PERCEPTION AND DISCRIMINATION AS A FUNCTION OF STIMULUS ORIENTATION:

THE "OBLIQUE EFFECT" IN MAN AND ANIMALS

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Performance for a large variety of perceptual tasks is superior for stimuli aligned in horizontal or vertical orientations, as compared to stimuli in oblique orientations. This phenomenon appears in the human adult and child, and throughout the animal kingdom. Neurophysiological mechanisms for orientation analysis have been found in the higher visual pathways of many animals, and the suggestive evidence is compelling that these mechanisms underly the orientation preferences reported behaviorally. This paper reviews both the behavioral and neurophysiological studies of orientation preferences, and suggests additional methods for determining the cause of these effects.

Stimulus orientation has received increased attention in the past decade from neurophysiological studies of visual pathways. These studies have located mechanisms for orientation analysis in single cells of mammalian visual systems. The study of stimulus orientation, however, has a long history in the behavioral and psychophysical literature. A persistent feature of these latter studies has been a small but consistent superiority in performance when visual stimuli are horizontal or vertical, as opposed to oblique. (For convenience, this phenomenon is subsequently referred to as the *oblique effect*.) The origin of the oblique effect has not been precisely determined, but a relationship between the behavioral results and the neurophysiological data is suggestive.

This paper deals with the oblique effect in two parts. First, it reviews the behavioral and psychophysical studies of orientation preferences. Second, it discusses the neurophysiological substrates of orientation perception. The first section helps define the oblique effect by elaborating on the many forms in which it appears. The second section amplifies the first by evaluating the neurophysiological findings in respect to these orientation preferences.

BEHAVIORAL STUDIES

Man

Acuity

Studies of visual acuity in man were among the first investigations to uncover preferences for vertical and horizontal stimuli. Emsley (1925) noticed acuity differences among subjects asked to resolve line gratings. Maximal acuity occurred when the gratings were in horizontal or vertical orientations. Visibility was poorest for stimuli 45 degrees or 110–140 degrees. Emsley initially attributed these results to astigmatism, but when lenses were used to correct for this disorder the effect remained. Emsley called this phenomenon "residual astigmatism."

Later studies (Hamblin & Winser, 1927; Higgins & Stultz, 1948; Leibowitz, 1953; Shlaer, 1937) confirmed these results for grating acuity, and also added a new dimension to the problem. It was discovered (Higgins & Stultz, 1948) that by tilting the head, so as to align the oblique stimuli with the retinal field, diagonal visibility improved. It seemed that orientation of the image was more important than orientation of the object, but later results have been more ambiguous on this point. For example, Luria (1963) determined acuity (in terms of pattern density) for checkerboard patterns while subjects were in upright or head-tilted conditions. Although vertical targets were significantly more visible than oblique patterns, this difference decreased with amount of

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head tilt. Attneave and Olson (1967) concluded from one experiment that orientation of the stimulus was most important, while they concluded the reverse from a second experiment (Attneave & Olson, 1970). Meanwhile, Attneave & Reid (1968) have suggested that perceived orientation, rather than actual orientation either in space or on the retina, is the critical factor. The ambiguity in these studies is further complicated by neurophysiological evidence from the cat, which suggests that cortical cells may compensate for head tilt by altering their response (Horn & Hill, 1969).

The difficulty with obliques on acuity tests was later found for a Landolt C test object (Hartridge, 1947), and Leibowitz (1955) demonstrated that the problem occurred in vernier acuity as well. Ogilvie and Taylor (1958, 1959) measured the visibility of very fine wires and found that oblique wires had to be twice as wide as vertical or horizontal wires to be seen.

Adjustment and Assessment of Stimulus Orientation

Perhaps the earliest discovery of an oblique effect was made by Jastrow (1893). Subjects required to reproduce visually presented lines, or to set other lines to some specified orientation, showed marked superiority with horizontal and vertical stimuli. More recent investigations have confirmed Jastrow's results. Smith (1962), for example, required observers to estimate the headings (radial position) of radar trails. Minimal errors were found at the horizontal and vertical axes. Discrepancies from these axes seemed to be perceptually exaggerated. Bouma and Andriessen (1968) determined perceived orientation by requiring subjects to adjust a dot to the perceived extension of a line segment. They tended to set the dots toward the nearest horizontal or vertical coordinate. Oblique lines seemed more horizontal or vertical than they were (by 3-10 degrees). Accuracy was lower for the oblique orientations and standard deviation was 2.5 times as great as for horizontal and vertical lines.

