

## Detection and identification of near-threshold visual patterns

Norma Graham

Department of Psychology, Columbia University, New York, New York 10027

Received January 18, 1985; accepted May 7, 1985

For a number of visual dimensions—spatial frequency, orientation, spatial position, and direction of motion (at velocities higher than 1 or 2 deg/sec)—experimental results at near-threshold contrasts can be explained by assuming that multiple mechanisms selectively sensitive along that dimension exist and have labeled outputs. For the temporal-position dimension, analogous experimental results can be explained by assuming that each mechanism's output at a particular time depends only on the recent past and is labeled. For the eye-of-origin dimension, however, although the evidence suggests selectively sensitive mechanisms (at least at some spatial and temporal frequencies), these mechanisms seem *not* to have labeled outputs. For the temporal-frequency dimension (at any fixed spatial frequency), evidence suggests that there are *not* narrowly tuned mechanisms although there may be very broadly tuned ones.

### INTRODUCTION

The aim of this paper is to summarize briefly what we know about near-threshold pattern vision. All the experiments considered in this summary used visual stimuli at contrasts near detection threshold (that is, patterns that were imperfectly discriminable from a blank field). All conclusions here are meant, therefore, to apply only in that range. In spite of this limitation in range, hundreds of psychophysical studies proved relevant. Since only a sample of these can actually be referenced here, the references should be considered only as entry points into the literature. Many other references to both near-threshold and suprathreshold pattern-vision studies can be found in other papers in this issue and in recent review articles including Braddick *et al.*, 1978; DeValois and DeValois, 1980; Graham, 1981; Julesz and Schumer, 1981; Kelly and Burbeck, 1984; Sekuler *et al.*, 1978; Westheimer, 1984.

### FIFTEEN DIMENSIONS OF PATTERNS

To organize this mass of experiments, a framework of 15 dimensions has proved useful. One way of viewing these is as the 15 dimensions of a recently popular and actually rather simple visual pattern—a patch of spatiotemporal sinusoidal grating. Such a sinusoidal patch looks like a circle or ellipse containing alternating dark and light fuzzy-edged stripes. The edges of the circle or ellipse are also fuzzy.

For such a stimulus, the spatial luminance profile along any line perpendicular to the stripes—the luminance as a function of spatial position along that line at any particular point in time—is a windowed sinusoid (Fig. 1). That is, it is a sinusoidal function multiplied by some window function. If the window function is Gaussian, the windowed sinusoid is often called a Gabor function. The spatial luminance profile along any line parallel to the stripes is simply a constant multiplied by a window function. If this window function is also a Gaussian, the stimulus is sometimes called a Gabor patch.

To introduce temporal variations, the sinusoidal function is either (a) drifted across the observer's visual field or (b)

flickered sinusoidally in counterphase. (In counterphase flicker, the boundaries between bars in the grating remain stationary, but each dark point in the grating becomes a light point, then again a dark point, etc., with the modulation in time being sinusoidal.) For either the drifting or flickering case, the temporal luminance profile—that is, the luminance as a function of time at any particular point in space—is again a windowed sinusoid (as in Fig. 1).

Although these patches of sinusoidal grating may seem an overly simple or unnatural kind of stimulus, every spatiotemporal pattern—every function giving luminance at each point on two spatial dimensions and one temporal dimension—can be constructed as the sum of spatiotemporal Gabor patches (of sinusoidal patches with Gaussian window functions). Further, as we shall see in the next section, these Gabor patches may correspond to the receptive fields of different mechanisms existing in the visual system. Perhaps for the two reasons just given (or perhaps a matter of sociology), all the literature on near-threshold pattern vision—in spite of the fact that it contains many experiments using nongrating stimuli—can be conveniently discussed using the dimensions characterizing a patch of sinusoidal grating.

To specify one such sinusoidal patch completely, values on 15 dimensions must be given. The value on any of these dimensions can be varied while keeping the values on the others constant (as, indeed, is done in a typical experiment).

Seven of these 15 dimensions are spatial dimensions and are illustrated in Fig. 2.

First—*spatial frequency*. Two sinusoidal patches, which are represented in the upper left of Fig. 2 by their spatial luminance profiles—can differ in the spatial frequency of the sine wave while being identical in all other dimensions listed below. The usual measure of spatial frequency is cycles per degree (c/deg) of visual angle. In Fig. 2, the two patches of different spatial frequency being identical in spatial extent is taken to mean that they have the same extent measured in number of cycles rather than in degrees of visual angle. This definition is less clumsy for some purposes, but it is essentially arbitrary.

Second—*orientation*. Two otherwise-identical sinusoidal

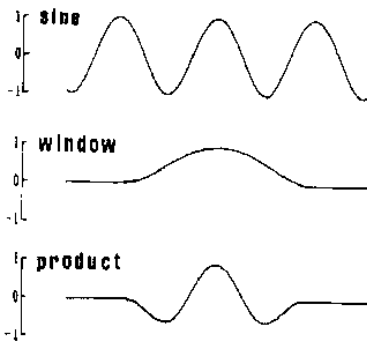


Fig. 1. The top row shows a sinusoidal function, the middle row a Gaussian function, and the bottom row the product of a sinusoid and a Gaussian—a windowed sinusoid. Such a function appears in several places in contemporary visual psychophysics and in this paper. When it describes the spatial or temporal luminance profile of a pattern, the vertical axis is luminance and the horizontal axis is spatial position or temporal position, respectively. When it describes the spatial or temporal weighting function of a neuron or hypothetical mechanism, the vertical axis gives the value by which the luminance profile of the pattern is weighted in computing the response of the neuron or the hypothetical mechanism (positive values are called excitation and negative values inhibition), and the horizontal axis again gives spatial or temporal position, respectively.

patches can have two different orientations. Two such patches are indicated in the upper right of Fig. 2, where they are represented by two-dimensional maps in which a plus indicates a region that is brighter than the mean luminance and a minus indicates a region that is darker.

Third and fourth—*spatial position in two orthogonal directions*. Two otherwise-identical sinusoidal patches can be centered at any two spatial positions along a horizontal dimension (as in the second row, left, Fig. 2) or at any two spatial positions along a vertical dimension (as in the second row, right, Fig. 2).

Fifth and sixth—*spatial extent in two orthogonal directions*. Two otherwise-identical sinusoidal patches can have window functions of different spatial extents. Either the extents perpendicular to the bars, that is, the number of cycles (as in the third row, left, Fig. 2) can be different or the extents parallel to the bars, that is, the length/width ratio (as in the third row, right, Fig. 2) can be different. Equivalently, two patches differing in extent perpendicular to the stripes can be described as varying in spatial-frequency bandwidth; for, as the number of cycles in a patch increases, the range of spatial frequencies the patch contains decreases. (See Graham, 1980, for an intuitive justification of this fact.) Similarly, two patches differing in extent parallel to the bars can be described as varying in orientation bandwidth.

Aperiodic stimuli (e.g., lines or disks) are simply a 0-c/deg spatial sinusoid (which is equivalent to a constant function) multiplied by a window function. That is, they are 0-c/deg sinusoidal patches. The spatial window functions used in such cases are more frequently rectangular than Gaussian, however. (See discussion of the effects of different window functions under miscellaneous factors below.) When such aperiodic stimuli are varied in width or height, they are equivalent to 0-c/deg sinusoidal patches varied in spatial extent.

Seventh—*spatial phase (spatial symmetry)*. Two otherwise-identical sinusoidal patches can differ in the relative spatial phase of the sinusoid with respect to the window function perpendicular to the bars. This variation produces spatial luminance profiles of different symmetries. Shown here (bottom row, Fig. 2) are an even-symmetric and an odd-symmetric one. Any other spatial phase (symmetry) of sinusoidal patch can be formed as a weighted sum of the two spatial phases shown here (or almost any other two given phases). Only two truly independent values along this spatial-phase dimension exist, therefore.

