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DISCRIMINATION AT THRESHOLD: LABELLED DETECTORS IN HUMAN VISION*

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Abstract—We examined discriminations between small patches of grating that differed in either spatial or temporal frequency. The patches were presented at contrasts near to detection threshold. For certain pairs of stimuli, each was correctly identified as often as it was detected. To explain this result, we hypothesize that the detectors of these stimuli are *labelled*, in the sense that the observer can distinguish the response of each detector from that of any other. Under this assumption, we find that the detectors form two non-overlapping sets in their selectivity for temporal frequency. In their selectivity for spatial frequency, the detectors of slowly varying stimuli can be partitioned into 7 distinct sets, but only 3 sets are evident among the detectors of rapidly modulated patterns.

INTRODUCTION

Many theories of visual contrast sensitivity assume the existence of a collection of selective detectors. Each detector responds to a different range of spatiotemporal luminance distributions, and a stimulus is seen whenever at least one detector is sufficiently active (Campbell and Robson, 1968; Kulikowski and Tolhurst, 1973; Graham, 1977; Wilson and Bergen, 1979; Watson, 1980).

But though these detector models may explain how an observer judges whether a stimulus is present, they cannot explain how the observer is able to distinguish one stimulus from another. This is because these models transform the visual stimulation into a single number which determines whether the stimulus is seen or not, and hence they provide no mechanism for the coding of sensory quality. In this paper we consider an elaboration to the detector model with which it may be applied to discrimination as well as detection.

Perhaps the most important hypothesis put forth to explain the sensory identification of stimuli is Muller's Law of Specific Nerve Energies. In his discussion of the physiological basis of sensory quality, Muller proposed that the nerves of each sense had a "specific energy", which ensured that they aroused only the appropriate sensation. Helmholtz extended this idea, proposing that the nerves within a sense might be "specific" as well (Boring, 1942). A modern interpretation of this doctrine is that each sensory nerve is a *labelled line*, capable of being distinguished from all other nerves. In this paper we consider the possibility that each detector is a labelled line, that is, that the observer can distinguish between the responses of any two detectors.

Consider one prediction of this hypothesis. If two stimuli are detected by different sets of labelled detectors, then the identity of the set mediating detection unambiguously identifies the stimulus. In this situation, each of the two stimuli will be correctly identified whenever it is detected. We say that the two stimuli are *perfectly discriminated.*

A number of previous reports of perfect discrimination support the idea that detectors may be labelled. For example, Nachmias and Weber (1975) found that sinusoidal gratings of 3 and 9 c/deg were discriminated perfectly at threshold. Furchner *et al.* (1977) have confirmed and extended this result, and Barker (1977) and Thomas and Gille (1979) have estimated spatial frequency and orientation bandwidths of individual detectors by this technique. Similarly, Tolhurst and Dealy (1975) have shown that bright and dark lines, or edges of opposite polarity, are correctly identified when barely detectable, and Watson *et al.* (1980) have shown that gratings which move rapidly in opposite directions are perfectly discriminated.

In this report, we examine the capacity of observers to distinguish perfectly between stimuli which differ in either temporal or spatial frequency. We then consider the consequences of our results for a labelled detector model of human contrast sensitivity.

METHODS

The stimuli in these experiments were small patches of vertical sinusoidal grating whose contrast was modulated sinusoidally in time. Their luminance is given by

$$L(x, y, t) = L_0[1 + cw(x, y, t) \times \sin(2\pi f_x x)\cos(2\pi f_t t)] \quad [1]$$

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* Some of these results were reported in May, 1979 at the meetings of the Association for Research in Vision and Ophthalmology (Watson and Robson, 1979).

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where L_0 is the mean luminance, c is the contrast, and f_x and f_t are the spatial and temporal frequencies. The window function $w(x, y, t)$ is given by

$$w(x, y, t) = \exp[-(x/s_x)^2 - (y/s_y)^2 - (t/s_t)^2] \qquad [2]$$

We adopt the term *spread* for the distance over which a Gaussian falls from 1 to 1/e. The window function is the product of horizontal, vertical and temporal Gaussians, with spreads of s_x, s_y, and s_t. All three windows were truncated at plus and minus two spreads.

