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Meridional anisotropy in visual processing: implications for the neural site of the oblique effect

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Abstract

The contention is examined that the oblique effect, i.e., the well-known performance deficit in detecting orientation difference in oblique lines as compared to vertical and horizontal ones, has its origin in a relative deficiency of neurons with obliquely-oriented receptive fields in the primary visual cortex. Psychophysical observations demonstrate a prominent oblique effect also in visual tasks involving widely-separated elements and other stimuli that would elicit little or no response in oriented neurons in the visual cortex. Conversely, some tasks, e.g. position discrimination, exhibit no oblique effect even with short, high-contrast lines. When the comparison with the reference can be accomplished during a single brief exposure rather than sequential ones, thresholds for orientation differences between adjacent contours in oblique meridians are also elevated compared to those in the vertical and horizontal, but to a lesser extent. In one particular texture discrimination task some but not all observers have a conspicuous oblique effect. The discrimination only of the direction of streaming random dots, not of their speed, is poorer for motions in oblique meridians. The findings imply that the neural locus for the oblique effect is more central than the primary visual cortex.

Keywords: Orientation discrimination; Visual cortex; Visual thresholds; Random-dot motion; Form discrimination

1. Introduction

That horizontal and vertical contours have an advantage over oblique ones was known already to Ernst Mach (1861), who found that observers were several times more accurate in setting a line parallel to a horizontal or vertical comparison line than when the task was to match the orientation of an oblique line. Since Mach's time, horizontal and vertical contours have been found superior in both animals and the human; the reduction in performance in oblique meridians has become known as the oblique effect (Appelle, 1972). References to various manifestations of the oblique effect abound in the literature.

Hubel and Wiesel's discovery of orientation-selective neurons in the primary visual cortex of the mammal soon was accepted as having the implication that contour orientation is an organizational feature right at the beginning of processing in the visual cortex. It was then a small step to postulate that the oblique effect had its root in an unequal angular distribution of these units (Bouma & Andriesson, 1968) and in fact there is evidence for this both in the cat and in the monkey cortex (Celebrini, Thorpe, Trotter, & Imbrie, 1993; DeValois, Yund, & Hepler, 1982; Mansfield, 1974). Even the receptive fields (Levick & Thibos, 1982) and dendritic trees (Passaglia, Troy, Rüttiger, & Lee, 2002) of retinal ganglion cells may show directional anisotropy.

It is, therefore, of interest to compare the oblique effect in a range of visual tasks and examine conclusions about the site in the stream of visual processing at which the orientational anisotropy might have its origin. Several of the experiments described here have been reported before in the 150-year history of the oblique effect, but performing them in a shared setting with substantially the same stimulus components, exposure conditions and observers endows them with some degree of commonality.

In a previous paper (Westheimer & Beard, 1998) the oblique effect was studied in visual tasks that depend primarily on the most distally-located visual apparatus, the retina. Simple thresholds such as detection and intensity-discrimination of lines in the fovea do not

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show much of an oblique effect. For resolution the evidence is mixed. Earlier results on acuity advantage for horizontal and vertical gratings (Mansfield, 1974; Mitchell, Freeman, & Westheimer, 1967) do not extend to the two-line resolution task with short, brief foveal stimuli. On the other hand there is strong consensus that orientation and vernier alignment discrimination thresholds are worse in oblique meridians than in the horizontal or vertical. This applies not only to the fovea but also in all positions in the retinal periphery (Davey & Zanker, 1998; Westheimer, in preparation). The experiments described here are designed to extend consideration to a variety of visual stimuli marked by a geometrical simplicity that permits unambiguous characterization of orientation. A start had already been made by the findings of an oblique effect in the orientation discrimination of virtual lines formed by a pair of blobs (Heeley & Buchanan-Smith, 1996) or dots (Westheimer, 2001) and by the axis of symmetry of ellipses or a pair of intersecting lines Li and Westheimer (1997).

2. Methods

Geometrical patterns were created under computer control on a black and white CRT monitor (Sony 15″ Trinitron) with 1074×768 pixel resolution. An antialiasing program step assured smooth contours in all orientations. Observation distance varied depending on the screen area needed to accommodate the targets, from 45 cm for target placement in the parafovea, to 5 m for foveal viewing. The screen luminance of the white areas was about 50 cd/m^2 and that of the unilluminated background less than 1 cd/m^2.