Sulzer and Zener (1953) determined the effect of orientation on the perception of parallelism. Two black lines were presented

on a white ground. One line could be rotated by the subject to bring it parallel with the second reference line. Variability of the settings was minimal with horizontal reference lines, poorer with vertical lines, and maximal with obliques. These results were replicated by Onley and Volkman (1958) and extended by Rochlin (1955). Andrews (1965, 1967a, 1967b) has pursued a similar analysis. Subjects were instructed to set a short bright line to an orientation parallel to a nearby standard or to make a forced-choice decision as to the lines' parallelism. When the test line was in a horizontal or vertical position, variability was at a minimum and acuity was best. Both Andrews and Bouma and Andriessen interpreted their experiments in terms of neural units responsive to particular orientations. Bouma and Andriessen (1968) have suggested a denser population of horizontal and vertical units. Andrews (1967a, 1967b) has suggested these units have a greater sensitivity.

These results are not restricted to straight line test objects. Leibowitz, Myers, and Grant (1955) obtained a measure of localization accuracy for circular test fields, 35 minutes in arc. The lights were presented in different radial positions, 4.2 degrees from a central fixation point. Localization accuracy was found to be poorest around the oblique positions and best at vertical and horizontal coordinates. In another experiment (Burns, Mandl, Pritchard, & Webb, 1969) observers were asked to give subjective impressions of target form and shape to a point source of light. Targets were generally reported as straight lines, while the slope was typically seen as near to horizontal regardless of stimulus position. Burns et al. suggest that some preferential treatment of horizontal stimuli in the visual system of man is implied in these data.

Other Studies on Object Orientation

Taylor (1963) has taken note of some studies to point out the difficulties with oblique positions; both the detection of stimuli and the assessment of line orientation are probably two aspects of the same problem. Meanwhile, other investigators have reported oblique effects in still other situations. For example, Craig and Lichtenstein (1953) had subjects report perceptual changes to a line during extended periods of fixation. Minimal disappearance occurred when the test line was along the vertical or horizontal axis, while maximal disappearance centered around a 45-degree oblique position. Similarly, Mc-Farland (1968) reported that right-angle stabilized images disappear with a much lower frequency than acute and obtuse angles or single horizontal lines.

Foley (1962) was concerned with the contribution of differential summation to the oblique effect. He hypothesized that area and luminance functions should be less for oblique stimuli in a critical flicker frequency test. The functions obtained, however, were parallel for a 60-degree oblique and a horizontal test line, indicating that observed differences with oblique and horizontal stimuli cannot be attributed to differential summation. Critical flicker frequency, however, was always lower with the oblique stimulus, a result that implies a lower effective luminance for stimuli in this orientation.

Several studies have examined the role of stimulus orientation in perceptual grouping. Beck (1966a, 1966b, 1967) presented stimuli composed of patterns of figure elements (short lines) arranged in different orientations. The figure elements in any one orientation composed a subdivision of the total figure. Subjects were required to segregate two overlapping stimulus fields, or divide three-boundary figures into two regions according to the division most naturally perceived in the overall figure. The results of these studies suggested that the most facilitating aspect of perceptual grouping was the change from horizontal or vertical orientations to diagonal orientations in the component lines of the figure elements.

Optical illusions are also subject to the oblique effect. The Poggendorf illusion consists of an oblique line that appears to pass behind a rectangle. This objectively straight line often looks broken or displaced. Green and Hoyle (1964) found that placing the oblique line in a horizontal orientation greatly reduces the illusion. Leibowitz and Toffey (1966) found that the illusion was reduced by one-half when the line was horizontal or vertical. The Zöllner illusion consists of long parallel lines intersected by a series of 45degree slashes. The parallel lines often appear to be slanted in respect to each other. This illusion is minimal when the lines are in a horizontal or vertical position and maximal for 45- and 135-degree obliques (Judd & Courten, 1905; Wallace, 1964). These studies suggest that rotating the distorted lines into vertical or horizontal positions greatly reduces the strength of the illusions.

