of 3 sec./ stimulus for 8 stimulus trials. The responses were summed and averaged for each stimulus seperately. The responses are shown in a polar form where the angle from the horizontal gives the direction of motion and the distance from the origin gives the response magnitude (spikes/second). The cell showed the same orientation and direction preference for luminance and subjective gratings ($0^{o}$ vertical moving to the right) but preferred a dot stimulus of different orientation and direction ($135^{o}$ and $315^{o}$ diagonal).

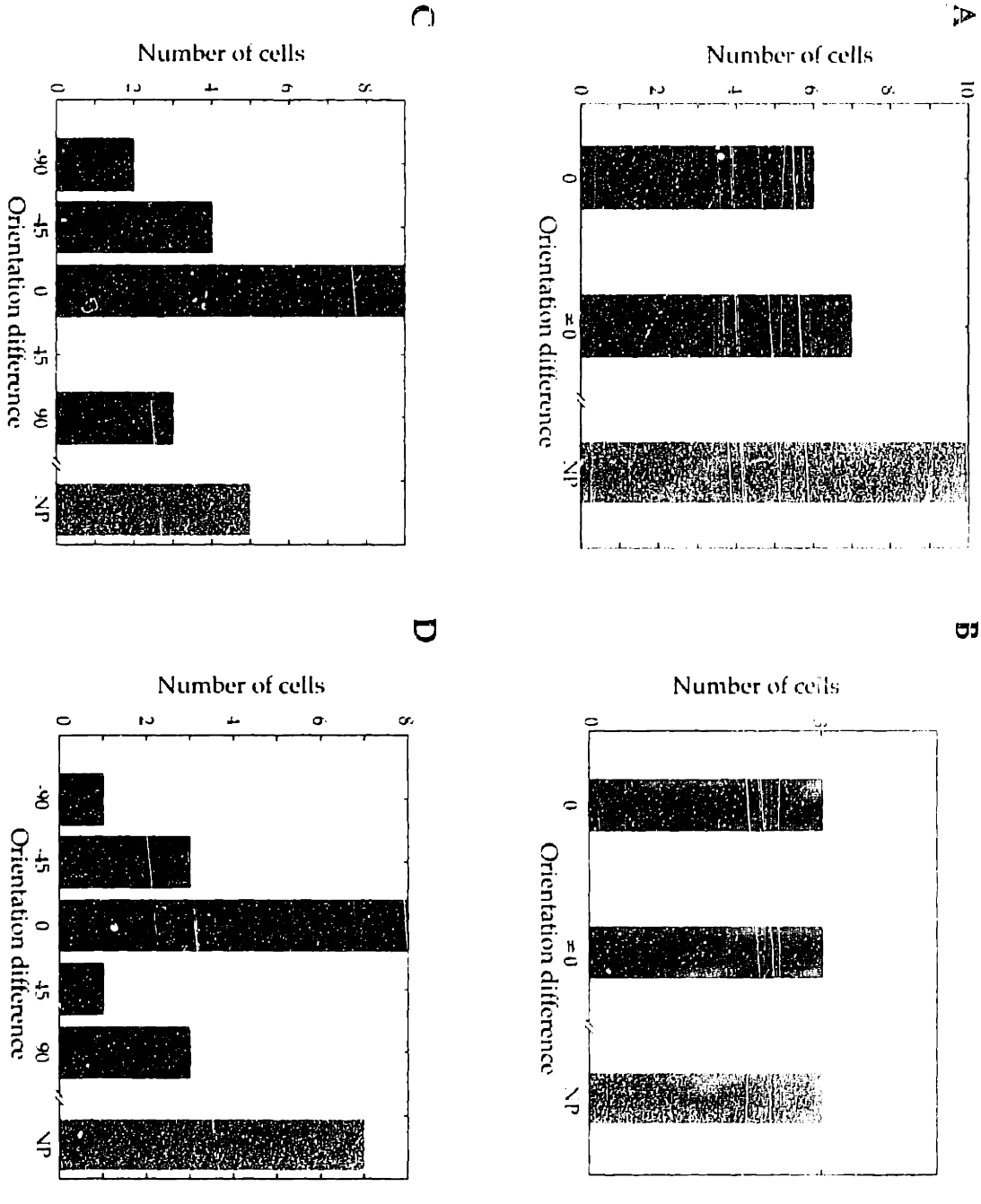

A
Number of cells
0
2
4
6
8
10
0
≠ 0
NP
Orientation difference
B
Number of cells
0
≠ 0
NP
Orientation difference
C
Number of cells
0
2
4
6
8
-90
-45
0
45
90
NP
Orientation difference
D
Number of cells
0
2
4
6
8
-90
-45
0
45
90
NP
Orientation difference