This window function served to confine the stimulus in space and time, as well as in spatial and temporal frequency. Specifically, the amplitude spectra were approximately Gaussian in both spatial and temporal frequency, centered upon f_x and f_t, with spreads of $1/(\pi s_x)$ and $1/(\pi s_t)$. The temporal spread was 250 msec, so the temporal frequency half-amplitude bandwidth was 2.12 Hz. The horizontal and vertical spreads were always equal to 1.5 periods of the lowest spatial frequency used in a session, so that the spatial frequency bandwidth for a patch was no longer than 0.52 octaves.

The stimuli were generated by computer on a large (20 × 30 cm), bright (340 cd/m^2) CRT with a P-31 phosphor. The screen was surrounded by a 61 × 61 cm surface of about the same brightness, but somewhat lower saturation. Horizontal and temporal modulation were produced by conventional means (Graham *et al.*, 1978). To produce the vertical modulation, the product of the horizontal and temporal waveforms was multiplied, once during each unblanked cycle of the 100 KHz raster, by the output of a digital-to-analog converter loaded from a very fast buffer memory.

To determine whether a pair of stimuli, arbitrarily called a and b, are perfectly discriminated we have used a *two-by-two forced-choice* (2 × 2FC) method (Nachmias and Weber, 1975). A trial consists of two time intervals, accompanied by tones, within just one of which a stimulus occurs. The stimulus is randomly either *a* or *b*. After each trial the observer must both select the interval in which the stimulus occurred, and identify the stimulus as *a* or *b*. We thereby measure concurrently the capacity to detect and to distinguish the pair of stimuli.

Within a session, the spatial and temporal frequencies of the two stimuli were fixed. Each was presented 48 times at each of 3 (occasionally 4) contrasts, which spanned in 3dB steps a previously determined threshold. In order to prevent possible discrimination based upon local features, for example, the proximity of a bright bar to the fixation point, the horizontal position of each patch was varied randomly from trial to trial over an interval of one period of the lower frequency, centered upon the fixation point. The display was viewed binocularly with natural pupils from distances of between 57 and 228 cm. Most results are from one observer (A.B.W.). A.B.W. was well practised in 2 × 2FC experiments, but had no substantial practice on any particular condition before the first session of that condition was run. In those conditions where several sessions were run, no consistent practice effects were observed. Additional results were obtained from three other observers (J.G.R., N.G. and D.G.P.). All three were experienced observers and were aware of the aims of the experiment.

RESULTS

We have analyzed the data in two ways. First, from the data of each session we have estimated separate detection and identification thresholds for each stimulus. If two stimuli are perfectly discriminated, each is identified as often as it is detected, so that detection and identification thresholds should be equal. The ratio of these two thresholds is therefore a simple measure of whether two stimuli are perfectly discriminated.

Our second analysis is a statistical test of whether the data of each session are consistent with the hypothesis that detection leads inevitably to correct identification. This is a direct test of whether the two stimuli are perfectly discriminated. Details of this test are given in the appendix.

The upper panels of Fig. 1 show the proportions of correct detections (circles) and identifications (triangles) from a session in which the stimuli were modulated at 0 Hz (left panel) or 2 Hz (right panel). The spatial pattern was a patch of 0.25 c/deg with horizontal and vertical spreads of 6 deg. The task was thus to distinguish between two rates of temporal modulation. To estimate detection and identification thresholds these proportions were fitted separately by a Weibull function with a slope parameter of 3.5, as shown by the solid and dashed curves. This fitting procedure is described elsewhere (Watson, 1979). Threshold is defined as that contrast at which the function equals 0.82.

Note that at 0 Hz the identification threshold is about 3 dB greater than the detection threshold: at 2 Hz the difference is about 2 dB. Evidently these two frequencies are not perfectly discriminated. The lower panel shows results for 0 and 8 Hz. Here the detection and identification thresholds are about equal, indicating that these two frequencies are perfectly discriminated.