Observers were required to make binary orientation judgments as described in detail for each experiment. The procedure employed the method of constant stimuli in which the pattern was displayed with orientation randomly at one of several values distributed in equal steps bracketing the null situation. On each trial, the observer registered the decision whether the test pattern appeared rotated in a clockwise or counterclockwise direction with respect to a standard; the latter was shown either before each test pattern in the manner of the two-interval forced choice (2-IFC) paradigm, or was included in the test presentation for simultaneous comparison. No error feedback was provided. Runs of 150 trials produced a psychometric curve and allowed the identification of slopes and mean values, with standard errors, by probit analysis. For each condition there were at least two runs, and often many more, on different days. Care was taken to preclude perceptual learning effects by giving the observers sufficient training sessions for the psychometric curves to have stabilized. Experiments were performed in a dark room excluding unwanted spatial and orientation clues. Presentation duration was usually 200 or 300 ms, short enough not to include refixation saccades. Where pattern elements were in the retinal periphery, there was always a small central fixation dot. All points plotted in the figures have standard errors between 5% and 10% of the indicated mean values. The index of obliquity effect is defined as the ratio of the threshold average in the 45° and 135° meridians to that in the vertical and horizontal. [1] As a general rule the volume of data accumulated in each particular experiment permits the conclusion that an obliquity index of about 1.15 is significantly different from unity at the 5% level. Fortunately, as can be seen in the tables and figures, the salient phenomena are sufficiently compelling to make detailed statistical analysis unnecessary.

Observers had experience in psychophysical research and their refractive and oculomotor status was unexceptional. They included the author and several biology undergraduate in their early twenties who at the outset were unaware of the ultimate purpose of the research. The protocol was approved by the institutional committee for the protection of human subjects.

3. Results

3.1. Two-interval forced choice thresholds

Because the adequate stimulus for orientation-selective neurons in the primary visual cortex is, in the first instance, a line or an edge, or a configuration composed of them, the first set of experiments concerns itself with patterns containing explicitly-drawn lines. Although grating and Gabor stimuli have become popular, their thresholds are either the same as lines' or under some conditions worse (Westheimer, 1998).

The orientation attribute of a pattern is traditionally probed by finding the minimum detectable difference in orientation; that is in fact what Mach had looked at. With modern psychophysical procedures and computer-driven displays, the orientation difference threshold can be determined simply and with good precision. In experiments seeking the minimum detectable difference, the observer must have the standard available: when the observer judges whether the test line in any given presentation appears tilted clockwise or counterclockwise with respect to, say, the vertical, we have to have

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[1] In an observer's visual field, a meridian is a plane containing the antero-posterior axis of the eye. With the head erect, the vertical meridian is defined by a plumb-line and the horizontal is orthogonal to it. By convention, the left half of the horizontal meridian as seen by the observer has zero angle, and meridional angles increase in a clockwise fashion, again as seen by the observer, so that a line going up and to the left from the fixation point would be along the 45° meridian.

assurance that the actual vertical is available for comparison. It is true that most observers have a remarkably good internal representation of the vertical, and usually also the horizontal, meridian. For example, even in a completely dark room, without feedback of results, the author has exhibited a 0.5° orientation discrimination threshold around the vertical for a foveal line 30′ in length shown just by itself. In general, however, such a performance cannot be taken for granted, and in any case it is never present for oblique lines. Hence, in the experiments to be described now, the standard was always shown in a separate presentation with spatial and temporal parameters identical to the test presentation, separated by a pause of 300 or 500 ms.

Orientation discrimination data with this 2-IFC paradigm for a foveal line stimulus, 20′ in length, are shown in Fig. 1. It is seen that the sensitivity is best for horizontal and vertical meridians and least for lines in the 45° and 135° meridians, intermediate meridians fitting in between. Vertical and horizontal are not always the same, depending on the individual, but these secondary differences will not be stressed in this study: attention is concentrated on the general impairment of performance in the obliques compared with the cardinal meridians, simply characterized by the threshold ratio (45° + 135°)/(H + V), the obliquity index. Its mean value for the five observers in Fig. 1 is 2.85.

In a series of steps, patterns were dissociated from the short line stimuli that would match the receptive field of foveal oriented receptive fields in the primary visual cortex. First, there were foveal lines 60′ long (row 2 of Fig. 2) and this increased the obliquity index somewhat. The next experiment dispensed with continuous straight lines and utilized only the distal 1° segments of a 5° line centered on the fovea, the central portion of the line being blocked out. The orientation discrimination threshold for this configuration is very good indeed for the horizontal and vertical, about 20′ of orientation, with the obliquity index remaining high (row 3 of Fig. 2). In the next configuration there was no explicit line; the virtual line whose orientation had to be discriminated was demarcated by a pair of rectangular arrow wings at each end. The line segments making up the arrow wings were tilted 45° either side of the virtual line axis (row 4, Fig. 2). The special property of this pattern is that when the orientation of the (virtual) oblique line is being tested, it is demarcated by explicit horizontal and vertical line segments, and the (virtual) horizontal one by explicit 45° and 135° line segments. In the experiment, the orientation of the whole configuration was changed; rotating the virtual line out of the 45° meridian, for example, was accomplished by rotating the arrow wings out of the horizontal and vertical. The outlining of the orientation of an absent real test line by 45°-offset configuring line segments affected the obliquity index only minimally. It should be remembered that even for short lines seen by themselves in the retinal periphery, there is an obliquity index of about 2 (Westheimer, 2003) so if the decision had been made on the basis of the tilt of the demarcating lines rather than of the configuration as a whole, the obliquity index