Figure 3. A. Frequency histogram of the difference in orientation preference between subjective gratings and gratings composed of a grid of dots for all of the V2 cells recorded (n = 23). 6 cells (26%) had the same orientation preference for both stimuli, while 7 cells (30%) did not share the same orientation preference for the two stimuli. 10 cells (43%) were silent to the subjective grating stimuli or to the dots stimulus and are shown in gray (NP = no subjective preference). These cells did not respond to any orientation of the subjective grating or the dots stimulus (or both).

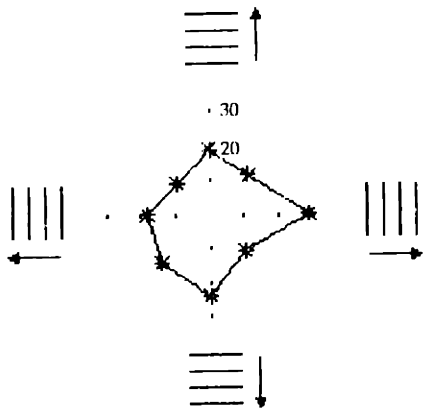
B. Frequency histogram of the difference in orientation preference between subjective gratings and gratings composed of a grid of dots for V2 cells that preferred the same luminance and subjective orientations (n = 9, contour cells). 3 cells (33%) had the same orientation preference for both stimuli, while 3 cells did not share the same orientation preference for the two stimuli. The remaining 3 cells were silent to the dots stimulus and are shown in gray (NP = no subjective preference). These cells did not respond to the dots stimulus in an orientation-specific manner (orientation selectivity index < 0.1).

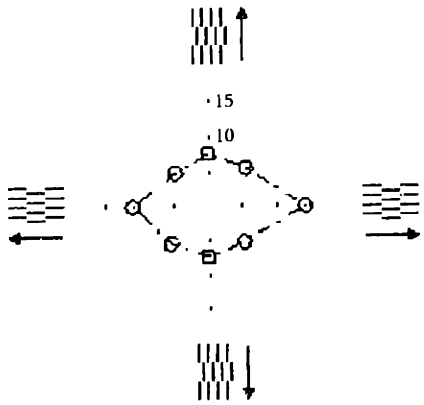
C. Frequency histogram of the difference in orientation preference between luminance and subjective gratings of V2 neurons (n = 23). 9 cells (39%) had the same orientation preference for luminance and subjective grating. 4 cells (17%) were found whose difference in orientation preference between luminance and subjective gratings was $\pm 45^{o}$. In 5 cells (22%), the difference between the two stimuli differed by $90^{o}$. 5 cells

were silent to the subjective grating stimuli and are shown in gray (NP = no subjective preference). These cells did not respond to the orientation of the subjective edges or the orientation of the inducing lines.

D. Frequency histogram of the difference in orientation preference between luminance gratings and gratings composed of dots over all V2 cells (n = 23). 8 cells (35%) had the same orientation preference for luminance and subjective grating. 4 cells (17%) were found whose difference in orientation preference between luminance and subjective gratings was $\pm 45^{\circ}$. In 4 cells (17%), the difference between the two stimuli differed by $90^{\circ}$. 7 cells (31%) were silent to the subjective grating stimuli and are shown in gray (NP = no subjective preference). These cells did not respond to the subjective edges or the inducing lines in an orientation-specific manner.