In addition to specifying values on seven spatial dimensions, one must also specify values on five temporal dimensions (Fig. 3) in order to describe a spatiotemporal sinusoidal patch. The first four are straightforwardly analogous to spatial dimensions. Two otherwise-identical sinusoidal patches, which are represented in the first four rows of Fig. 3 by their temporal luminance profiles, can have temporal luminance profiles that differ in the following:

### SPATIAL DIMENSIONS

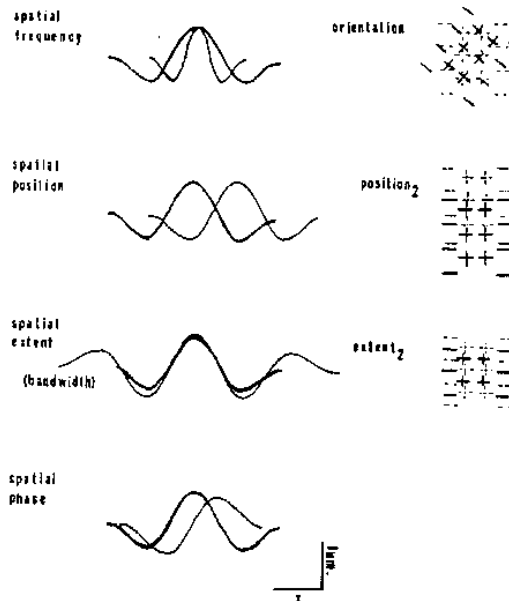


Fig. 2. Seven spatial dimensions on which patterns can differ. Alternatively, the sensitivities of neurons or hypothetical mechanisms can differ on these spatial dimensions. Each subpart of the figure represents two sinusoidal patches (or, alternatively, two neurons or hypothetical mechanisms) that are presumed identical on all dimensions except the indicated dimension. In each drawing in the left half of the figure, the two patches (or, alternatively, the two neurons or mechanisms) are represented by spatial luminance profiles (or, alternatively, spatial weighting functions). In the right half of the figure, the two patches (or, alternatively, the two neurons or mechanisms) are represented by two-dimensional spatial maps in which pluses indicate brighter parts of a stimulus (or, alternatively, excitatory regions of a receptive field or spatial weighting function) and minuses indicate dimmer parts of a stimulus (or, alternatively, inhibitory parts of a receptive field or spatial weighting function).

### TEMPORAL DIMENSIONS

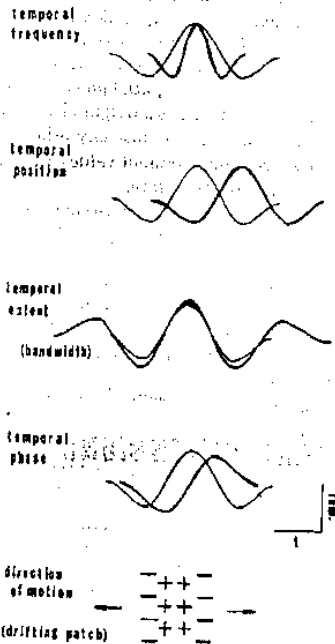


Fig. 3. Five temporal dimensions on which patterns (or neurons or hypothetical mechanisms) can differ. Each subpart represents two sinusoidal patches (or neurons or hypothetical mechanisms) that are presumed identical on all dimensions except on the indicated dimension. The two patches (neurons, mechanisms) are represented in the top four rows by temporal luminance profiles (temporal weighting functions) and in the bottom row by two-dimensional spatial maps with arrows indicating direction of motion.

First—*temporal frequency*, the usual measure of which is cycles/second (c/sec or Hz).

Second—*temporal position* (relative to the start of a trial, for example).

Third—*temporal extent* or, equivalently, temporal-frequency bandwidth (the larger the temporal extent, the smaller the temporal-frequency bandwidth).

Fourth—*temporal phase* of the temporal window relative to the temporal sinusoid.

The fifth temporal dimension—*direction-of-motion*—actually involves an interaction between space and time. Two otherwise-identical drifting sinusoidal patches differing in direction of motion are represented in the fifth row of Fig. 3 by stationary two-dimensional maps (as in the right column of Fig. 2) and an arrow indicating direction of motion. For a sinusoidal grating of infinite spatial extent (both parallel and perpendicular to the bars), there are only two distinct directions of motion (those indicated by the arrow).

A flickering sinusoidal grating is equivalent to the sum of two sinusoidal gratings drifting in opposite directions (where each of the two has the same spatial frequency, temporal frequency, and orientation as the original flickering grating is of half the contrast).

The next diagram (Fig. 4) shows three other dimensions on which values must be given in order to specify completely a sinusoidal patch stimulus:

First—*contrast*.

Second—*mean luminance*.

Third—*which eye they stimulate*.

Finally, a brief mention of some of the many other factors that could differ between experiments but that will be ignored here.

Color is important, but we will consider here only experiments that used monochromatic stimuli. No conclusions here will depend on what that one color was (to my knowledge).

The binocular disparity between two patches stimulating separate eyes could be manipulated to produce stimuli appearing to be at different depths, but we will consider only the experiments (which are in the great majority) that used either monocular stimuli or binocular stimuli in which the two identical monocular images fell on corresponding points in the two eyes.

The exact shapes of the spatial and temporal window functions have differed from one experiment to another, but the effects of such variation—to the extent that they have been studied at this point—seem readily explainable on the basis of the dimensions already considered and so will not be separately considered here. For example, relative to a Gaussian window function, a rectangular window function introduces high spatial frequencies at its edges. That is, a sinusoid multiplied by a rectangular window function is

### OTHER DIMENSIONS

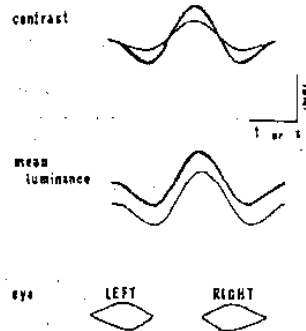


Fig. 4. Three other dimensions on which patterns (or neurons or mechanisms) can differ. Each subpart represents two sinusoidal patches (neurons, mechanisms) that are presumed identical on all dimensions except the indicated dimension. The two patches (neurons, mechanisms) are represented by spatial luminance profiles (spatial weighting functions) in the top two rows. The eyes themselves are represented in the third row.

- ignore: color
- depth
- windows' shapes (x,y,t)
- observers' eyes
- pathology of color

equivalent to the sum of (a) the same sinusoid multiplied by a Gaussian, where the Gaussian is of approximately the same extent as the rectangular function and centered at the same position, and (b) many other sinusoids all of higher frequencies than the original and each of which is multiplied by a Gaussian function that is centered near the edge of the rectangular window function rather than at its center. To put it still another way, a rectangularly windowed patch can be treated as a compound of many Gaussian-windowed patches of different frequencies and positions.

Further factors will also be ignored here for lack of space, although many of them are important, e.g., observers' ages, observers' pathologies, the exact psychophysical method including instructions, observers' expectancies, and the nature of the visual field surrounding the pattern under study. (This surround ideally would be—but in actuality never is—an infinitely extended field at the mean luminance of the grating. This is the ideal surround since that is what theoretical accounts generally assume either explicitly or implicitly.)

Note that all the dimensions are defined above in retinal coordinates (e.g., cycles per degree of visual angle) rather than in world coordinates (e.g., cycles per centimeter) as it is retinal value that seems the important determiner for experimental results of the type considered here.

## EXPERIMENTS

The conclusions below are based on evidence from five common kinds of psychophysical experiment. As mentioned above, all use stimuli that are imperfectly discriminable from a blank field or, in other words, stimuli that are near their own detection threshold. Each of these five kinds of experiment can, in principle, be done with stimuli that vary along any one of the 15 dimensions above. The five, listed in order from most to least common, are as follows:

*Parametric contrast sensitivity*—The observer's detection threshold is measured for simple patterns as a function of value along some dimension of interest (see, e.g., Kelly, 1984). (A simple pattern contains only a single value along the dimension of interest.)

*Summation at threshold*—Thresholds for a compound stimulus containing two or more values along some dimension of interest are compared with the thresholds for the component simple stimuli (see, e.g., Graham *et al.*, 1978).

*Adaptation at threshold*—Thresholds for various test stimuli after adaptation to different adapting stimuli (including a blank field) are compared (see, e.g., Blakemore and Campbell, 1969). Typically, both the test and adapting patterns are simple stimuli. Here I will consider only experiments in which the adapting stimulus was turned off decidedly before the test stimulus was presented. For, when the adapting and test stimuli are on simultaneously, experimental results become less consistent and more difficult to explain (presumably for some of the same reasons that results of pure masking experiments are).