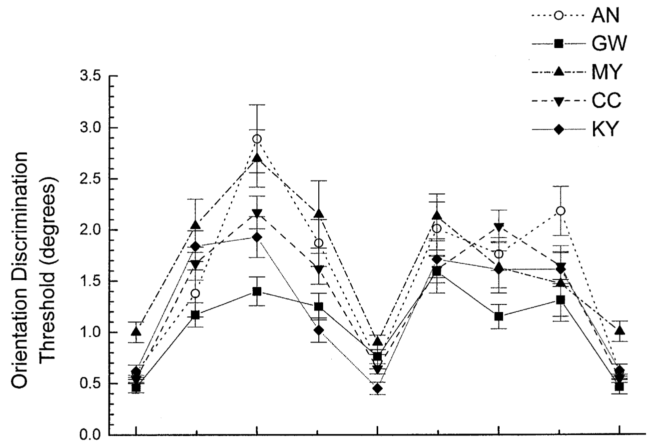

Fig. 1. Orientation discrimination for foveal lines, 20′ in length, in eight meridians 22.5° apart, for five observers. 2-IFC psychophysical procedure in which the standard is shown first, followed after a pause by the test. Overall obliquity index ((45° + 135°)/(H + V)) for all observers is 2.85. Obliquity index > 1 signifies a poorer performance when configurations are in oblique meridians than when they are in the vertical and horizontal. Standard error of each determination is about 10% of its value.

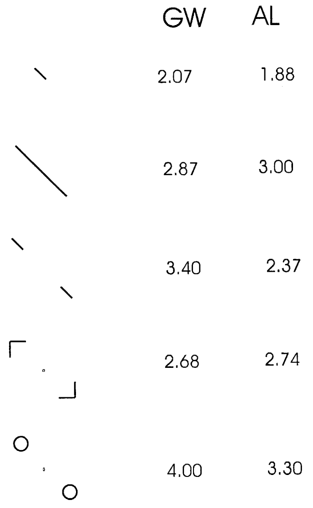

Fig. 2. Obliquity index in two observers for five different orientation discrimination tasks. Fixation in center of configurations, explicitly marked by a fixation point in some of the configurations. In each case a comparison is shown first (300 ms exposures). From top to bottom: foveal line 15′ in length; line 1° in length; virtual orientation of 5° line marked by only its outer 1° segments; virtual orientation of a 5° line marked by a pair of rectangular arrow wings each 1° in length, tilted 45° with respect to the orientation of the virtual line; virtual line joining two circles 5° apart.

would have been less than 1. Finally, the virtual axes whose orientation had to be discriminated were demarcated not by lines at all but by circles 20′ in diameter, to which oriented receptive fields are not very responsive. Yet there was a most prominent oblique effect (row 5, Fig. 2). The last experiment was duplicated in observer GW with 1° diameter circles that were 20° apart; the obliquity index was found to be of about the same magnitude, 3.68. These results should be read in association with earlier ones demonstrating a powerful oblique effect for the orientation of an ellipse and for the axis of symmetry of more complex configurations (Li & Westheimer, 1997).

So far, evidence has been presented that overt oblique line segments are not a necessary condition for the oblique effect. Other configurations show even stronger performance deficits in oblique meridians. But this is not to say that oblique lines in general fare more poorly in vision than vertical and horizontal ones. That some simple visual thresholds believed to have an underlying retinal origin exhibit no oblique effect has been mentioned above; in addition there are some spatial tasks clearly needing sophisticated processing, presumably cortical, where there is no essential difference in the performance with horizontal and vertical line segments compared with oblique ones. Some have already been described (Westheimer, 2001): there is no oblique effect in experiments with the same spatial and temporal parameters (and even an overlap of observers) as the ones used here, in which the discrimination of the length of lines and of their separation is measured. To provide a ready comparison with the data in Fig. 2, the obliquity factors for lateral displacement of 15′ foveal lines, for a three-line bisection task and for the discrimination of the spatial interval separating two dots have been determined afresh and are shown in Table 1. They do not differ from unity. The argument whether this is compelling evidence for equal representation of all orientations in the primary visual cortex will not be joined here; suffice it to say that there is no oblique effect in some spatial thresholds where short lines segments are the stimulus, whereas a powerful oblique effect is seen when judging the virtual orientation of a configuration of elements which by themselves are not elongated and presumable only minimally address the classical orientation-selective receptive fields.