## Unit k0b04



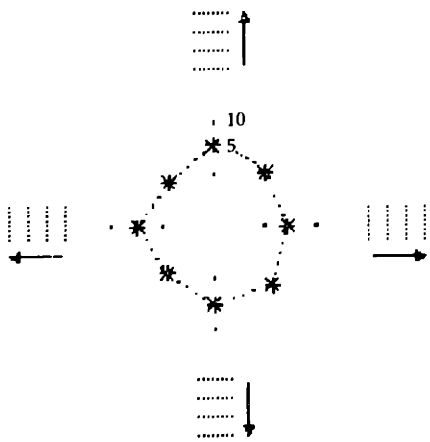
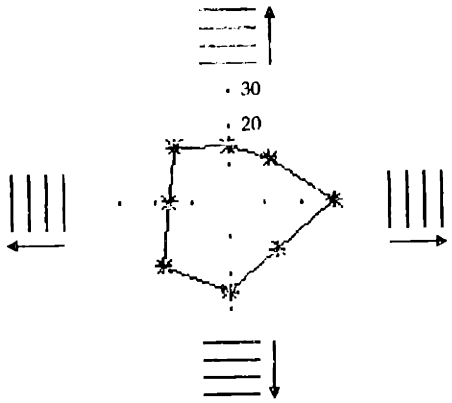
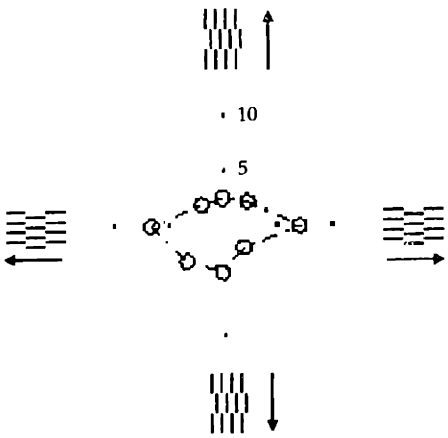



Figure 4. A simple, non end-stopped subjective contour cell (cf. subjective criterion, Chapter 3) in V2 obtained at 1770 μm depth below the cortical surface. Luminance gratings (0.15 cycles/deg.) (continuous lines) were shown (12 trials, 3 sec./stimulus presentation). Subjective gratings (0.15 cycles /deg. subjective frequency, 0.45 cycles/ deg. inducing lines frequency) (broken lines) and gratings composed of dots (same parameters as subjective grating) were interleaved for a time duration of 3 sec./ stimulus for 12 stimulus trials. The responses were summed and averaged for each stimulus separately. The responses are shown in a polar form where the angle from the horizontal gives the direction of motion and the distance from the origin gives the response magnitude (spikes/second). The cell showed the same orientation and direction preference for luminance and subjective gratings ($0^{o}$ vertical moving to the right) and showed no orientation tuning for the dots stimulus. The orientation tuning for subjective gratings was sharper (orientation selectivity index (OSI) = 0.25) than for the dots stimulus (OSI = -.03). The cell responded more vigorously to a $0^{o}$ subjective grating stimulus (14.2 spikes/sec.) as compared to a $0^{o}$ dots stimulus (7.2 spikes/sec.).

**Unit k0b01**



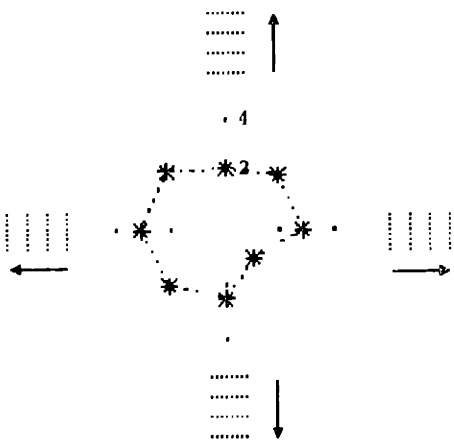



Figure 5. Another subjective contour cell (cf. subjective criterion, Chapter 3) in V2 obtained at 1779 μm depth below the cortical surface. Luminance gratings (0.15 cycles/ deg.) (continuous lines), subjective gratings (0.15 cycles /deg. subjective frequency, 0.45 cycles/deg. inducing lines frequency) (broken lines) and gratings composed of dots (same parameters as subjective grating) were interleaved for a time duration of 3 sec./ stimulus for 16 stimulus trials. The responses were summed and averaged for each stimulus seperately. The responses are shown in a polar form where the angle from the horizontal gives the direction of motion and the distance from the origin gives the response magnitude (spikes/second). The cell showed the same orientation and direction preference for luminance and subjective gratings ($0^{o}$ vertical moving to the right) and showed no orientation tuning for the dots stimulus. The orientation tuning for subjective gratings was sharper (orientation selectivity index (OSI) = 0.36) than for the dots stimulus (OSI = 0.15). The cell responded more vigorously to a $0^{o}$ subjective grating stimulus (7.0 spikes/sec.) as compared to a $0^{o}$ dots stimulus (2.8 spikes/sec.).