In the lower panels, 8 Hz is identified correctly at the lowest contrast more often than it is detected, while for 0 Hz the converse is true. This is probably due to a bias towards reporting the stimulus as 8 Hz when it has not been detected. A bias towards one stimulus will result in an overestimate of its detection-to-identification threshold ratio, and an underestimate in the ratio for the other stimulus. To compensate somewhat for this effect, we have averaged the two decibel ratios from each session.

Discrimination of temporal frequencies

The upper panel of Fig. 2 shows the detection-to-identification threshold ratios for stimuli which dif-

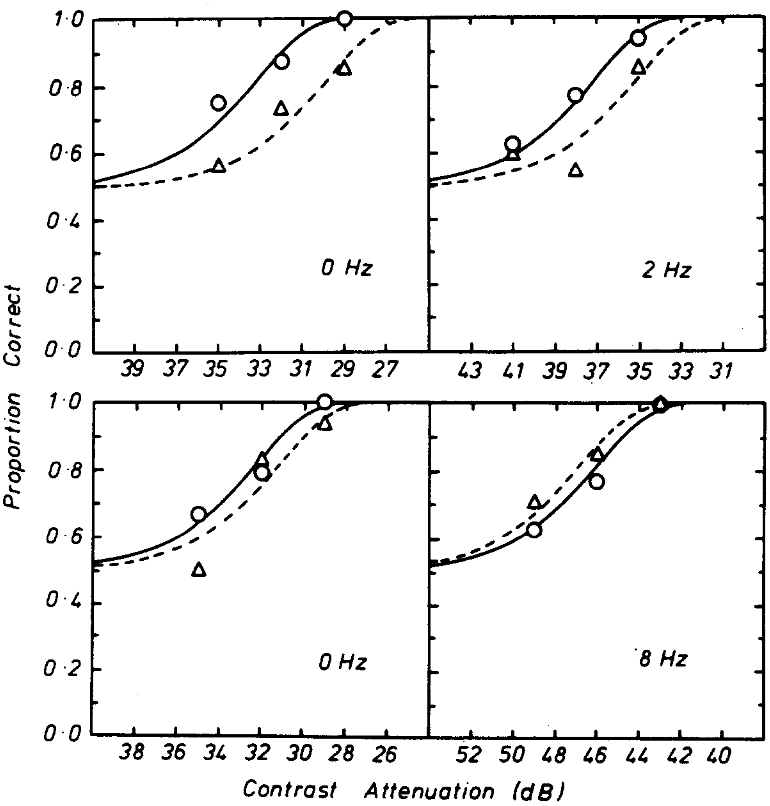

Fig. 1. Each panel shows proportions of correct judgements of interval (circles) and identify (triangles) for the indicated frequency. The solid curve is fit to the circles, the dashed curve to the triangles. The upper panels are from a session containing 0 and 2 Hz, the lower, 0 and 8 Hz.

fered only in temporal frequency. The spatial stimulus was always a patch of 0.25 c/deg with horizontal and vertical spreads of 6 deg.

Each point represents the average threshold ratio from a session in which the two temporal frequencies were a "base", and the frequency shown on the abscissa. The lines connect points sharing a common base, which is indicated by the arrow at the upper end of the dashed segment. The data in the upper panel of Fig. 1 are represented by the circular symbol at 2 Hz, those in the lower panel of Fig. 1 by the symbol at 8 Hz.

The outcome of the statistical test applied to each session is indicated by whether the relevant symbol is open or filled. If it is filled, we cannot reject ($P < 0.05$) the perfect discrimination hypothesis.

The circles show that 8 Hz is perfectly discriminated from 0 Hz, but that 2 Hz and 4 Hz are not. The triangles show that 2 Hz is perfectly discriminated from 16 Hz, but that 4 Hz is not. The three square symbols show that 4 Hz is no more readily discriminated from 32 Hz than from 16 Hz.

The lower panel of Fig. 2 shows the results obtained when the spatial stimulus is a patch of 16 c/deg with horizontal and vertical spreads of 3/32 deg. Filled symbols again indicate acceptance of the perfect discrimination hypothesis. Here only 0 and 8 Hz, and 0 and 16 Hz are discriminated without error at threshold. To summarize the results in Fig. 2, at both a high and low spatial frequency, only quite high and quite low temporal frequencies are discriminated perfectly.