Table 1
Obliquity index for (a) detection of overall displacement in direction orthogonal to line length, (b) bisection, and (c) discrimination of spatial interval separating two features

	GW	AL
(a) 15′ foveal line—lateral jump	0.85	1.05
(b) 15′ foveal line simultaneous comparison (bisection)	0.83	1.05
(c) Spatial interval discrimination of two dots 4° apart	0.91	1.00

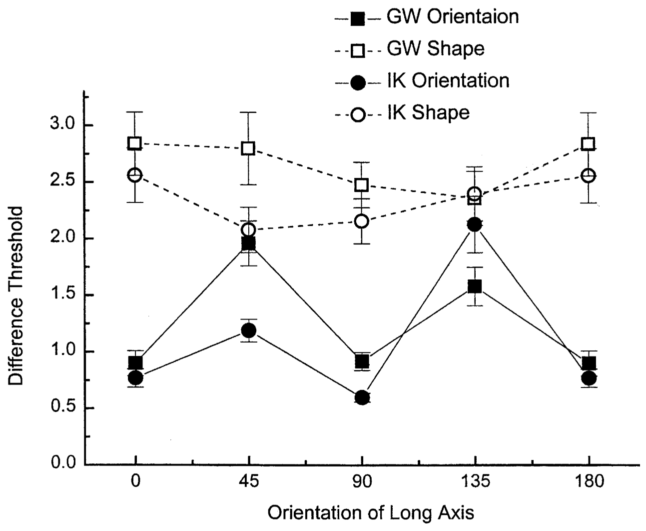

Fig. 3. Thresholds for differences in the orientation (solid symbols and lines) and length/width ratio (open symbols and dashed lines) of ellipses, 45′ long axis, 30′ short axis. Foveal fixation. Reference and test stimuli exposed for 200 ms each, separated by a 500 ms pause. Scale of axis of ordinates reads as degrees of orientation, or percent change in ratio of the axes of the ellipse. Obliquity index for GW (squares) 1.95 for orientation, 0.97 for shape; for IK (circles) 2.42 for orientation and 0.95 for shape.

A good illustration of the task-dependent difference in the oblique effect measured on identical configurations is given in Fig. 3. The pattern here is an ellipse, long axis 45′ and short axis 30′, foveally presented for 200 ms in a 2-IFC procedure. In one set of experiments, the threshold was determined for detecting differences in the ellipse's orientation, in the other, in the ellipse's shape, i.e., the just detectable change in the ratio of the long and short axes. In all other respects the situations were identical. The figure shows that the oblique effect is prominent for orientation discrimination (obliquity index 1.95 and 2.42 for the two observers) but absent for eccentricity discrimination (obliquity index 0.97 and 0.95). As was pointed out by Li and Westheimer (1997), who first described the oblique effect in ellipse orientation, it is the ellipse's axes of symmetry rather than the individual contour segments of which it is composed that determine the oblique effect.

3.2. Sequential versus simultaneous presentation

As has been stressed earlier, it is mandatory in these experiments to provide the observer with a standard against which the orientation of the test stimulus is to be judged. So far this was accomplished by the 2-IFC procedure in which the standard always preceded the test. It has been shown by Heeley and Buchanan-Smith

(1992) that there was less of an oblique effect if the standard (in their experiment an annulus containing a grating) is shown at the same time as the stimulus (a 1.5° circular grating patch) than when the two appear successively.

Two reexamine the issue, the comparison–pause–test sequence that has been employed in the experiments so far described in this study was replaced with one in which both the test and the standard stimuli appeared in a single 300 ms exposure. The test line whose orientation had to be judged was accompanied by the reference which must necessarily be in a non-overlapping location. The results can be affected by the spatial gap between them, a parameter that had been investigated separately earlier (Westheimer, Shimamura, & McKee, 1976); a 12′ separation was used here, sufficiently wide to minimize any orientation interaction between comparison and test lines.

Fig. 4 gives data on the obliquity index for the orientation discrimination of a single foveal 15′ line in which the comparison is in a preceding exposure followed by a pause, and also when the comparison, now a pair of laterally flanking lines 12 min to each side, is contained in the same exposure. There is less of an oblique effect in the second situation. Using a configuration in which a single comparison line is positioned collinearly, there is a similar reduction. Overall for all observers and the two patterns, the obliquity index for sequential comparison is 2.69 and for simultaneous comparison 1.40. It is evident that some portion of the oblique effect in orientation discrimination may be explained by a poorer very-short term memory for oblique orientations compared to that for the vertical and horizontal. However, when both test and reference are seen at the same time, the discrimination may, in addition to the orientation difference, involve a component of relative spatial location of the line ends, which is known to have distinguishably different processing characteristics (Westheimer, 1996).