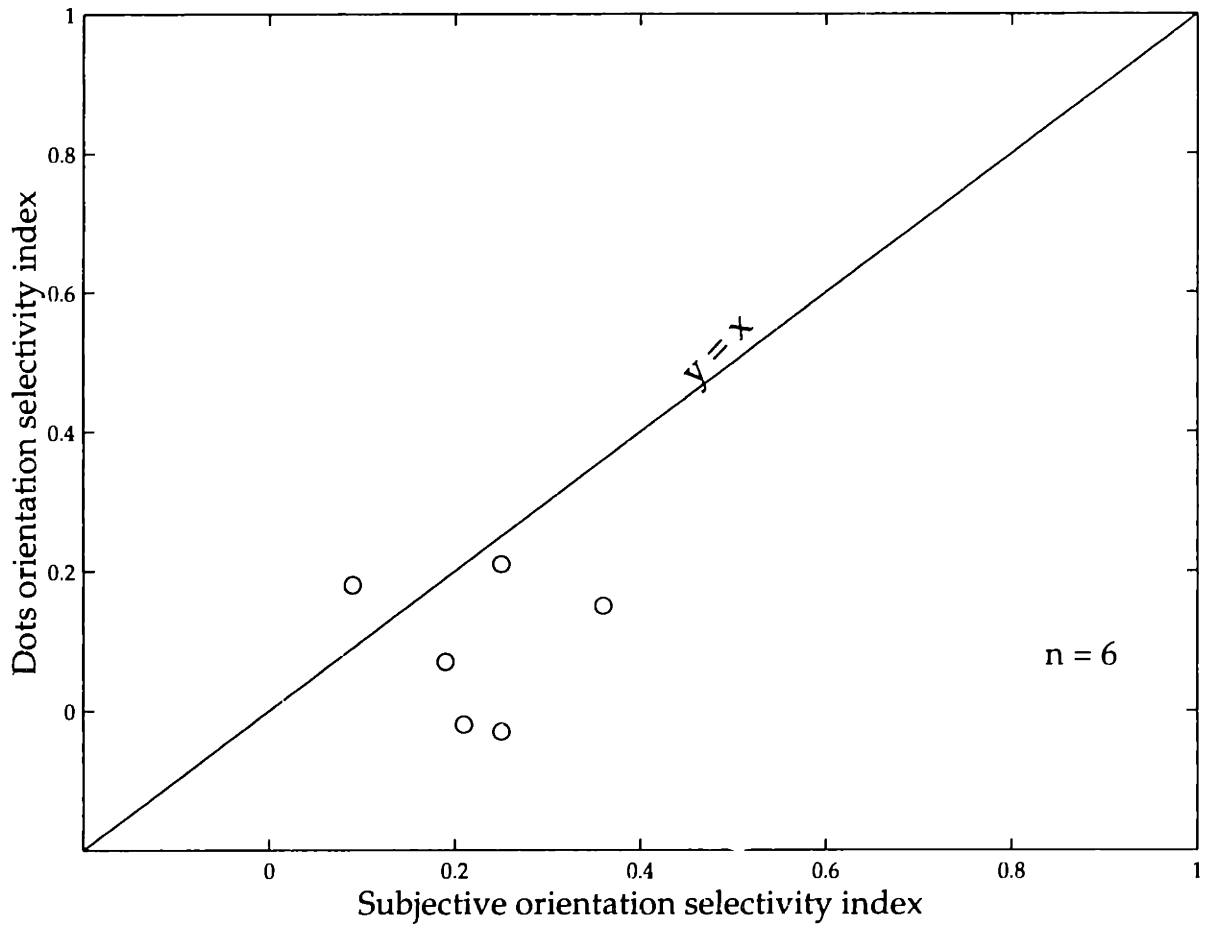

Dots orientation selectivity index
Subjective orientation selectivity index
y = x
n = 6
0
0.2
0.4
0.6
0.8
1

Figure 6. A comparison of orientation tunings between subjective gratings and gratings composed of dots for cells in V2 that preferred the same luminance and subjective orientations and whose orientation preference for the dots stimulus did not differ(6 cells). The orientation selectivity index for each stimulus was calculated by using the following formula :

$$(response_{optimal} - response_{ortho.}) / (response_{optimal} + response_{ortho.}),$$

The formula yields a number in the range [0,1] with higher values signifying sharper orientation tuning. For each cell, the orientation selectivity index for subjective gratings and the dots stimulus is plotted. $y = x$ is the line at which the orientation indices for both gratings is equal; above the line the subjective orientation index has a higher value than the luminance orientation index and vice-versa for the region below the line. Most cells have sharper orientation selectivity for subjective gratings (mean = 0.23) than for the dots stimulus (mean = 0.09) as indicated by the fact that most points (5/6 cells) fall below the line. The difference between the two indices is statistically significant (two-tailed t-test, $p < 0.05$). The correlation between the orientation indices for the two stimuli is negligible ($r = -0.04$).