Children

Children as well as adults are susceptible to the oblique effect. Gibson, Gibson, Pick, and Osser (1962) tested 4-8-year-olds on visual discrimination of letterlike forms. Standard forms were matched against comparisons rotated 45, 90, or 180 degrees. The greatest errors occurred with the 45-degree transformations. Rudel and Teuber (1963) tested $3\frac{1}{2}-8\frac{1}{2}$ year-old children with vertical, horizontal, and oblique lines and U shapes. Stimuli were simultaneously presented in pairs, and the children were asked to guess which member of the pair was "correct." While virtually no children failed to learn the horizontal-vertical discrimination, almost all the 3-5-year-olds and one-third of the 81/2-year-olds failed to discriminate left and right obliques. Also, successive presentations proved even more difficult to master, a fact that suggested a memorial component to the problem.

Over (1967), in fact, has suggested that the oblique effect may be due to memory variables per se rather than any visual mechanisms. This hypothesis was tested by Over and Over (1967) with 31-61-year-old children. Two procedures were used: One (recognition task) required the children to remember an oblique stimulus as an oblique from trial to trial, and the other (detection task) only required that the correct stimulus be detected from a two-comparison array. The experimenters found that most children could distinguish between obliques with the detection task but that many failed to discriminate obliques with the recognition task. All subjects, however, could make a horizontal-vertical discrimination. Although this result suggests the role of memory, when time intervals of 15-90 seconds separated presentation of

standard and comparison in a third task, many previously unsuccessful subjects were now successful at all time delays. Over and Over (1967) suggested that some factors beyond memory must be involved in the recognition of mirror-image obliques.

Bryant (1969) tested 5-7-year-olds on simultaneous and successive matching tasks and found successive discrimination of mirror-image obliques to be most difficult. Bryant then went on to test difficulty on non-mirrorimage obliques. Since difficulty in discriminating between mirror-image stimuli among children has been demonstrated for stimuli other than oblique lines (Huttenlocher, 1967; Rudel & Teuber, 1963; Sekular & Rosenblith, 1964) performance with 45-degree versus 135-degree objects could be ascribed to either the mirror image or oblique characteristic of the discrimination. Comparison of two obliques led to chance-level discrimination whether they were mirror images or not. Bryant concluded that oblique lines are seen as oblique but that the particular direction of slope is not encoded in memory.

Animals

Preferences for horizontal and vertical stimuli appear in many different organisms. These preferences are investigated by training animals to differentially respond to two or more stimuli to obtain reward (usually food). Rate of learning can thereby be used as a measure of ability to discriminate between objects in different orientations.

Octopus

Sutherland (1957) trained octopuses to respond to various rectangular bar shapes. The animal was rewarded with a crab when it attacked a positive rectangle and was shocked if it attacked a negative rectangle. It learned to respond to horizontal and vertical bars with about 90% accuracy. With a leftright oblique discrimination, however, there was no evidence of learning after 100 trials. Sutherland (1958) later tested octopuses on horizontal versus oblique and vertical versus oblique discriminations. Both were considerably more accurate than an oblique-oblique discrimination and much less accurate than a vertical-horizontal discrimination. Wells (1960) has shown that orientation discrimination in the octopus is dependent on the position of the retinal image. In the normal animal, the eyes rotate so that they are always horizontal to the environment regardless of the animal's position. When the octopus' statocysts are removed, the eyes stay horizontal in relation to the head rather than in relation to the gravitational (environmental) axes. Octopuses are incapable of discriminating orientation after the statocysts are removed.

Goldfish

Mackintosh and Sutherland (1963) have shown that goldfish have difficulty learning to discriminate objects in oblique orientations. The fish were trained to take food from rewarded rectangular shapes. One group of fish was trained to discriminate between horizontal and vertical rectangles, a second group between left and right oblique rectangles. The second group required twice as many trials to learn the oblique discrimination.