Discrimination of spatial frequencies

The upper panel of Fig. 3 shows detection-to-identification threshold ratios for stimuli modulated at 0 Hz which differ in spatial frequency. As in Fig. 2, filled symbols indicate results of sessions which are compatible with the perfect discrimination hypothesis. Again, each set of connected points represents sessions sharing a common base, which is indicated at the upper end of the dashed line. Within each set the horizontal and vertical spreads were 1.5 periods of the base frequency.

Note that each adjacent pair of bases are perfectly discriminated. Thus the figure shows that the spectrum between 0.25 and 30.0 c/deg is spanned by seven frequencies that are discriminated without error at threshold. The difference in frequency required for perfect discrimination is slightly more than an octave at low frequencies, slightly less than an octave at high.

Modulation of the stimuli at 16 Hz results in the threshold ratios in the lower panel of Fig. 3. Here the spectrum accommodates only two perfectly dis-

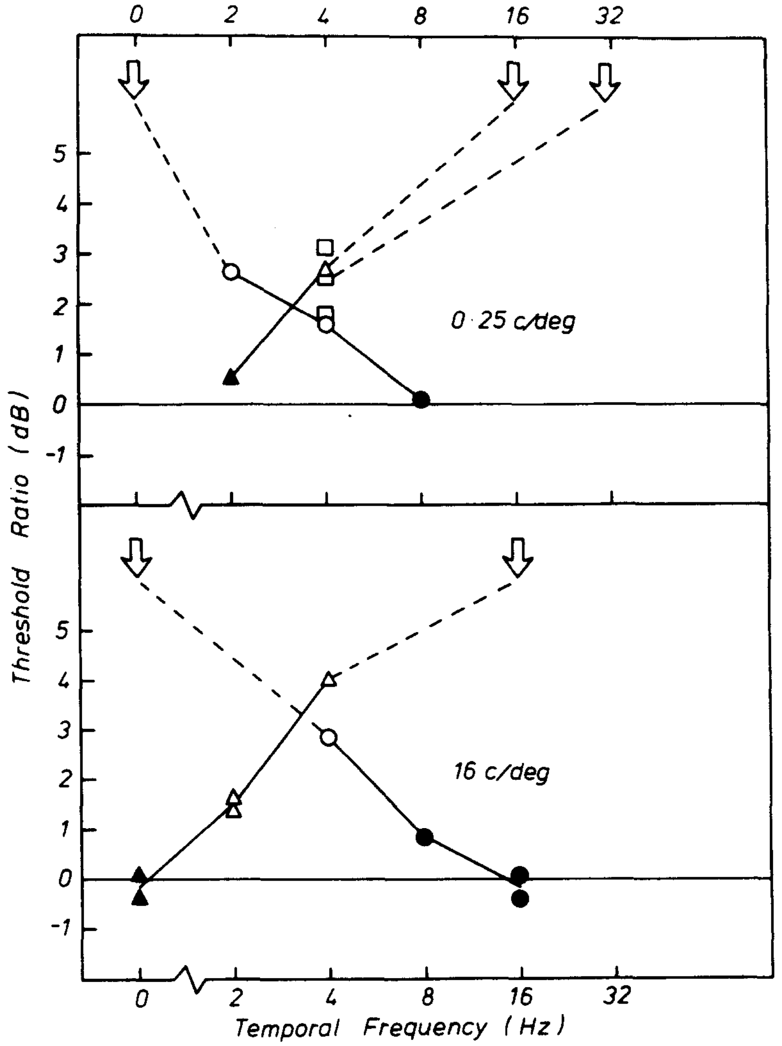

Fig. 2. Detection-to-identification threshold ratios for stimuli differing in temporal frequency. Each point is the average ratio from one session in which the two frequencies were that indicated by the arrow in the upper margin and that given by the position of the point. Sessions which do not reject the perfect discrimination hypothesis are indicated by filled symbols. Stimuli for the upper panel were patches of 0.25 c deg with horizontal and vertical spreads of 6 deg. In the lower panel, the frequency was 16 c/deg and the spread 3/32 deg.

tinguishable frequency pairs. The stimuli are identified at threshold only when separated by about three octaves in frequency.