*Uncertainty at threshold*—Detectability of a stimulus (typically a simple stimulus) is measured both when the observer is certain as to which stimulus will be presented and when the observer is uncertain (typically because trials of many different stimuli are randomly intermixed (see, e.g., Ball and Sekuler, 1980).

*Identification near threshold*—The observer's ability to identify which of several near-threshold stimuli has been presented is measured. A number of rather different experimental paradigms are being grouped together under this title: (i) identification of which of several simple stimuli was presented on a single-interval trial (see, e.g., Yager *et al.*, 1984); (ii) identification of which of several simple or compound stimuli were presented on a single-interval trial (see, e.g., Hirsch *et al.*, 1982; Olzak, 1981); (iii) the two-by-two paradigm (see, e.g., Watson and Robson, 1981; see description in Thomas, 1985; and (iv) forced-choice discrimination between two equally detectable stimuli (see, e.g., Olzak and Thomas, 1981). In many near-threshold identification experiments, the observer's ability to detect each pattern, that is, to discriminate each from a blank field, is measured simultaneously with the ability to identify which pattern it was.

Although, in principle, each of these five kinds of experiments can be done on each of the 15 dimensions, some of these 75 possibilities are problematical to interpret or essentially equivalent to each other. At least 65 of the 75 possibilities are distinct and sensible experiments to do, however. To get complete information about pattern vision, each of these 65 (e.g., adaptation on the spatial-frequency dimension) ought to be done at all possible combinations of values on the 14 nonexperimental dimensions (orientation, spatial position, spatial extent, temporal frequency, mean luminance, etc.). Thus, even if there were only two values of interest on each dimension, the total number of experiments would be more than a million; they would take at least 50 journal years to report (at 2000 pages/year and 10 experiments/page). The number of near-threshold pattern experiments that have been done may be large (there were 738 references in the lists I collated in 1982), but not that large. We obviously do not yet know what happens in all regions of pattern vision's parameter space. And we probably never would if we had to learn about it by doing a complete factorial set of experiments and reporting the results piecemeal. Not only would such an enterprise be boring, but we would not be able to encode or remember the results. As it happens, however, we do know a good deal about pattern vision, because the experiments that have been done have been guided by theory, and the results have added up to a coherent theory of near-threshold pattern vision.

The following caution is necessary, however. The conclusions to be given below apply only within the parameter ranges explored to date. As giving such details for each of the conclusions below would take a book, the following list attempts to give some idea of what these ranges are by showing the values commonly used on each dimension when it is *not* the experimental dimension. (The full range has usually been explored when a dimension is the experimental dimension).

List of typical parameter ranges:

SPATIAL FREQUENCY—low to medium (0 to 10 c/deg)

ORIENTATION—vertical, horizontal

SPATIAL POSITION—centered at fixation point

SPATIAL EXTENT—2 to 6 degrees (CRT face)

TEMPORAL FREQUENCY—low to medium (1–10 c/sec) unstabilized viewing

TEMPORAL EXTENT—long (many temporal cycles)

MEAN LUMINANCE—low to moderate photopic

**BINOcular VIEWING**

**MISCELLANEOUS**—observer's ordinary refractive correction  
 —broadband white or bluish to yellowish-green  
 —young adult to middle-aged (human)

**MULTIPLE-MECHANISM MODEL**

Current models of pattern vision postulate the existence of multiple individual mechanisms, where by mechanism is meant the entity in a psychophysical model that is analogous to an individual neuron. (Some authors use terms other than mechanism; for example, detector, channel, neural unit, neuron, filter, and sensor have all been used.) The sensitivities of these mechanisms might well be postulated to vary on any of the 15 dimensions listed above, and indeed, they have been on almost all of them.

Figures 2-4 can be reinterpreted as representing the potential sensitivities of these individual mechanisms. The little drawings in these figures are then taken to be the mechanisms' spatial (Figs. 2 and 4) or temporal (Fig. 3) weighting functions. Or, speaking loosely using terminology drawn from the possible physiological analog; the drawings represent possible receptive fields (spatial or temporal appropriately) of individual neurons. (Note, however, that the temporal weighting functions of individual mechanisms would presumably be strongly asymmetric on the time axis since effects never go backward in time; but most of the drawings in Fig. 3 are even-symmetric, as is typical of visual stimuli.)

A model must contain more than lower-order mechanisms, however, in order to account for psychophysical data. Figure 5 is a diagram illustrating the shared features of current multiple-mechanism models of pattern vision. As a class, these models have had considerable success at quantitatively accounting for near-threshold pattern vision (see, e.g., Mostafavi and Sakrison, 1976; Quick *et al.*, 1978; Robson and Graham, 1981; Thomas *et al.*, 1982; Watson and Ahumada, 1986; Wilson and Bergen, 1979; Yager *et al.*, 1984). In these models, there are an indefinite number of individual mechanisms, only three of which are illustrated in Fig. 5. Each mechanism can be thought of as containing two stages, the

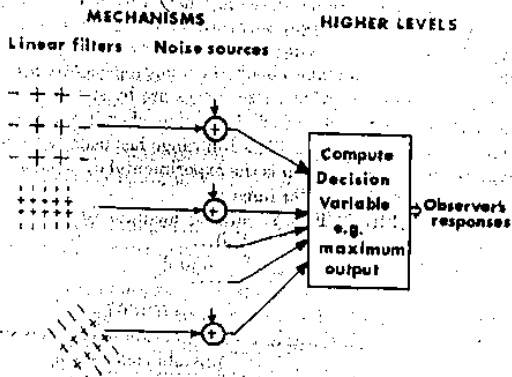


Fig. 5. Sketch of shared features of current models of near-threshold pattern vision. See text for more detail.

first of which is deterministic and is represented in Fig. 5 by a two-dimensional map of its spatial weighting function (spatial receptive field). This stage is generally assumed to be a linear system, that is, its output to a sum of two stimuli is the sum of its outputs to each stimulus alone, but exact linearity is not crucial to the conclusions here. Since this stage responds only to limited ranges of spatial and temporal parameters; it is frequently called a filter.

Second, the output of each mechanism to a particular pattern is assumed to be variable across presentations of the same stimulus. This variability can be modeled—as in Fig. 5—by assuming that the first deterministic stage of each mechanism is followed by a second probabilistic stage that adds time-varying noise.

Third, although not indicated on the figure, these mechanisms are assumed to fatigue or be adaptable in the following sense: After a period of producing an output above baseline (above the level evoked by a steady blank field), the mechanism will be less sensitive to a given pattern than it is after a period of producing a baseline output.

Finally, as indicated on the right side of Fig. 5, the multiple outputs from the various mechanisms are combined to form a decision variable. When accounting for detection results, this decision variable is frequently taken to be the maximum of the individual mechanisms' outputs. (For example, the observer is assumed to respond "yes, a pattern was presented" if and only if the maximum of the outputs from the various mechanisms is bigger than some criterion.) When accounting for near-threshold identification results, the decision variable is frequently taken to be the identity of the mechanism producing the maximum output. (For example, in an orientation identification experiment, the observer may be assumed to identify the stimulus as being the horizontal one if and only if the mechanism producing the maximum output is most sensitive to the horizontal orientation.) Further, the computation of the decision variable is sometimes assumed to be based, not on the full set of mechanisms' outputs but on a subset that is particularly informative for the task under consideration (e.g., outputs from all the mechanisms that are sensitive to at least one of the stimuli that the observer knows might be presented).

Many features of any complete receptive-field model have obviously been left unspecified in the general framework sketched in Fig. 5.

**QUESTIONS**

The results from the five kinds of near-threshold pattern-vision experiments listed above will be summarized below by answering, for each of the 15 dimensions in turn, five further questions about features of the general multiple receptive-field model described above.

(1) **PARAMETRIC SENSITIVITY?** What is sensitivity as a function of value along the dimension? (If there are multiple mechanisms, this function is approximately the envelope of their sensitivity functions. If there is only a single mechanism, this function is approximately its sensitivity function.)

(2) **MULTIPLE MECHANISMS?** Are there mechanisms sensitive to different values along that dimension?