Pigeon

Zeigler and Schmerler (1965) presented pigeons with white rectangles on black backgrounds in vertical, horizontal, 60-degree, and 120-degree orientations. These stimuli were projected on keys to which the pigeons responded for reward. A 15-second fixed-interval reinforcement schedule was used for training. Both simultaneous and successive discriminations were studied. Discrimination, as measured by differential rate of responding, was found to be essentially the same for vertical-horizontal, vertical (or horizontal)oblique, and oblique-oblique discriminations. Although oblique stimuli do not seem to present a problem to pigeons in a discrimination task, Mello (1965, 1966a, 1966b, 1967) has shown that pigeons monocularly trained to respond to an oblique line will respond maximally to its mirror image when the untrained eye is tested. It has been argued (Beale & Corballis, 1968), however, that this "paradoxical transfer" phenomenon may be a procedural artifact. This issue has not yet been satisfactorily resolved.

Rabbit

Rabbits have been trained to discriminate either rectangular bars (Van Hof, 1965) or rows of dots (Van Hof, 1969) in different orientations. These studies found that both horizontal-vertical and oblique-oblique discriminations could be performed with close to 100% accuracy. Rate of acquisition, however, is slower for oblique discriminations (Van Hof. 1970a. 1970b). Van Hof and Wiersma (1967) determined the minimum angular difference that could be detected around a horizontal, vertical, and 45-degree oblique axis. Threshold discrimination was 5-10 degrees around the vertical and horizontal axes, and 10-15 degrees around the 45-degree oblique axis. These studies suggest that although rabbits can learn oblique discriminations, obliques present more difficulty than verticalhorizontal discriminations.

Rat and Squirrel

An early and comprehensive study on discriminative abilities in rats by Lashley (1938) revealed that rats learned to discriminate more rapidly between vertical and horizontal striated patterns than between 45- and 135degree striations, Koronakos and Arnold (1957) studied the formation of learning sets in rats using eight different oddity problems. In one problem a vertically striped door had to be selected from four other horizontally striped doors. Another problem required a left-oblique-lined door to be selected from four other right-oblique-lined doors. This second problem proved to be the more difficult to master.

Dodwell (1970) has recently shown that rats' difficulty with oblique discriminations persists, regardless of the type of testing apparatus used. In addition, Dodwell compared the discrimination of rats with squirrels. Like rats, squirrels had more difficulty learning to discriminate between a diagonal and vertical than a horizontal and vertical. A diagonalhorizontal discrimination could not be learned at all.

Cat

Sutherland (1963a) trained cats to discriminate between horizontal and vertical, or 45-degree and 135-degree oblique rectangles. The cats learned to discriminate either problem in an average of about 11 days. Performance on the horizontal-vertical problem was 75% correct; performance was 78% correct on the mirror-image obliques. Warren (1969) replicated these results on another apparatus, while eliminating the possibility of influence from contextual cues.

The problem presented to Sutherland's (1963a) and Warren's (1969) cats was a simultaneous discrimination. Parriss (1964) was interested in cats' performance when a successive discrimination was required. Four cats responded to rectangular shapes on two doors for food. The cats were confronted with a locked door when responding to the negative door. Training covered 20 trials per day, for five consecutive days each week. Training was terminated when the animal's performance was 90% correct over 80 consecutive trials. Two cats learned a horizontal-vertical discrimination first, then a 45-135-degree discrimination. The other cats learned in the opposite order. In the first group, the oblique discrimination took twice as many trials as the horizontal-vertical task and produced three and five times as many errors. When the oblique discrimination was the first problem learned, three times as many trials were required, and four and six times as many errors were made. It would seem that cats are no better with oblique stimuli than other animals, at least when the stimuli are presented in successive fashion.