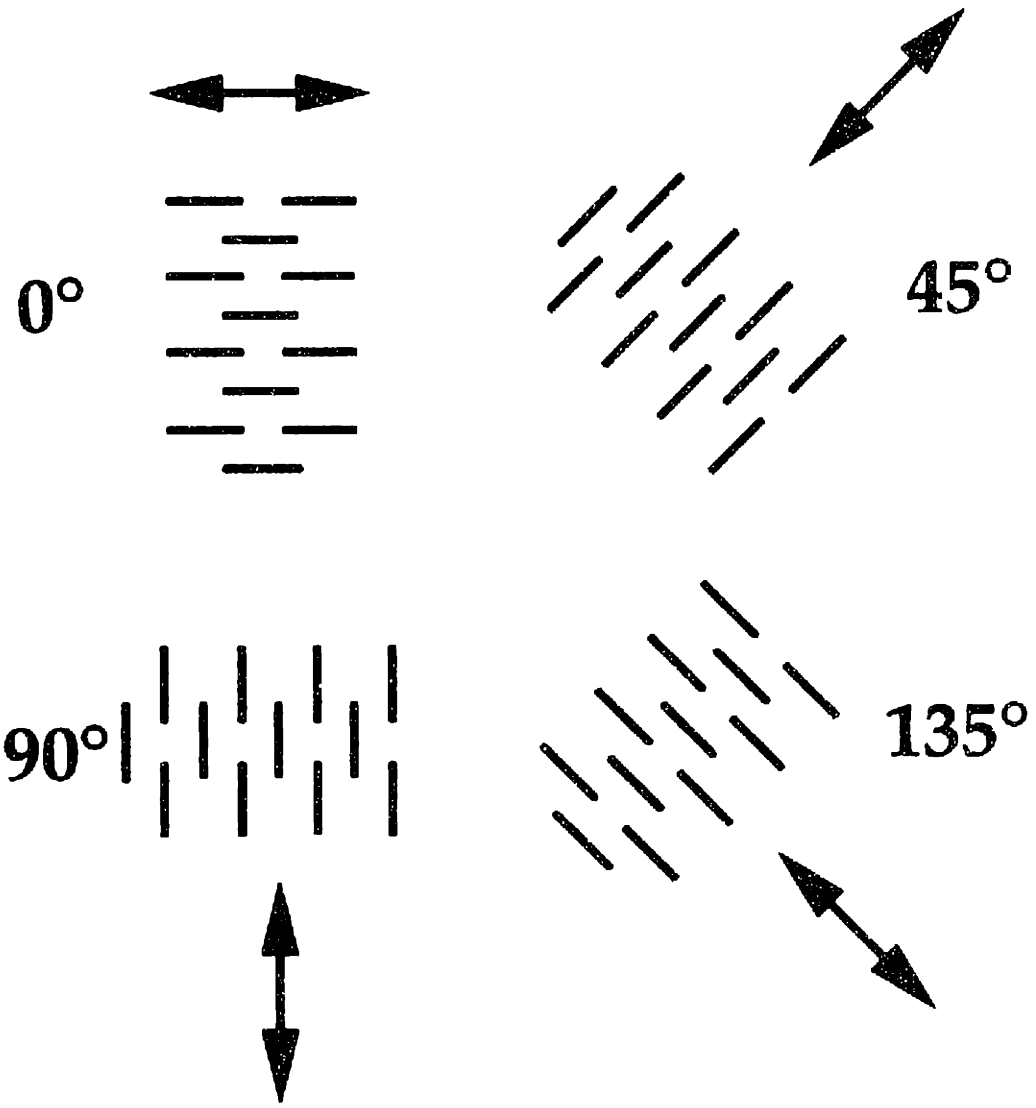

0°
45°
90°
135°

Figure 7. Partially overlapped gratings used in single-unit studies on contour cells in V2 and imaging studies on V1. Overlapped grating stimuli of four different orientations (0°, 45°, 90° and 135°) were shown. The overlap measured a quarter of the inducing line length. The inducing line lengths were the same as those used for the subjective gratings. Overlapped gratings have a luminance gradient along each "edge" formed by the inducing line ends. There are twice as many lines on one side as the other, which results in the luminance gradient.