To answer unambiguously this question along any one dimension, certain issues involving two or more dimensions

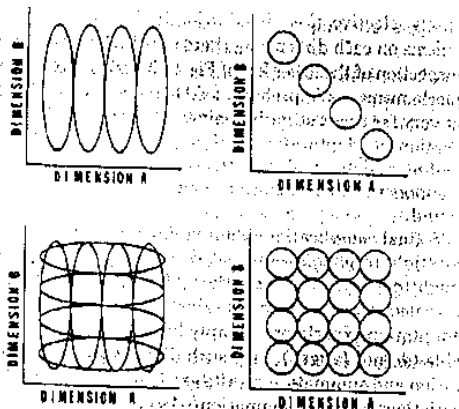


Fig. 6. Four hypothetical cases of sensitivities along two dimensions. The horizontal axis gives value along dimension A; the vertical axis gives value along dimension B. Each circle or ellipse encloses the region of values to which an individual mechanism is sensitive (more exactly, the region where its sensitivity is greater than some criterion). Upper left: Multiple mechanisms along dimension A with a single mechanism along dimension B. Upper right: A single mechanism along each dimension (at each point on the other dimension). Lower left: Singly selective mechanisms sensitive to a narrow range along one of the dimensions but sensitive to the full range of visible values along the other. Lower right: Doubly selective mechanisms sensitive to narrow ranges along both of the dimensions.

must be briefly considered. Figure 8 illustrates several different hypothetical cases of how sensitivities of mechanisms along two different dimensions might interact. The horizontal axis in each case gives value along dimension A; the vertical axis gives value along dimension B. Each circle or ellipse encloses the region of values to which an individual mechanism is sensitive (more exactly, the region where its sensitivity is greater than some criterion). The clearest case of a "yes" answer to the question of whether there are multiple mechanisms on a particular dimension is the following: There exist mechanisms sensitive to different ranges along that dimension (e.g., spatial frequency) but all sensitive to the same ranges along all other dimensions (e.g., all sensitive to near-vertical orientations, to far-peripheral spatial positions, to low temporal frequencies, to the left eye, etc.). Both bottom panels of Fig. 6 illustrate clear cases of "yes" answers for both dimension A and dimension B, although the panels differ in another important respect discussed further below.

The clearest case of a "no" answer is one—as illustrated for dimension B in the upper left panel of Fig. 6—in which every mechanism has exactly the same sensitivity along that dimension (B in this case) no matter what its sensitivity along other dimensions (e.g., whether it is sensitive to low or to high values on dimension A).

A priori, it is unclear what answer should be given to question (2) in cases like that in the upper right of Fig. 6, however. If you consider all mechanisms, no matter what their sensitivities on other dimensions (e.g., dimension B), there are multiple mechanisms sensitive to different ranges on dimension A. But if you hold values on all other dimensions constant (e.g., consider only very low values on dimension B), there is only a single mechanism on dimension A. In the following, the answer to the question in this case would be

said to be "no." A "yes" answer will mean that there are multiple mechanisms sensitive to different ranges along the dimension of interest while holding values on all other dimensions constant.

In addition to knowing whether there are multiple mechanisms on each pattern dimension, one would like to know about joint selectivity along all sets of two or more dimensions. As illustrated in the lower left of Fig. 6, for example, each mechanism might be sensitive to a narrow range along one of the dimensions but sensitive to the full range of visible values along the other; mechanisms of this sort will be called "singly selective." Or, as illustrated in the lower right of Fig. 6, each mechanism might be sensitive to narrow ranges along both dimensions; mechanisms of this sort will be called "doubly selective." By extension one could discuss triple selectivity, etc.

(3) LABELED? If there are multiple mechanisms on a particular dimension, are these mechanisms' outputs labeled in the following sense: the higher stages that compute the decision variable can keep track of which output comes from which mechanism (at least well enough to predict, for simple stimuli of far-apart values, decrements due to uncertainty and identification that is as good as detection)?

(4) PROBABILISTIC INDEPENDENCE? If there are multiple mechanisms on the dimension, are their noise sources probabilistically independent (uncorrelated) or not? In other words, are the outputs of any pair of mechanisms uncorrelated over different presentations of the same stimulus?

(5) INHIBITION (OR EXCITATION) AMONG MECHANISMS? If there are multiple mechanisms on the dimension, does one mechanism's output ever directly affect (excite or inhibit) another's or (as in Fig. 5) can each mechanism's average output to a particular stimulus (which is equivalent to the output from the linear filter) be computed directly as a function only of the stimulus parameters? Notice that the answer to this question is logically independent of the answer to question (4).

How such questions are answered:

Although no attempt will be made here to justify the answers to these questions rigorously (such justification far exceeding reasonable space limits for a single paper), some brief intuition into the logic underlying the answers might be useful.

(1) PARAMETRIC SENSITIVITY? Answering this question as asked above is a simple matter of plotting sensitivity as a function of value. This is the only one of the five questions that can be answered by the first kind of experiment listed above—the parametric experiment. Interpreting this parametric sensitivity function, however, depends on other features of the model. For one thing, whether there are multiple mechanisms [the answer to question (2)] determines which theoretical function—the envelope of multiple mechanisms' sensitivity functions or a single mechanism's sensitivity function—is closer to the measured parametric sensitivity function. Second, the exact relationship between the measured parametric sensitivity function and the theoretical function depends on whether there is independent variability [probability summation—the answer to question (4)] and/or intermechanism interaction [the answer to question (5)].

(2) MULTIPLE MECHANISMS? The second question can be answered by any of the second through the fifth kinds of experiment. The existence of multiple mechanisms shows

up as value-selective (e.g., spatial-frequency-selective, direction-of-motion-selective) behavior, that is, as more observed interaction between close-together stimuli than between far-apart stimuli where observed interaction needs to be defined separately for each kind of experiment.

In summation experiments, more observed interaction means greater detectability of the compound relative to the components.

In adaptation experiments, more observed interaction means greater threshold elevation.

In uncertainty experiments, more means smaller differences between the condition in which the observer is certain and that in which the observer is uncertain.

In identification experiments, it means more confusability.

After having discovered experimentally whether there is value-selective behavior on a given dimension (more observed interaction at close values than at far ones), some quite tricky interpretational steps remain in order to answer this question about multiple mechanisms. Indeed, value-specific behavior in an experiment on one dimension may often be explainable by mechanisms selectively sensitive on that dimension. However, it is often the case that value-specific behavior on one dimension (e.g., using stimuli varying in spatial extent as in the third row of Fig. 1) can also be explained by mechanisms on some other dimension (e.g., mechanisms differing in peak spatial frequency as in the top row of Fig. 1) because the stimuli used in studying the experimental dimension (e.g., spatial extent), necessarily vary in bandwidth on the other dimension (e.g., spatial frequency) although the dominant value on that other dimension may be kept constant. To find out which is the correct explanation—the explanation that will explain not only the results of experiments along the one dimension but all other results as well—may require extensive theoretical calculations (e.g., as it does in the case of experiments on the spatial-extent dimension; see Graham, 1977; 1980).

A closely related interpretational problem frequently arises when stimuli that are broadband on some dimension (e.g., spatially aperiodic stimuli) are used in experiments on another dimension (e.g., are flickered at different temporal frequencies in a summation or adaptation or identification experiment). When value-selective behavior is found, it is not clear whether (as in the lower right of Fig. 6) there are really multiple mechanisms on the experimental dimension (temporal frequency) at each value on the other dimension (spatial frequency) or whether instead the situation is more like that in the upper right of Fig. 6. Comparing the results with further experiments using stimuli that are narrow band on the nonexperimental dimension (e.g., of narrow spatial-frequency bandwidth) will disentangle the two possibilities.

In cases where evidence indicates multiple mechanisms on each of two or more dimensions (e.g., spatial frequency and orientation) there remains the question of deciding whether these mechanisms are singly selective (left bottom panel of Fig. 6) or doubly selective (right bottom panel of Fig. 6) or have some other pattern. In fact, in all such cases considered here, the evidence from adaptation and summation experiments that indicates multiple mechanisms on each dimension also suggests that each mechanism is narrowly tuned on every such dimension (doubly selective on any pair of such dimensions) rather than singly selective. For, if the mechanisms were

singly selective, then, in addition to the narrow-band mechanisms on each dimension, there are also broadband ones (as inspection of the lower left of Fig. 6 shows). These broadband mechanisms would probably lead to more observed interaction at very far-apart stimulus values (that is, more threshold elevation in adaptation experiments even at far-apart values and more detectability of the compound relative to the two components in summation experiments) than is typically found.