Chimpanzee

Chimpanzees are close to man phylogenetically and have similar visual systems. It would be interesting to know how well they can discriminate orientations, however, not many studies are available on these animals' orientation preferences. Nissen and McCulloch (1937) tested monkeys, but their main concern was the effect of different learning techniques on discrimination, and it is difficult to interpret their data in terms of the oblique effect. However, the data do suggest that the animals had more difficulty learning to discriminate between opposing diagonally striped patterns than between vertical and horizontal stripes. One animal failed to discriminate diagonal patterns after 800 trials.

Behavioral Studies: Summary

Wherever stimulus orientation has been manipulated, performance has been consistently better with objects in vertical or horizontal orientations, as compared to stimuli in oblique orientations. This phenomenon has been demonstrated for the resolving power of the human eye (grating acuity, vernier acuity, Landolt C test object, and fine-line acuity), critical flicker frequency, fading of stabilized images, setting of lines to specified orientations, estimation of stimulus position, reaction times, perceptual grouping, matching and learning tasks, stimulus discrimination and generalization, and optical illusions. It has appeared in the human adult and child, and in the octopus, goldfish, pigeon, rabbit, squirrel, rat, cat, and chimpanzee. These studies clearly establish the reality of preferences for vertical and horizontal orientation. They are less clear in identifying the origin of these preferences. One approach to that problem has been to look for underlying mechanisms in the neurophysiological substrates of orientation perception. In reviewing the behavioral studies, it has occasionally been necessary to refer to these systems. The second section of this paper examines the neurological evidence in detail, and pays special attention to any possible connection to oblique effects.

NEUROPHYSIOLOGICAL MECHANISMS OF ORIENTATION ANALYSIS

A number of attempts have been made to relate the psychophysical evidence for an oblique effect with anatomical or neurophysiological data. The approach is an encouraging one. Sutherland (1963b) has referred to

the exciting possibility that when both neurophysiological and behavioral evidence are available for a variety of species, we may be able to correlate variations in behavior with variations in the proportions of different types of receptive fields present in the brain of different species [p. 122].

With this in mind, the present section reviews the neurophysiological studies of orientation perception.

Animals

The visual systems of a number of animals have been studied, but the earliest and most exhaustive studies have been carried out on the cat. It seems advisable to discuss these investigations first. Hubel and Wiesel (1962), using perfected microelectrode techniques, were able to record electrical activity from single cells in the cat's visual cortex. Anesthetized animals were presented with barshaped stimuli, which were moved around the visual field while the recordings were being made. By mapping out the region of the retina that could influence the firing of particular cells, the "receptive field" of those cells could be determined. Hubel and Wiesel discovered that the cells in cat striate (Hubel & Wiesel, 1962, 1963) and nonstriate cortex (Hubel & Wiesel, 1965) responded maximally to bars or contours of particular size, position, and orientation. Departure from the optimal characteristics would diminish or eliminate that cell's response. For example, a change of 5–10 degrees in orientation could abolish a cell's response completely. Monkey cortex was found to be organized in a way quite similar to that described for the cat (Hubel & Wiesel, 1968). The pigeon retina (Maturana & Frenk, 1963), goldfish tectum (Jacobson & Gaze, 1964), and rabbit ganglion cell (Levick, 1965, 1967) also seem to be organized to discriminate orientation.

Several studies of restricted rearing have confirmed the dependence of orientation discrimination on orientation-sensitive neurons in the cat. Wiesel and Hubel (1965) and Ganz, Fitch, and Satterberg (1968) have shown that if kittens are deprived of early visual experience, cortical cells will respond with no specificity with regard to orientation. The kittens will be behaviorally blind. Ganz and Fitch (1968) reared cats with one eye shut for 1-6 months. With the experienced eye, 85% accuracy on a vertical-horizontal discrimination was reached after 100 trials. There was no learning after 2,000 trials with the nonexperienced eye. More specific demonstrations of the relationship between experience and cortical function have come from Blakemore and Cooper (1970) and Hirsch and Spinelli (1970). These investigators

showed that cells in cat cortex will respond only to the particular orientations experienced during rearing.