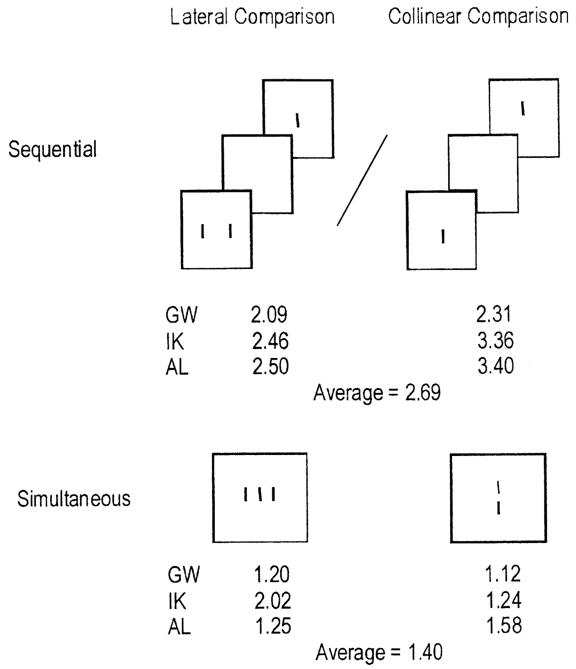

Fig. 4. Obliquity index for orientation discrimination for three observers when reference is shown in a separate, preceding exposure with a 500 ms pause, and when reference and test lines are in same exposure. Lines were 15′ long and reference was either a flanking pair (left side of figure) or a single collinear line (right).

This does not by any means exhaust the causative factors, as is illustrated in the next experiment, which is a modification of the one of row 5 of Fig. 2. There were three circles, each 10′ in diameter and the task consisted of the detection of the direction of misalignment of the middle circle with respect to the virtual line joining the outer two, whose overall separation was either 40′ or 120′. Thresholds for three observers and for orientations 22.5° apart are shown in Fig. 5. There is a measurable oblique effect, particularly for the wider separation. Calculations of the average obliquity index for all three observers gives a value of 1.18 for the 20′ and 1.45 for 1° center-to-center separation, the latter significantly larger than unity at the 1% level. In this experiment there are no complications about lack of simultaneity (all picture elements always appeared simultaneously and the configuration contained its own reference) nor could any convincing arguments be developed for the immediate involvement of orientation-selective receptive fields in the primary visual cortex, because the configuration contained no explicitly drawn linear contours. To confirm the conclusion from the data in Fig. 2 that the oblique effect increases with component separation, measurements were obtained on observer GW with 1° circles separated by 10° in addition to ones with 20′ and 60′ separation shown in Fig. 5. The obliquity index increased to 2.04, compared to 1.27 and 1.47 for 20′ and 60′ separation respectively for this observer.

3.3. Streaming random dots

3.3.1. Orientation discrimination for dynamic random dot patterns in different meridians

A 100% correlated cinematogram consisting of 76 bright dots in random locations within a circular area 3.75° in diameter, 50 ms frame interval, was shown for 500 ms, moving at the rate of 3.6° s^{-1}. Preceding the exposure the observer was shown a line indicating the reference meridian. In each trial the streaming random dots moved in one of seven directions, bracketing the reference meridian in equal steps, and the observer had to indicate whether the motion appeared to differ from the reference in a clockwise or counterclockwise direction. The experiment was performed with motion directions bracketing the horizontal, 45°, vertical and 135°