A final complication in answering question (2) is that the multiple mechanisms revealed by one kind of experiment might not show up in another. For example, mechanisms revealed in summation experiments might not show up in adaptation experiments simply because they are not adaptable (do not fatigue). No such dissociation between adaptation and summation results exists to my knowledge. Dissociations between summation/adaptation and identification results certainly do, however, and are discussed below.

(3) LABELLED? Value-specific behavior in adaptation or summation experiments can be explained by multiple mechanisms even if the outputs of these mechanisms are not labeled according to which mechanism produced them, that is, even if the subsequent stages use only the sizes of the mechanisms' outputs without knowing anything about which mechanism produced which output. To explain value-specific behavior in uncertainty and identification experiments, however, seems to require that the outputs of the mechanisms be labeled (not necessarily perfectly) by which mechanism produced them. Therefore, we will conclude here that mechanisms' outputs are labeled if and only if value-specific behavior is found in uncertainty and/or identification experiments on the appropriate dimension.

(4) INDEPENDENT NOISE? Probabilistic independence among the outputs of different mechanisms may show up as (a) probability summation in summation experiments, that is, sensitivity for a compound containing far-apart values is a little higher than that for either component (e.g., Sachs *et al.*, 1971); (b) uncorrelated responses by the observer to the two component values in concurrent identification experiments (e.g., Hirsch *et al.*, 1981; Graham *et al.*, 1985; Olzak, 1981) and (c) the appropriate size of decrement due to uncertainty (e.g., Davis *et al.*, 1983; Kramer *et al.*, 1985; Yager *et al.*, 1984). Thus finding any of these effects is some evidence for such probabilistic independence.

(5) INHIBITION? Support for the notion of inhibition among mechanisms far apart on some dimension of interest can come from finding with far-apart simple stimuli—in adaptation, summation, uncertainty, or identification experiments—an effect that is the opposite of the effect found at close values. By opposite is meant the other side of the baseline expected from the case when two stimuli affect two entirely different sets of mechanisms and these mechanisms do not interact in any way. The baseline depends on many features of the overall model and will not, in general, be the same as zero effect. Although in adaptation experiments, for example, the baseline is zero, so that the opposite effect is the lowering of thresholds after adaptation (e.g., DeValois, 1977), in summation experiments the baseline is the small amount of summation expected from independent variability in separate mechanisms (probability summation).

Another piece of evidence suggesting inhibition can come from finding that adapting to a compound stimulus produces

less effect than adapting to one of its components (e.g., Levinson and Sekuler, 1975a; Tolhurst, 1972).

The problem with all the evidence is that there are always several reasonable alternative explanations not requiring inhibition as, for example, Graham *et al.* (1985), Hirsch *et al.* (1982), Klein (1985), and Thomas (1985) discuss for identification experiments. Consequently, the evidence to date for inhibition on any dimension is—in my opinion—noncompelling. In the summary below, therefore, a tentatively affirmative answer given to this fifth question means only that effects have been reported at far values that are opposite to those at close values. It should not be taken to imply compelling evidence for inhibition.

Many features necessary to specify completely a multiple receptive-field model will still remain undiscussed after the above questions are answered. For example:

(a) What is the probability density function describing an individual mechanism's output (the probability density characterizing the noise source in Fig. 5), and does it depend on signal strength?

(b) What is the exact form of the decision variable? For example: Is it the maximum output or some weighted sum or the more complicated calculation of likelihood ratio required for an optimal observer?

(c) What mechanisms form the subset of mechanisms that enter into the decision variable in any given task? (What mechanisms does the observer pay attention to or monitor?)

(d) Are the initial filters truly linear filters, or, for example, do they embody a compressive or rectifying nonlinearity?

To calculate the quantitative predictions of a multiple receptive-field model all these features and more must be specified. Changing any of these features, therefore, might well affect the conclusions drawn about any other feature including the features discussed here. The attempt here, however, is only to summarize qualitatively the broad and impressive consistencies found between results from different kinds of experiments done by different investigators. I suspect that these general conclusions will be little affected by details of the other features of the model (with one exception—the decision rule for identification—which will be discussed later).

More complete and rigorous descriptions of ways in which answers to questions (2) through (5) above can be derived from psychophysical results can be found in many sources, including Georgeon and Harris, 1984 (for adaptation experiments); Graham, 1980, and Graham *et al.*, 1978 (for summation experiments); Yager *et al.*, 1984 (for uncertainty and identification experiments); Thomas, 1985, and Watson, 1983 (for identification experiments). For discussion of the features of multiple-mechanism models not discussed here—as in questions (a) through (d) above—see, for example, Kramer *et al.*, 1985; Nachmias, 1972, 1981; Nachmias and Kocher, 1970; Pelli, 1985; Yager *et al.*, 1984.

## ANSWERS

### Spatial Frequency

(1) PEAKED sensitivity function. Typically (in parameter ranges listed above) sensitivity peaks at medium spatial frequencies (3–10 c/deg), declines slightly for lower spatial

frequencies, and declines strongly for higher spatial frequencies, becoming zero above 60 c/deg for ordinary gratings (see, e.g., Kelly, 1984; Robson, 1966).

The high-spatial-frequency decline derives from both optical and neural spatial integration (see, e.g., Williams *et al.*, 1984).

(2) YES, multiple mechanisms. Bandwidths are sufficiently narrow that there are at least several effectively nonoverlapping ranges at any constant combination of values on the other dimensions (see, e.g., Blakemore and Campbell, 1969; Campbell and Robson, 1968; Graham and Nachmias, 1971; Graham *et al.*, 1978; Pantle and Sekuler, 1968; Sachs *et al.*, 1971; Thomas, 1970; Wilson and Bergen, 1979). At high temporal frequencies, the bandwidths may be slightly broader. (An apparent discrepancy between adaptation/summation and identification results on the spatial-frequency dimension at high temporal frequencies will be discussed below.) That multiple spatial-frequency mechanisms exist at a single spatial position (rather than being distributed with the highest spatial-frequency ones in the fovea and the lower spatial-frequency ones further out) has been verified by experiments with localized patches (see, e.g., Graham *et al.*, 1978; Watson and Robson, 1981).

(3) YES, labeled (see, e.g., Hirsch *et al.*, 1982; Olzak, 1981; Thomas *et al.*, 1982; Watson and Robson, 1981; Yager *et al.*, 1984).

(4) YES, probabilistically independent at least to a large extent (see, e.g., Hirsch *et al.*, 1982; Sachs *et al.*, 1971).

(5) MAYBE inhibition. Some opposite effects have been reported in adaptation (see, e.g., DeValois, 1977; Tolhurst and Barfield, 1978), in identification (see Graham *et al.*, 1985; Hirsch *et al.*, 1982; Olzak, 1981; Olzak and Thomas, 1981), and sometimes in summation experiments (Olzak and Thomas, 1981) but not always (Kramer, 1984). Further, adapting to a compound stimulus produces less adaptation than adapting to either component alone (see, e.g., Stecher *et al.*, 1973; Tolhurst, 1972).

### Orientation

(1) FLAT sensitivity function, at least approximately. Sensitivity is often reported to be slightly less (a fraction of a log unit) at the oblique than at the vertical and horizontal orientations.

(2) YES, multiple mechanisms, at least several of which are effectively nonoverlapping (see, e.g., Kulikowski *et al.*, 1973; Mostafavi and Sakrison, 1976; Movshon and Blakemore, 1973).

(3) YES, labeled (see, e.g., Thomas and Gille, 1979).

(4) YES, apparently probabilistically independent (see, e.g., Kelly, 1982; Thomas and Gille, 1979).

(5) MAYBE inhibition. Some opposite effects have been reported (see, e.g., Thomas and Shimamura, 1975, but see Thomas, 1985): although primarily using suprathreshold patterns.

### Spatial Position (Horizontal and Vertical)

(1) PEAKED sensitivity function with sensitivity generally greatest at the foveal center and decreasing approximately as a function of the number of periods away from foveal center (at least within parameter ranges listed above—see, e.g., Robson and Graham, 1981).