The studies on visual deprivation, along with the microelectrode evidence from normal animals, strongly support the contention that cortical cells are responsible for orientation discrimination, if not for the oblique effect itelf. Some studies have found differences that do seem capable of explaining an oblique effect, Pettigrew, Nikara, and Bishop (1968) studied cells with receptive fields located within 5 degrees of the visual axis (area centralis). These experimenters classified cells into several different categories. One kind of unit, a "simple cell" directionally sensitive to movement and giving just a single excitatory response, is of particular interest here. Among these cells, a distinct preference for vertical and horizontal orientations was found. This offers at least initial support for a neurophysiological explanation of the oblique effect. In the rabbit (Levick, 1965, 1967) ganglion cells have been found that respond to a horizontal or a vertical border, but none responding to obliques. Since rabbits can discriminate between oblique stimuli, these results suggest that these animals must use some other mechanism in making oblique discriminations.

Histological Evidence

If neurons responsible for orientation analysis favor a particular orientation, it would be expected that some anatomical organization must provide a basis for this preference. Several studies suggest that the dendritic fields of sensory neurons provide such a code. In the optic lobe of the octopus, for example, cell dendrites have elongated oval fields with axes predominantly found in the horizontal plane, and to a lesser extent in the vertical (Young, 1960, 1962). Few fields have been found in oblique orientations.

Colonnier (1964) examined dendritic field orientation in cat, rat, and monkey cortex. He found that the number of dendritic segments was slightly greater in the horizontally or vertically oriented fields. The length of these segments was much greater than for oblique fields. Vertically oriented dendritic fields were especially predominant. Such an

organization could account for differences in perception along different meridians.

The orientation of elongated dendritic trees permits a differential sensitivity of the receptor cells to groups of differently oriented axons. . . The preferential orientation of dendritic trees along one axis would ensure that a specific input coming in the same direction would be better focused upon the cells of that area [Colonnier, 1964, p. 341].

Colonnier suggested these preferences could be the morphological basis of an oblique effect. Although enough obliquely oriented fibers exist to make oblique discriminations possible, they should be less accurate than other discriminations.

Man

Before going directly to a discussion of neurophysiological mechanisms in man, it should be pointed out that many investigators have tried to relate orientation preferences in man to optical factors. The earliest investigators attributed the results to astigmatism. Later studies, however, took steps to eliminate astigmatic contributions. The persistence of the preferences and consistency of astigmatism along two meridians argued against this explanation. Still, Beck (1965) showed that accommodation could lead to astigmatism for the near distances even where no astigmatism could be detected in the relaxed eye. Howard and Templeton (1966) have also criticized earlier studies for their inability to definitely eliminate astigmatism as a cause of the oblique effect.

Meanwhile, other optical theories had also been advanced. Leibowitz (1953) studied the role of dioptric factors by determining threshold angle resolution for test gratings in different orientations. Horizontal and vertical thresholds were found to be not different from each other, but markedly superior (by 7%) to all other orientations. Leibowitz reasoned that if dioptric aberrations were responsible for such results, the oblique effect should be enhanced under conditions where dioptric aberration was made more effective. However, the differences persisted even under these conditions. Leibowitz (1953) felt the data required a nondioptric explanation.

A later study on localization accuracy (Leibowitz, Myers, & Grant, 1955) supported this conclusion. The authors found that the detection of a patch of light was influenced by luminance and duration, but localization accuracy was not. Thus, the factors limiting localization performance were not governed by the photochemical events in the retina. Leibowitz et al. suggested this "points to the locus of contributing factors in events occurring after the activation of the end organs [p. 78]."

Weymouth (1959), however, persisted in explaining the oblique effect in optical terms. The characteristic effect of a point of light to form an image with horizontal and vertical rays (as in viewing a star) was argued to accentuate or increase the contrast of vertical and horizontal stimuli, while blurring an oblique.