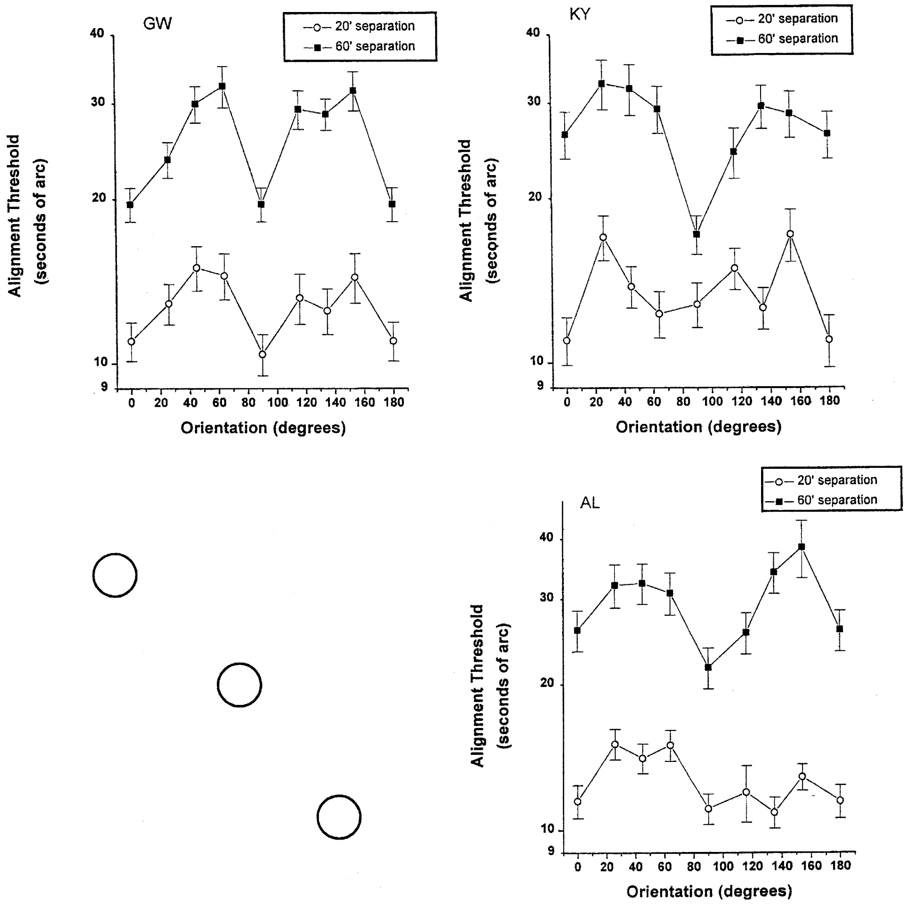

Fig. 5. Alignment thresholds in the three-circle task (shown schematically) in three observers as a function of orientation of the virtual axis along which circles are arrayed. Center-to-center separation of circles 20′ and 60′; circle diameter 10′.

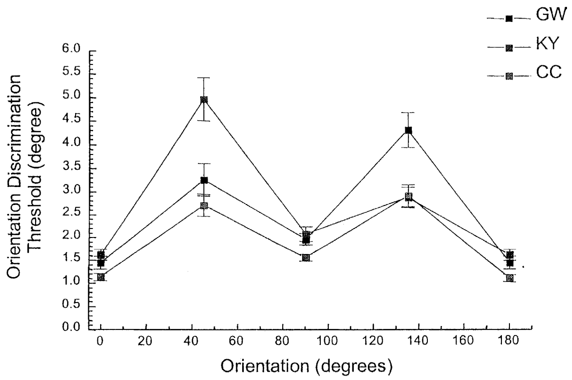

Fig. 6. Orientation discrimination of axis-of motion of streaming random dots. Just discriminable difference in orientation of a 100% correlated random dot cinematogram, as a function of meridian in which the motion took place. Exposure duration 500 ms, velocity 3.6° s^{-1}, circular area 3.75° in diameter, 2.23 dots/square degree. The obliquity index for the three observers was 2.21, 2.12, and 2.09.

meridians. As can be seen in Fig. 6, the observers had better motion-orientation thresholds in the vertical and horizontal than in the obliques. The obliquity index was 2.21, 2.12 and 2.09 for observers GW, KY and CC respectively.

3.3.2. Weber fraction for speed of stroboscopic motion in a random-dot cinematogram

A 100% correlated cinematogram consisting of 76 bright dots in random locations within a circular area 3.75° in diameter, 50 ms frame interval, moving at a rate of 3.6° s^{-1}, was shown for 500 ms, and then again, after a pause, with a speed that was randomly faster or slower, in a constant stimuli arrangement. The just-discriminable difference in speed, expressed as a percentage of the reference speed, is shown in Fig. 7 for three observers. The obliquity was 0.98, 0.94 and 1.04 for observers GW, KY and CC, respectively.

These results, illustrating that for an identical stimulus situation there is an oblique effect in one discrimination task and not in another, confirm the findings in a recent similar study by Matthews and Qian (1999).

3.4. Oblique effect in texture discrimination

Finally, an experiment will be described whose equivocal results illustrate an additional facet of the problem. The task involved the decision whether in a square array of texture elements, “ribs” of size differ-

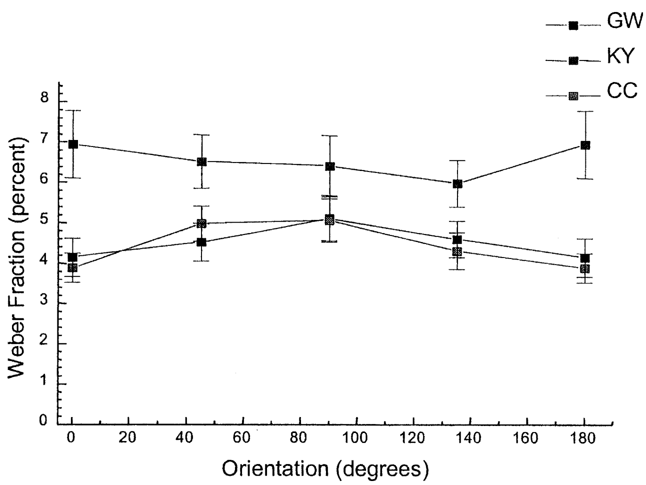

Fig. 7. Just discriminable difference in speed of streaming random dots as a function of the orientation of their axis of motion. Parameters as in Fig. 6. There is no oblique effect for this task.