As a result, sensitivity as a function of spatial frequency (at



a constant temporal frequency) cuts off at much lower spatial frequencies peripherally than centrally. Interestingly, sensitivity as a function of temporal frequency (at a constant spatial frequency) is less affected and, indeed, at very low spatial frequencies, high temporal frequency sensitivity may even improve in the periphery (see, e.g., Kelly, 1984).

A question of current interest is whether these effects of eccentricity can be explained simply as the result of a scaling the size of receptive fields as a function of distance from foveal center (see, e.g., Kelly, 1984; Koenderink *et al.*, 1978a, 1978b, 1978c, 1978d; Royamo *et al.*, 1978; Watson, 1983). The scale factor is sometimes called the cortical magnification factor.

(2) YES; multiple mechanisms, as has been assumed for decades (see, e.g., Barlow, 1958). The range of spatial positions covered by any one mechanism is a narrow subrange of the visible range (which is the whole visual field). Thus there are effectively a great number of mechanisms having non-overlapping ranges on these two spatial-position dimensions.

(3) YES, labeled (see, e.g., Davis *et al.*, 1983; Graham *et al.*, 1985; King-Smith and Kulikowski, 1981).

(4) YES, probabilistically independent (see, e.g., King-Smith and Kulikowski, 1981; Robson and Graham, 1981).

(5) MAYBE inhibition. Some opposite effects have occasionally been reported at far values, but the difficulties in interpretation are numerous (see, e.g., Graham *et al.*, 1985; Wilson *et al.*, 1979).

#### Spatial Extent (Parallel and Perpendicular to Bars)

(1) INCREASING SENSITIVITY FUNCTION. As spatial extent (of either a grating or an aperiodic stimulus) is increased, sensitivity tends first to increase quickly and then to slow down; nonmonotonicities (decreases in sensitivity) are sometimes seen. (A patch of greater extent can be viewed as a compound of two side-by-side patches of half the extent. Thus parametric experiments on the spatial-extent dimension can also be viewed as summation experiments on a spatial-position dimension.) To explain these changes in sensitivity as a function of spatial extent, three factors need to be taken into account.

First, at relatively small extents, effects of spatial integration within the spatial weighting functions (spatial receptive fields) of individual mechanisms will be seen. In the mechanisms tuned to the spatial frequency and orientation of the stimulus, the effect of this integration is an increase in sensitivity as spatial extent increases. In general, the increase in these mechanisms' sensitivity dominates the observer's sensitivity, and thus the observer's sensitivity also increases.

Zero cycles/degree is a special case, however, as there may well be no mechanisms tuned to 0-c/deg, that is, no mechanisms lacking an inhibitory surround. Thus, increasing the extent of aperiodic stimuli (0-c/deg sinusoids multiplied by a window function) should produce, in each individual mechanism, an initial increase in sensitivity (spatial integration within the excitatory center) followed by a decrease (due to the inhibitory surround). Such decreases may be hidden by the second factor described below but are sometimes reported (Shapley, 1974; Thomas, 1978).

Also, for sinusoids of very high spatial frequency, all effects of integration within the spatial weighting functions of individual mechanisms may be entirely hidden by an initial decrease due to the second factor discussed below.

The second factor that one must consider is the changing spatial-frequency and orientation content as spatial extent is increased. Spatial frequency and orientation bandwidth become narrower as spatial extent increases. Thus which spatial-frequency and orientation mechanisms are most sensitive to the stimulus may change as the stimulus increases in spatial extent. This effect can lead to decreases in sensitivity (e.g., for high-spatial-frequency sinusoids) or to increases (e.g., for aperiodic stimuli see demonstration in Fig. 2 of Thomas, 1970; or Fig. 6 of Bergen *et al.*, 1979, of the switch from receptive fields having smaller centers to those with larger centers).

The third factor that one must consider is the effect of probabilistic independence of mechanisms at different spatial positions (i.e., spatial probability summation) taking retinal nonuniformity, that is, sensitivity as a function of spatial position, into account. Across regions of relatively uniform sensitivity, spatial probability summation produces a slow increase as spatial extent is increased even out to large extents (Robson and Graham, 1981). For patterns centered at the fovea, however, no such increase is predicted in general because of the rapid drop-off in sensitivity moving away from the fovea (see, e.g., Robson and Graham, 1981).

(2) PROBABLY NOT multiple mechanisms near threshold. Adaptation and summation experiments using stimuli of different spatial extent (different spatial-frequency or orientation bandwidth) have indeed shown selectivity on both spatial-extent dimensions (see, e.g., Kulikowski and King-Smith, 1973; Wright, 1982). But, within a multiple-mechanisms model, this observed selectivity with stimuli of different spatial extents does not necessarily require multiple mechanisms of different spatial extents. For, when you increase the spatial extent of a stimulus, you also necessarily decrease the range of spatial frequencies and/or orientations contained in the stimulus and you increase the range of spatial positions covered by the stimulus. Thus you change the population of responsive mechanisms even if there is only one spatial extent of mechanism at a given best spatial frequency, best orientation, and center spatial position.

In fact, the success of the predictions for the spatial-extent summation experiments assuming only mechanisms having different best spatial frequencies (although all of the same spatial extent) but allowing for independent variability in their outputs (Graham, 1977, 1980) provides some evidence against the existence of multiple spatial extents of mechanisms (multiple-spatial-frequency bandwidths—near threshold, of course). For, if such mechanisms existed, they should have affected the predictions.

(3-5). Not applicable.

#### Spatial Phase

(1) FLAT, presumably uniform sensitivity for all phases.

(2) UNCLEAR whether there are multiple mechanisms near threshold. For one thing, few experiments have used different phases of near-threshold stimuli. Second, all experiments manipulating spatial phase (i.e., spatial symmetry) of stimuli perforce change the spatial-position content as well, thereby changing the population of responsive mechanisms even if all mechanisms have the same symmetry of spatial weighting function. Thus to argue that selectivity when using stimuli of different spatial phases of stimuli is due to mecha-

nisms with different phases (symmetries) of receptive field requires some careful calculation. On the other hand, I know of no good evidence against the existence of multiple spatial phases, and it is an attractive idea.

(3-5) No information.

#### Temporal Frequency

(1) **PEAKED SENSITIVITY FUNCTIONS.** In many circumstances (in particular, in the parameter ranges listed above) sensitivity is greatest at medium temporal frequencies (3 to 10 Hz) and drops off slowly toward low frequencies and quickly toward high frequencies, looking, in fact, remarkably like sensitivity plotted as a function of spatial frequency (see, e.g., Kelly, 1984; Robson, 1966). Dependence on eccentricity is briefly discussed above under spatial position.

There is a strong interaction between spatial frequency and temporal frequency; for example, at moderate mean luminances, the low-frequency decline in the sensitivity function on either dimension disappears when measured at high values of the other (see, e.g., Robson, 1966). In other words, the function giving sensitivity for each temporal frequency and spatial frequency is not separable—it cannot be expressed as the product of two functions, one giving sensitivity at each temporal frequency and one giving sensitivity at each spatial frequency.

(2) **NO multiple mechanisms except highly overlapping, broadly tuned ones.** In spite of the similarity in overall sensitivity functions on the spatial-frequency and temporal-frequency dimensions, and in spite of an exact formal analogy between temporal frequency and spatial frequency; near-threshold psychophysical results using stimuli of different temporal frequencies are entirely different from those using stimuli of different spatial frequencies. (This difference should erase any fears that, in some artifactual way, sinusoids magically generate their own results.) In the case of temporal frequency, there is much less selectivity than in the case of spatial frequency. This is true for adaptation (see, e.g., Moulden, Renshaw, and Mather, 1984; Pantle, 1971; Smith, 1971), summation (Watson, 1977), and identification (Mandler and Makous, 1984; Thompson, 1983; Watson and Robson, 1981). Uncertainty experiments have not been tried to my knowledge. That identification results indicate somewhat greater selectivity than do detection results is discussed below.