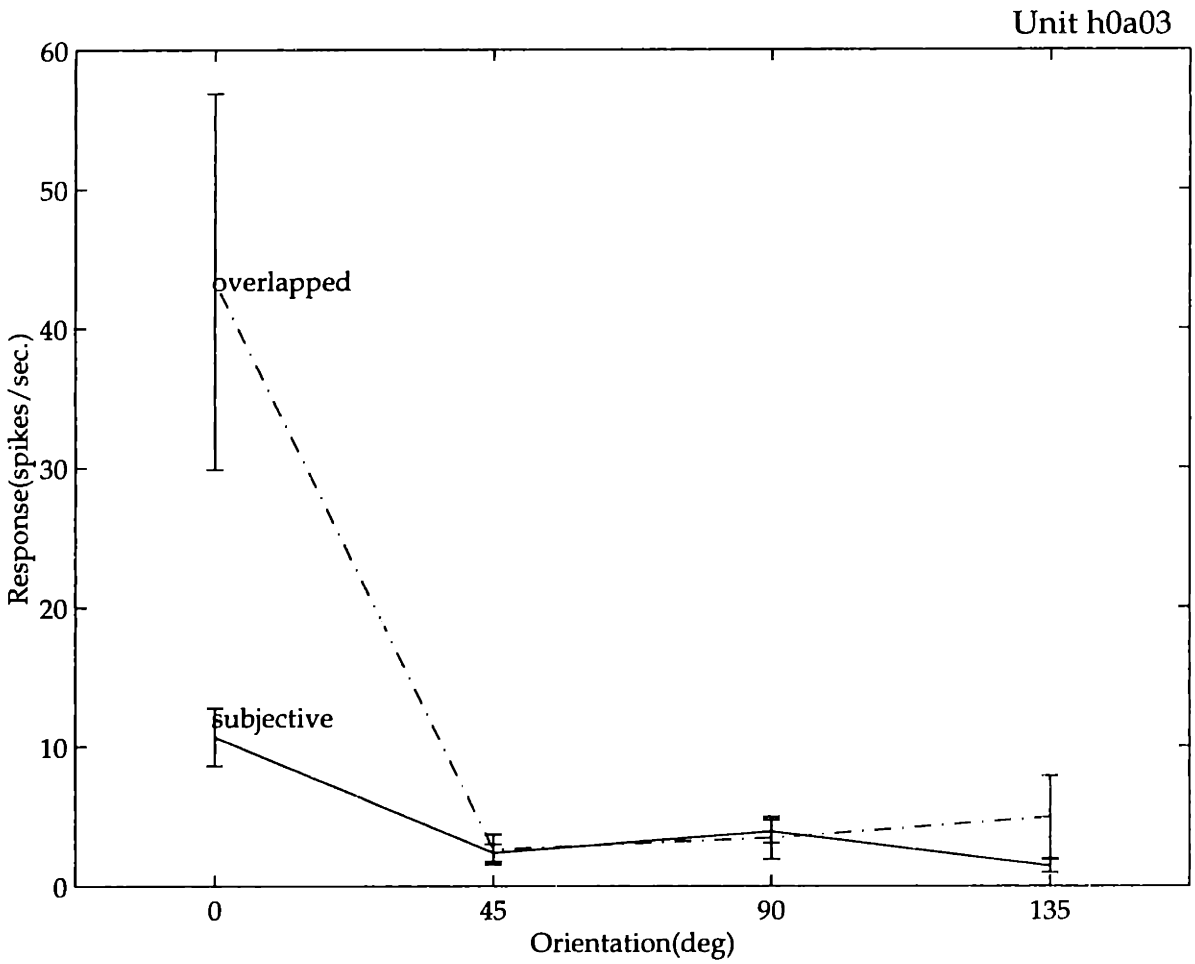

Unit h0a03
60
50
40
30
20
10
0
Response(spikes/sec.)
overlapped
subjective
0
45
90
135
Orientation(deg)

Figure 8. A pure subjective contour cell in V2 that exhibited a greater response to an overlapped grating of $0^{o}$ orientation than a subjective grating of the same orientation. The cell's tuning curves for subjective and overlapped gratings are shown in continuous lines and broken lines respectively. The cell preferred a $0^{o}$ orientation grating for luminance (not shown), subjective and overlapped gratings.