ences appeared along rows or along columns. The configurations consisted of a 9×9 array of circles, each 8.6′ in diameter with center-to-center separations of 20′. For each presentation, which lasted 300 ms, the configuration was modified by increasing the diameter of the elements in randomly either alternate rows or alternate columns. The increase was randomly 0′, 1′, 2′ or 3′ and the observer had to signal whether there was a texture difference along rows or along columns. In this way the minimal size difference of the elements was determined for which the observer could on 75% of occasions correctly identify the direction of the texture difference. The experiment was performed with the edges of the square array making angles of 0°, 22.5°, 45°, and 67.5° with the horizontal. Data for five observers are shown in Fig. 8. A clear oblique effect, thresholds peaking for the 45°/135° meridians, was exhibited by three of the five observers, and none by the other two. Although the results were robust and showed no practice effect on the three experimental days, it remains to be demonstrated whether long-term training with error feedback would change the situation. As in the three-circle alignment configuration (Fig. 5), the pattern here also contained its own reference and hence did not need a comparison, and its component features were as far as possible decoupled from the adequate stimulus for orientation-selective neurons in the primary visual cortex.

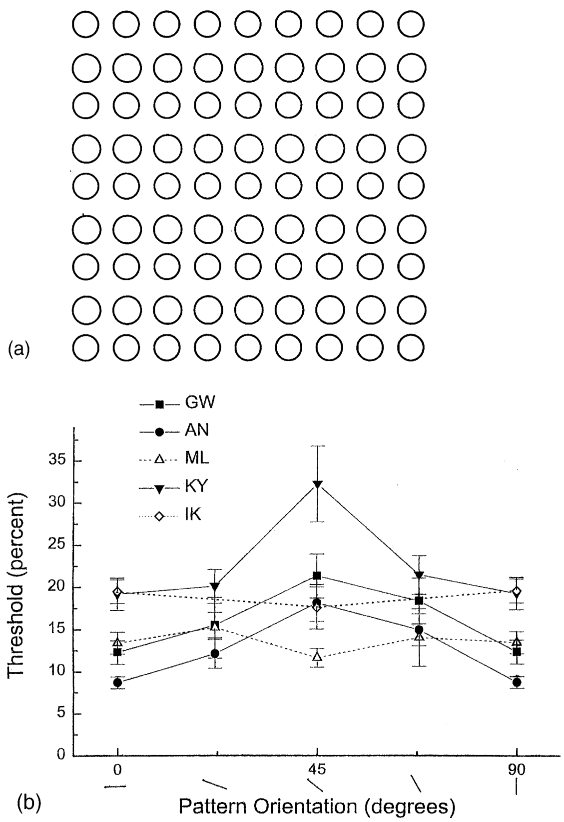

Fig. 8. (a) Texture pattern. Observer had to identify whether circles were of unequal size along rows or columns. (b) Threshold in terms of percent difference in circle size for 75% correct response in texture discrimination task, as a function of orientation of pattern. Three observers clearly exhibited an oblique effect, two did not.

4. Discussion

Neurophysiological studies of the primary visual cortex and psychophysical investigations in “early” visual processing have been proceeding side by side with the insistent expectation that findings from the two will match and hence that the neural substrate for the latter will have been discovered. The oblique effect is paradigmatic for this approach. It has been observed widely and in a variety of situations, and the orientation attribute which underlies it makes plausible an association with orientation-selective neurons in the primary visual cortex. And once it was reported that there appear to be fewer neurons in the visual cortex tuned to oblique meridians than to the horizontal and vertical, the case seemed to have been made: the paucity of obliquely-tuned neurons and the diminished performance in some tasks involving obliquely-oriented contours puts the neural substrate of the latter in the former.

The question is reopened here by collecting and extending the variety of visual thresholds in which oblique effects are observed and yet close association with the responses of orientation-selective cortical neurons is lacking. Conversely no oblique effect is found in situations where this association would seem to be firm. The generic difference between the two sets is that tasks exhibiting an oblique effect involve stimulus perturbations in a tangential direction, i.e., in a direction normal to the length of the contour. In those with no oblique effect, on the other hand, the changes are in the radial direction, i.e., along the length of the contour.

There is as yet no consensus on how the spatial thresholds that are the subject of this study arise. Central to the discussion is the fact that receptive field of neurons anywhere in the visual stream do not have the properties that would allow them by themselves to signal the stimulus differences that can be perceived. However, it is seldom claimed nowadays that a percept arises from the activity of a single neuron (an argument raised and rejected by von Kries, 1901 already). [2] There just are not enough neurons for a simplistic interpretation of this view. It has long been realized that reconciliation was needed between the relatively wide tuning curves of cortical neurons and the acute sensitivity for orientation differences. If it is unsatisfactory to look to single neurons to act as the substrate for the percept of an attribute, let alone the whole object, perhaps ensembles of neurons might be involved whose state of activity would represent—or would allow to emerge—signals of such fine gradations. For example, the tilt angle of a line might be identified by the firing within a circumscribed ensemble of orientation-specific neurons in the primary visual cortex in a given retinotopic location. Their classical receptive field covers at most 1° of visual angle in the near periphery (and only a fraction of that in the fovea). Non-classical surround areas may, of course, be involved, particularly because they have recently been proved to have close synaptic connection from adjacent regions. Those arising within V1, which share the orientation-selectivity of the target cells (Stettler, Das, Bennett, & Gilbert, 2002) and might therefore be considered part of the apparatus from which perceptual orientation arises, cover an area of several degrees. There is also feedback to V1, covering about the same area, both from V2, which does not preserve the orientation selectivity (Stettler et al., 2002) and from V3 (Angelucci et al., 2002). To make the connection between these neurons and a paucity of members tuned to oblique orientations with the oblique effect highlighted in this paper, the allowable separation of pattern components is relevant. Very prominent oblique effects are seen with pattern components 10° and 20° apart, several times higher than the largest receptive fields and synaptic confluences within the primate primary visual cortex and the feedback field from higher visual areas; hence even an interpretation of V1 processing more sophisticated than one of merely passive spatial filtering will not suffice.