Most of the experiments with temporal frequency have been done using spatially aperiodic stimuli; and thus the evidence for something more than a single mechanism (perhaps two broad bandwidth mechanisms) might not indicate more than a single mechanism at a given spatial frequency. Instead it might be a by-product of the existence of multiple mechanisms on the spatial-frequency dimension coupled with some interaction between temporal and spatial frequency (e.g., the mechanisms sensitive to low spatial frequencies are quite sensitive to high as well as to low temporal frequencies unlike the mechanisms sensitive to high spatial frequencies). (Or, letting dimension *A* in Fig. 6 be spatial frequency and dimension *B* be temporal frequency, the situation might be like the one in the upper right of Fig. 6 except with the circles elongated downward into ellipses that have their long axes parallel to temporal frequency.) Some temporal-frequency experiments have, however, been done with spatial sinusoids (see, e.g., Watson, 1977; Watson and Robson, 1981) and do

seem to indicate more than a single mechanism at a single spatial frequency.

In short, if there are mechanisms (e.g., sustained and transient) sensitive to different temporal-frequency ranges at any particular spatial frequency, orientation, spatial-position, etc. (near threshold!), they seem to have highly overlapping sensitivity functions.

(3-5) Probably not applicable, therefore.

#### Temporal Position

(1) **FLAT sensitivity function.** Sensitivity as a function of temporal position (from, for example, the beginning of a trial) is presumably uniform although rarely measured. Assuming that it is completely uniform is probably a mistake, however.

(2) **YES, multiple "mechanisms."** All available near-threshold evidence indicates, as has been assumed for decades, that there is selectivity for temporal position: (i) two stimuli presented far apart in time do not sum completely in determining threshold, as has been shown in dozens of temporal-summation studies (see, e.g., Barlow, 1968; Rashbaas, 1970; Watson and Nachmias, 1977); (ii) an observer can identify at which of several relatively far-apart times a stimulus was presented (as is consistent with the regular use of two-interval forced-choice paradigms); (iii) uncertainty about temporal position causes a decrement in performance (see, e.g., Lasley and Cohn, 1981). Rather than attributing this selectivity to literally separate mechanisms (e.g., separate neurons, each one responding at a single moment in time), one ordinarily assumes that an individual mechanism gives different responses at different moments in time. Thus this dimension might well be expected to act differently from other dimensions in some respects; indeed, the region of interaction along the temporal-position dimension indicated by adaptation experiments (many minutes) is much bigger than that indicated by, for example, summation or identification experiments (fractions of seconds).

(3) **YES, labeled** (see, e.g., Lasley and Cohn, 1981).

(4) **YES, probabilistic independence** (e.g., probability summation across time; Watson, 1979).

(5) **Unknown.**

#### Temporal Extent

(1) **INCREASING sensitivity function, analogous to that for spatial extent.** As temporal extent (either of temporally sinusoidal or of temporally aperiodic stimuli) increases, sensitivity increases dramatically at small values (presumably owing to temporal integration within single temporal weighting functions) and then increases more slowly (presumably owing to independent variability in the responses at different points in time, that is, to temporal probability summation).

(2-5) **UNKNOWN.** Possible selectivity for temporal extent has been relatively little studied but has been reported in an identification paradigm (Zacks, 1970). Interpreting it, however, runs into a problem analogous to that for spatial extent. Namely, such selectivity might well be due to mechanisms having sensitivities that vary along the temporal-frequency or temporal-position dimensions. Some quantitative predictions will probably be necessary to untangle the answer.

**Temporal Phase** (number of peaks) *temporal phase* (number of peaks) *temporal phase* (number of peaks)

- (1) FLAT sensitivity function presumably.  
 (2-5) Possible selectivity for temporal phase has been little investigated. Were selectively found in experiments using stimuli that vary in temporal phase; interpreting it would run into problems analogous to those with spatial phase.

#### Direction of Motion

- (1) FLAT sensitivity function. Sensitivity is approximately uniform for different directions (with exceptions in some subjects and with possible differences depending on whether the direction is toward or away from the fovea).  
 (2) YES AT HIGH VELOCITIES, NO AT LOW. In near-threshold experiments using stimuli differing in direction of motion, direction selectivity is found at low spatial frequencies and high temporal frequencies (that is, at high ratios of temporal to spatial frequency or, equivalently for drifting stimuli, at high velocities); no (or much less) direction selectivity is found at high spatial frequencies and low temporal frequencies (at low velocities).

There may even be an exact dependence on the ratio of temporal to spatial frequency (for drifting stimuli, on velocity) with the boundary region between about 0.5 and 2 deg/sec. (Using equal-velocity stimuli has usually shown some dependence on spatial frequency as well, however; see, e.g., Arditi *et al.*, 1981.)

Summation (see, e.g., Arditi *et al.*, 1981; Stromeyer *et al.*, 1978; Watson *et al.*, 1980) and identification (see, e.g., Green, 1983; Lennie, 1980; Thompson, 1984) experiments have been done in both ranges, and one identification experiment has even been done using stabilized vision (Mansfield and Nachmias, 1981). Adaptation (see, e.g., Levinson and Sekuler, 1975a, 1975b; Pantle and Sekuler, 1969; Stromeyer *et al.*, 1979) and uncertainty experiments (see, e.g., Ball and Sekuler, 1980) seem only to have been done in the high-velocity range.

It is at least provocative and perhaps important that this dependence on spatial frequency and temporal frequency shows up in two more places: (i) neurons in V1 and V2 of primates tuned to high temporal and low spatial frequencies are more directionally selective than those tuned to low temporal and high spatial frequencies (Foster, *et al.*, in press); and (ii) spatiotemporal patterns at detection threshold are reported (see, e.g., Harris 1980; Koenderink and van Doorn, 1979) to have either a predominantly temporal (moving, fluctuating) appearance or a predominantly spatial (clear spatial forms) appearance depending on whether the velocity (or the ratio of temporal frequency divided by spatial frequency) is higher or lower than about 1 deg/sec.

Somewhat above detection threshold at high velocities, observers may be able to set a pattern threshold—the minimum contrast at which the stimulus has a clear spatial appearance. Interestingly, although the effect of adaptation on detection threshold is direction selective in this velocity range, its effect on this pattern-appearance threshold seems not to be (Levinson and Sekuler, 1980).

- (3) YES, labeled (at low spatial and high temporal frequencies where direction selectivity is found) as indicated both by uncertainty effects and by good identification of near-threshold stimuli. The uncertainty effect for direction

of motion (which has been reported only for random-dot patterns) is much larger than that for other pattern dimensions (see, e.g., Ball and Sekuler, 1980). It is too large to be explained merely on the basis of probabilistically independent noise, in fact, but requires postulating something like limited-capacity attention (e.g., some inability of the observer to monitor all mechanisms at once). Whether this result would also hold with simple grating patterns is not clear.

- (4) PROBABLY YES. The directionally selective mechanisms are presumably probabilistically independent (at low spatial and high temporal frequencies) as the amount of summation seen between opposite directions in a summation experiment is of the correct order of magnitude for probability summation (see, e.g., Watson *et al.*, 1980), although that small amount of summation might also be explained by mechanisms having some sensitivity to the opposite direction. (See similar discussion on EYE dimension below.)

- (5) MAYBE inhibition (at high velocities). Although little information about possible opposite effects is available, the result of adapting to a compound has been reported to be less than that of adapting to a single component (Levinson and Sekuler, 1975a).

#### Contrast

- (1) NOT APPLICABLE. Measuring sensitivity (reciprocal of contrast at threshold) as a function of contrast does not make sense. However, one often measures performance (e.g., percent-correct detection in a two-alternative forced-choice task) as a function of contrast, typically finding an S-shaped function going from chance to perfect performance over a range of about 0.3 log unit—a factor of 2 of contrast. (This function is frequently called the psychometric function.)

- (2) PROBABLY NOT multiple mechanisms. The absence of an uncertainty effect when intermixing contrasts (Davis *et al.*, 1983) suggests that there are *not* multiple mechanisms, at least not ones with labeled outputs, on the contrast dimension. This conclusion applies, obviously, only within the narrow range of near-threshold contrasts that can be studied in this uncertainty paradigm.

- (3-5) Not applicable.

#### Mean Luminance

- (1) INCREASING sensitivity function. The function relating contrast sensitivity to mean luminance has the same shape for every spatial and temporal frequency (see, e.g., van Ness *et al.*, 1967). At low mean luminances, contrast sensitivity increases linearly or, to put it two other equivalent ways: contrast threshold decreases linearly and absolute luminance increment threshold remains constant. Then, with further increases in mean luminance the rate of decrease slows down until finally it stops, with contrast sensitivity remaining constant at all high mean luminances or, equivalently, absolute luminance increment threshold increasing linearly with mean luminance (the Weber function range).