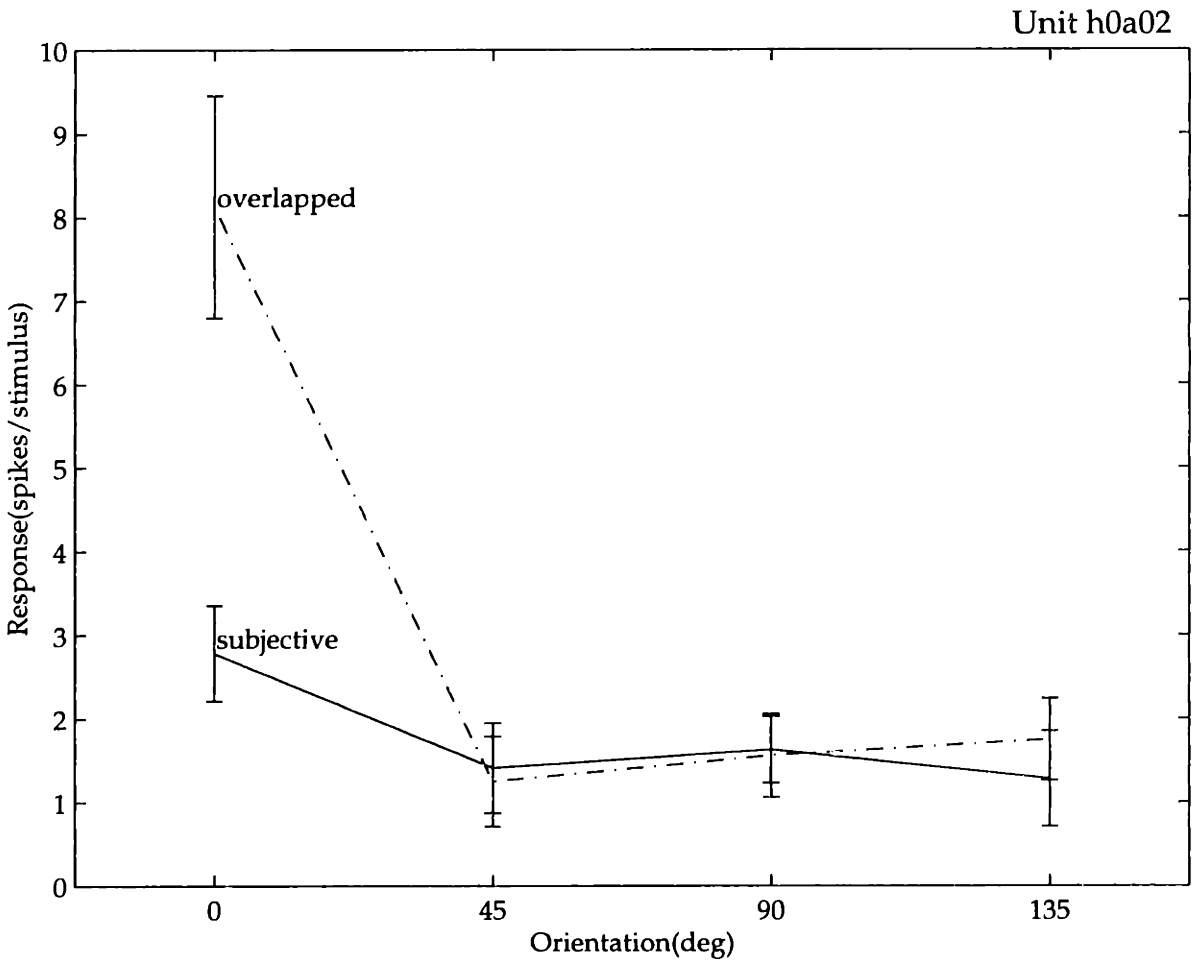

Unit h0a02
overlapped
subjective
Response(spikes/stimulus)
Orientation(deg)
0
45
90
135
1
2
3
4
5
6
7
8
9
10

Figure 9. Another contour cell in V2 that also responded more vigorously to an overlapped grating than to a subjective grating.