Currently neither the nature of the neural circuitry leading to low orientation difference thresholds nor its location in the brain are known. The receptive field size of neurons generally increases the further removed a visual area is from the thalamic input to the cortex. Because psychopysical measurements of signal interaction (e.g., Westheimer et al., 1976) and transfer of perceptual training (Crist, Kapadia, Westheimer, & Gilbert, 1997; Schoups, Vogels, & Orban, 1995) are spatially restricted to areas of the order of the synaptic field of V1 neurons, it is generally supposed that circuits for fine spatial processing are located near the beginning of the cortical visual stream. Global rather than local factors are, however, implicated in at least some spatial hyperacuities (e.g., Loffler, Wilkinson, & Wilson, 2003). Nor need it be assumed that even such related tasks as the discrimination of the orientation and the length of single short lines are subserved by circuitry closely related in kind and location; after all only the former exhibits an oblique effect (Westheimer, 2001) and a severe deficit at low contrast (Morgan & Regan, 1987; Westheimer, Brincat, & Wehrhahn, 1999).

The results of the present study invite the conjecture that the oblique effect has its origin in a more distributed specialization that favors the horizontal and vertical. In the anatomy of the visual pathways evidence for organization around the horizontal and vertical axes within the organism abound. In the retina there is the horizontal raphe and the vertical dividing line between locations projecting to the right and left hemispheres. Horizontal axes are part of the vestibular and oculomotor organization. There is a clear distinction between horizontal and vertical binocular disparity. Thus there is no conceptual impediment in presuming a preference for horizontal and vertical interconnection. The impaired perceptual saliency of oblique sequences of contiguous oriented contour elements (Li & Gilbert, 2002) is of interest here, but it has also been demonstrated above that isolated circular features, many degrees apart, projecting to cortical locations in different hemispheres show an oblique effect for detecting a perturbation in the tangential direction.

Another possible association of the oblique effect with a putative horizontal/vertical grain of the visual neural system would be the assumption, though rather far-fetched, that feature localization took place within a horizontal/vertical cartesian grid of spatial elements. A tangential displacement about the 45° and 135° meridians would have to be $\sqrt{2}$ larger to end up in an adjoining element than a tangential displacement around the vertical or horizontal. But this would apply also to radial displacements which, as has been demonstrated, do not exhibit an oblique effect, hence there is no need to entertain such a hypothesis further.

The dissociation between one property of fine spatial visual processing, the oblique effect, from the neural level in which it has widely been conceded to be operating, the primary visual cortex, poses a dilemma. It is difficult to conceive that a meridional preference oper-

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[2] "If we ask ourselves how we are to think about the central representation of a specific visual impression, the first thing to reject is the idea that each such impression has its own specific cell ... it founders in that it is impossible for each new class of impression to have a number of cells waiting for them."

ating over such large distances and wide variety of stimulus components would be a feature of localized neurons and circuits that do not at the same time exhibit it in other, closely related tasks. On the other hand, one hesitates to relegate spatial hyperacuity processing, with its high local specificity (short distances of interaction, lack of transfer of training across tasks and neighboring positions) to neural stages quite far removed from the primary visual cortex. To be sure a short-term memory deficit, demonstrated here (Fig. 4), appears to be a contributing factor. Yet the presence of an oblique effect in single, brief presentations in naïve observers and its wide-spread manifestation all across the peripheral visual field and for configurations whose pattern elements are tens of degrees apart, suggests an innate organizational feature in the visual system. It is some interest in this connection that an oblique effect is also exhibited for the discrimination of the orientation of the axis of symmetry of configurations composed of individual lines whose own orientations are predominantly vertical and horizontal (Li & Westheimer, 1997). Thus a configuration as a whole displays a property absent from its components, very much in the spirit of the Gestalt teaching and something that is often discussed as the binding problem. Suffice it to say that it is insufficient to seek an explanation in the reportedly sparser population of orientation-selective units tuned to the oblique compared to those tuned to the horizontal and vertical.

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