The exact luminances at which these transitions occur, however, do depend on spatial frequency, temporal frequency, and spatial position and probably on the values on some other dimensions as well (see, e.g., Koenderink *et al.*, 1978d; van Ness *et al.*, 1967). Thus the shape of the functions relating

sensitivity to other dimensions (e.g., spatial frequency, temporal frequency) does change somewhat depending on the mean luminance (e.g., lose its low-frequency decline).

(2-5) NOT APPLICABLE. The four near-threshold kinds of experiment that might reveal the existence of multiple mechanisms are problematical on the mean-luminance dimension, partly because of the manifest processes of light adaptation. Consequently, although mechanisms sensitive in different ranges of mean luminance might exist (that is, mechanisms having sensitivity functions on the mean-luminance dimension that are either peaked like those on other dimensions or perhaps functions that decline only at the low end staying sensitive for all high luminances), the mechanisms' properties cannot be straightforwardly determined from the kinds of experiment considered here.

#### Eyes

(1) FLAT sensitivity function. In general, sensitivity is similar in the two eyes, although many individuals show some differences.

(2) YES multiple mechanisms. Both adaptation and summation experiments show selectivity along this dimension (that is, the phenomena known as incomplete interocular transfer (see, e.g., Blakemore and Campbell, 1969) and incomplete binocular summation (see, e.g., Arditi *et al.*, 1981)). These results suggest the existence of multiple mechanisms that are differentially sensitive to inputs from the two eyes. Note, however, that the sensitivities are probably overlapping as some interocular transfer is apparently always found, and the amount of summation is usually reported to be somewhat greater than that expected on the basis of probability summation (greater than that between far-apart spatial frequencies, for example).

(3) NO, not labeled (in the sense of providing enough information to allow identification or selective monitoring). Although information about which eye produced which response is presumably used in stereopsis, information about which eye is connected to which mechanism seems to be lost upstream. Evidence for this statement comes from both the uncertainty and the identification paradigms. Uncertainty about eye of origin does not decrease detectability (see, e.g., Cormack and Blake, 1979), nor can observers identify eye of origin (particularly not at high spatial frequencies and low temporal frequencies—which is exactly the range where evidence for multiple analyzers from adaptation and summation experiments is strongest; see, e.g., Blake and Cormack, 1979).

The eye dimension is thus the only dimension on which there is abundant evidence that results from the four kinds of near-threshold mechanisms-revealing experiment are dissociated, with some (adaptation and summation) showing selectivity and others (uncertainty and identification) not. This particular discrepancy seems reasonably explained by assuming that, although multiple mechanisms exist, their outputs are not labeled. Indeed, if the labels used by an observer in identification and uncertainty experiments occur at some level above stereopsis (above the level at which the two eyes' outputs are used to compute the depth of objects), it would seem quite sensible to lose information about the eye of origin *per se*.

(4) UNCLEAR. The question of whether there is inde-

pendent variability or not is hard to answer on this dimension. A compound-pattern stimulating both eyes is always more detectable than either component—often by an amount that might be interpreted as due to independent variability in the two eyes but usually by a somewhat greater amount than, for example, two far-apart spatial frequencies. As mentioned above, this and the partial interocular transfer suggest that most mechanisms are somewhat sensitive to both eyes. (Since there are only two values on this eye dimension, you cannot look at values even further apart to help disambiguate the situation.) So all the partial summation seen between the two eyes could just as well be entirely due to broadband mechanisms having sensitivity to both eyes rather than due to independent variability. Since corroborating evidence from uncertainty and identification experiments on this dimension cannot be gained, one is at a dead end.

(5) UNCLEAR for much the same reasons as the answer to (4) is.

#### DISCREPANCIES BETWEEN DETECTION AND IDENTIFICATION RESULTS

This discrepancy between results from different kinds of experiment on the eye dimension leads naturally back to two other discrepancies—briefly mentioned earlier—between identification and detection (in particular, adaptation/summation) results.

On the spatial-frequency dimension, adaptation (Graham, 1972) and summation (Arend and Lange, 1979; Pantle, 1973; Thompson, 1981) experiments show only a little broadening of bandwidth as temporal frequency is raised, but identification experiments seem to show a large increase in bandwidth (Watson and Robson, 1981). If this discrepancy proves robust, e.g., can be found with the same observers in the same conditions, one could explain this discrepancy by saying that, at high temporal frequencies (but not at low) the spatial-frequency channels are unlabeled. Postulating unlabeled mechanisms seems less pleasing here than on the eye dimension, however.

In any case, the other discrepancy between identification and adaptation/summation results—one on the temporal-frequency dimension (in the typical low-to-middle spatial frequency range)—is in the wrong direction for this explanation. Adaptation (see, e.g., Pantle, 1971; Smith, 1971) and summation (Watson, 1977) experiments show less selectivity for temporal frequency than do identification experiments. The latter (Mandler and Makous, 1984; Thompson, 1983; Watson and Robson, 1981) show evidence for at least two nonoverlapping ranges.

These so-called discrepancies depend, of course, on all the details of the models used to interpret the adaptation, summation, and identification experiments. And it seems to me likely that the cause of both discrepancies just mentioned is with the model used in interpreting identification results, in particular, with the simple kind of decision rule used (e.g., the identity of the maximally responding mechanism). The substantial practice and instructional effects that are found in identification experiments (particularly with supra-threshold stimuli; but we have seen them with near-threshold stimuli (see, e.g., Graham *et al.*, 1985)) reinforce this not very surprising guess. Some (e.g., Thomas, 1984; Watson and Ah-

umada, 1985) have begun work on more plausible decision rules for identification experiments, rules that assume that the observer makes more use of available information than, for example, simply computing the identity of the maximally responding mechanism.

### A PHYSIOLOGICAL ASIDE

In addition to the two best-known visual cortical areas (V1 and V2 in primates), recent neurophysiological and anatomical work has uncovered many other, higher visual areas. (Recent reviews can be found in Cowey, 1985; Van Essen, *In press*; Van Essen and Maunsell, 1983.) For many years, people have wondered if the mechanisms postulated by psychophysical models could be identified with neurons in V1 and, perhaps, V2. Although it is notoriously difficult—on both logical and practical grounds—to confirm such an identification, the neurophysiological and psychophysical evidence uncovered in intervening years has certainly not disconfirmed it. On the contrary, V1 and V2 neurons do show selective sensitivities analogous to those of the mechanisms in the psychophysical model. (A recent review can be found in Shapley and Lennie, 1986.) Indeed, if anything, the neurons in V1 and V2 seem to be more complicated than do the mechanisms in the model for near-threshold psychophysical behavior (e.g., show selectivity on more dimensions, for example, on the spatial extent dimensions; DeValois *et al.*, 1982a, 1982b; Foster *et al.*, *in press*). The majority of visual areas in the cortex, therefore, may be represented in Fig. 5 in only a simple form—all lumped together into the "compute decision variable" box. Presumably all that neural machinery is used for something more complicated than computing the simple decision rules, e.g., maximum output, adequate to explain quantitatively near-threshold behavior. Perhaps the only reason such simple rules work near threshold is that—near threshold—they happen to be near optimal (see, e.g., Noll and Jaarsma, 1967).

### CONCLUSION

Although I suspect that our understanding of the higher stages (decision processes) in identification tasks even near threshold is less than it might be, our understanding of the higher stages (decision processes) in detection tasks may be substantially correct. Further, and the main point of this paper, the many hundreds of published near-threshold pattern-vision experiments form an impressive body of evidence in support of the current models of pattern vision, models in which the fundamental stage is a set of multiple mechanisms with different ranges of sensitivities along certain dimensions. There is remarkable agreement across different experimental paradigms and across different laboratories about which dimensions do have and which dimensions do not have multiple mechanisms, as well as substantial agreement about other properties of those mechanisms.

### ACKNOWLEDGMENTS

This paper is based on a talk given at the Symposium on Relation of Detection to Identification in Vision: History, Theory, and Applications, held at the Optical Society of

America Meeting, October 30, 1984, San Diego, California. I am grateful to Elizabeth Davis, Patricia Kramer, and James Thomas for their helpful comments on an earlier draft.

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