Despite the appeal of these theories, recent studies have shown all theories based on the image-forming properties of the eve (astigmatism, diffraction characteristics, etc.) to be untenable. Campbell, Kulikowski, and Levinson (1966) effectively bypassed dioptric effects by projecting images directly onto the retina by means of laser-generated sinusoidal interference fringes. These are high-contrast gratings that are not degraded by ordinary optical effects. Resolving power was found to be worst for oblique patterns and best for vertical and horizontal gratings. Mitchell, Freeman, and Westheimer (1967) confirmed these results using the same technique. Both research groups concluded that orientation differences cannot be attributed to optical factors, and that retinal or higher mechanisms must be involved. Shlaer (1937) and Hartridge (1947) have argued for retinal mechanisms. They have suggested that density of retinal cells might be greatest along the horizontal and vertical meridians, and that this could lead to a corresponding enhancement in the perception of similarly aligned stimuli. This explanation, however, is not in agreement with histological evidence (see Polyak, 1941).

Still other investigators have ascribed the oblique effect to differential eye movements. Brown (1949) suggested that an asymmetrical distribution in the pattern of eye movements (resulting from preferential vibrations in the vertical and horizontal planes) may cause blurring along certain directions due to retinal image motion. Higgins and Stultz (1950) tested this hypothesis by presenting striped test objects to subjects at durations too short for eye movements to occur. In spite of the absence of eye movements, acuity for vertical and horizontal patterns was 20% better than for oblique objects. Nachmias (1960) recorded eye movements during threshold measurements and determined that they made no contribution at all to the observed differences.

In summary, investigators have tried to account for the oblique effect in terms of eye movements, optical disorders, and various dioptric characteristics. The composition of the retinal mosaic has also been proposed as a cause. Experimental studies show all of these explanations to be unacceptable, and therefore point to a postretinal origin. The evidence for this position is presented in the following sections.

Psychophysical Evidence

One promising psychophysical approach to the study of neurophysiological mechanisms is visual masking (see Weisstein, 1969). Sekular (1965), for example, studied adaptation using a backward masking paradigm. Detection thresholds were studied as a function of the masking field orientation. It was found that detection of the test stimulus decreased as the masking stimulus approached the orientation of the test field. Beyond 45 degrees the masking effect appeared to be independent of orientation. Similar findings are reported by Houlihan and Sekular (1968) and Parlee (1969). Blakemore, Nachmias, and Sutton (1970) have reported orientation-specific masking for gratings of similar spatial frequencies.

Since effective masking suggests an inhibitory or interfering effect by certain units on the activity of others, these results imply the presence of separate sets of analyzers for different orientations. This is supported by other orientation-specific masking phenomena such as in direction-sensitive analyzers (Sekular, Rubin, & Cushman, 1968) and orientation-specific color aftereffects (Fidell, 1970; Harris & Gibson, 1968; Hepler, 1968; McCollough, 1965). The fact that a number of similar psychophysical investigations have discovered preferences for horizontal and vertical orientations suggests these systems are responsible for the oblique effect as well. Campbell and Kulikowski (1966) found that when a 45-degree test grating was used in place of a vertical field, angular selectivity as measured by the masking effect was reduced by 25%. Gilinsky (1968) and Gilinsky and Doherty (1969) also reported a different masking effect for obliques, while Bouma and Andriessen (1970) reported similar differences between obliques and horizontal or vertical lines for an angular interaction effect.

Neurophysiological Evidence

The psychophysical studies support a neurophysiological theory for orientation perception and for the oblique effect in humans. More direct evidence, however, is available from some neurophysiological studies. Blakemore and Campbell (1969a, 1969b) reported that after 30 seconds of viewing an adapting grating of high contrast, a fivefold rise in threshold is obtained for a similarly oriented test object. This is accompanied by a suppression of the visual evoked potential, which only slowly returns to a detectable level. Since the visual evoked potential measures averaged activity of cortical cells, the source of this effect seems to be in the cortex.

Other studies have also found differences in the evoked potential to different orientations, Campbell and Maffei (1970) found that the amplitude of the evoked potential was .3 log units less for viewing an oblique test pattern than for vertical or horizontal patterns. This correlated with psychophysically derived thresholds for spatial frequency and contrast. Maffei and Campbell (1970) simultaneously recorded the evoked potential and the electroretinogram, thereby obtaining measures of electrical activity at both retinal and cortical levels. They found no differences in wave form or amplitude in the electroretinogram among vertical, horizontal, and oblique patterns. However, the evoked potential was decreased for the oblique patterns. Maffei and Campbell concluded:

that there is an electrophysiological correlate to the psychophysical observation that the visual resolving power in oblique orientations is less than in the vertical and horizontal, and that the mechanism of this phenomenon arises between the site of origin of the electroretinogram and the evoked potential from the visual cortex [p. 387].

The most direct evidence for cortical analysis of orientation in man comes from Marg. Adams, and Rutkin (1968). These investigators were able to record activity from five cortical units in two conscious patients with intractable seizures. The subjects fixated a point on a screen while the receptive fields were plotted with moving bar-shaped or disc stimuli. Two of the receptive fields were circular and the others were rectangular. Among the rectangular fields, two were horizontal and the third was nearly vertical in orientation (95 degrees). Five units is hardly a sufficient sample on which to base conclusions. but the finding of only horizontal and vertical preferences certainly does not detract from other psychophysical and neurophysiological evidence that the oblique effect has a central origin in man.

DISCUSSION

A review of the literature has shown that perception and discrimination vary with stimulus orientation. The most characteristic finding in these studies is a preference for vertical or horizontal orientations over obliques. This preference manifests itself in the resolution of targets, estimation of stimulus position, learning and discrimination of objects, and a wide assortment of other perceptual phenomena. These preferences are found throughout the animal kingdom, from man to octopus,

Neurophysiological research has firmly established the presence of cells in the cortex of cat, monkey, and man that are selectively sensitive to orientation. Ganglion cells in rabbit, pigeon, and goldfish have been found that perform similar functions. Histological evidence from octopus, rat, cat, and monkey suggest an anatomical substrate for orientation preferences.

It has become increasingly more popular to account for orientation preferences as reported in the behavioral literature in terms of these neurophysiological discoveries. Typically, it is assumed that preferences for horizontal and vertical orientations imply a dis-

proportionate number of cells optimally sensitive to stimuli in these preferred positions. The distribution of preferred orientation does seem to be disproportionate in optic fibers of octopus, rabbit ganglion cells, and at least some subcategories of units in cat visual cortex. An anatomical basis for a bias in the orientation systems of rat, cat, and monkey has been found histologically. In man, psychophysical, evoked potential, and microelectrode evidence converge to suggest biases in the human visual system as well. In all cases the biases or disproportional distributions of analyzers have always favored the horizontal and vertical orientations at the expense of obliques.

These findings suggest that the oblique effect is a function of the number of cells responsible for analyzing stimuli in vertical, horizontal, and oblique positions. However, this is not a necessary assumption. The oblique effect can be accounted for in terms of differential sensitivity as well as distribution. So far, this theory has not been tested neurophysiologically. Two lines of inquiry seem useful in evaluating these positions. First, selectivity in single cells should be studied not only in terms of response maxima but in regard to the response distribution to a range of orientations. This would reveal whether cells preferring horizontal or vertical orientations are more "finely tuned" than obliques. Andrews (1967a, 1967b) has suggested such a mechanism. Second, a more thorough investigation should be made for any possible biases in the distribution of cell orientation preferences. Hubel and Wiesel (1968), for example, have admitted that their investigations were not extensive enough to reveal small predominances in any one orientation. It would also seem advisable to conduct a more extensive investigation of receptive fields in the peripheral retina. Only a few of these areas have been mapped to any degree. Distributions in the periphery might prove to be different from those encountered in more central regions.

Evidence continues to accumulate, and more specific data on these speculations should be forthcoming. But the data certainly suggest now that preferences for horizontal and vertical orientations, as reported in the behavioral literature, correspond to similar biases in neurological orientation-analyzing systems. The site of the oblique effect would seem to be well established in the higher visual pathways of man and animal. However, it would be remiss to imply that all aspects of this problem can be most successfully described in sensory or neurophysiological terms. For example, memorial or attentional components may exist, and these also deserve further study. In fact, if the suggested neurophysiological substrates of the oblique effect are real, the presence of attentional or memorial deficits would be expected. On the other hand, these factors could be important independent (in the absence) of neurophysiological biases.

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