Some results from other observers are shown in Fig. 4. The curve in each panel is a replica of the comparable data from observer A.B.W. The experimental conditions were as for A.B.W., except that for observer D.G.P. (Fig. 4b) the temporal spread was 70 msec rather than 250 msec. The data are quite similar to those for A.B.W., except perhaps for J.G.R. at 16 HZ (circles in Fig. 4c) who shows somewhat better discrimination between 0.25 and 1 c/deg.

Finally, to illustrate the relation between the threshold ratio and the statistic, the two have been plotted against one another in Fig. 5. All the data from Figs 2, 3, and 4 are included. The critical value ($P < 0.05$) of the statistic is indicated by the horizontal line. A vertical lines has been drawn at a threshold ratio of 1 dB. There is a rough correspondence between these two criteria, since a ratio of 1 dB or less coincides with a failure to reject the perfect discrimination hypothesis on 31 out of 35 occasions.

DISCUSSION

According to the theory outlined in the introduction, two stimuli will be perfectly discriminated if they are detected by different sets of labelled detectors. Is the converse also true? Must stimuli that are perfectly discriminated be detected by different labelled detectors? This notion may seem extreme. Traditionally, discriminations have been thought to be based upon a

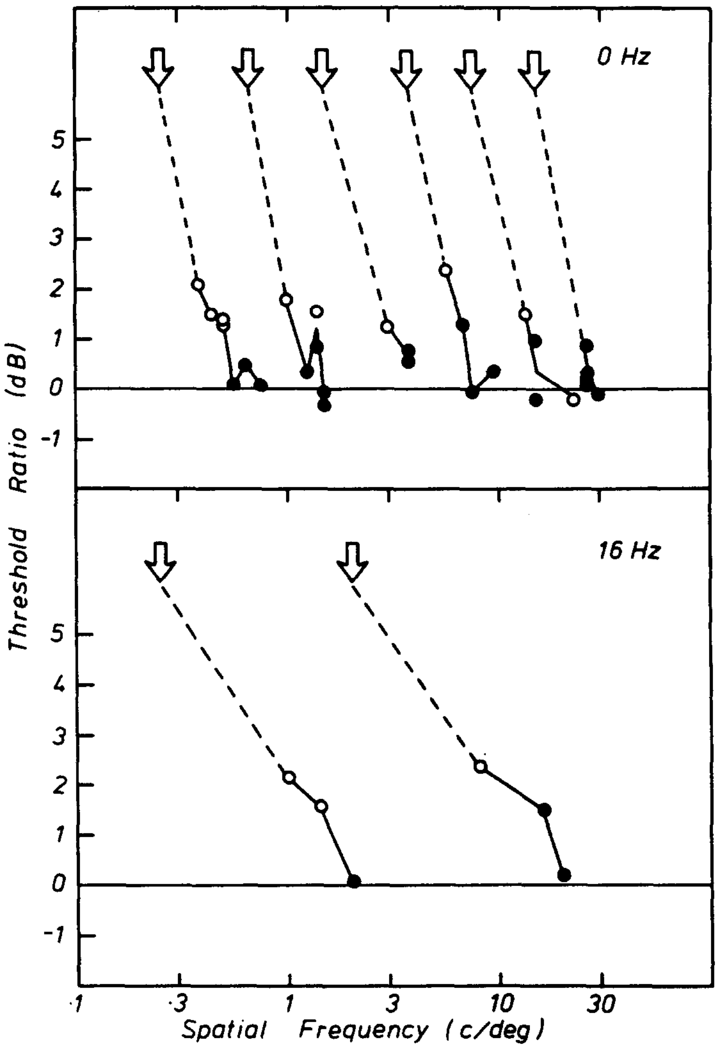

Fig. 3. Detection-to-identification threshold ratios for stimuli differing in spatial frequency. Data in the upper panel are for stimuli modulated at 0 Hz; these in the lower panel, at 16 Hz. Other details are as in Fig. 2.

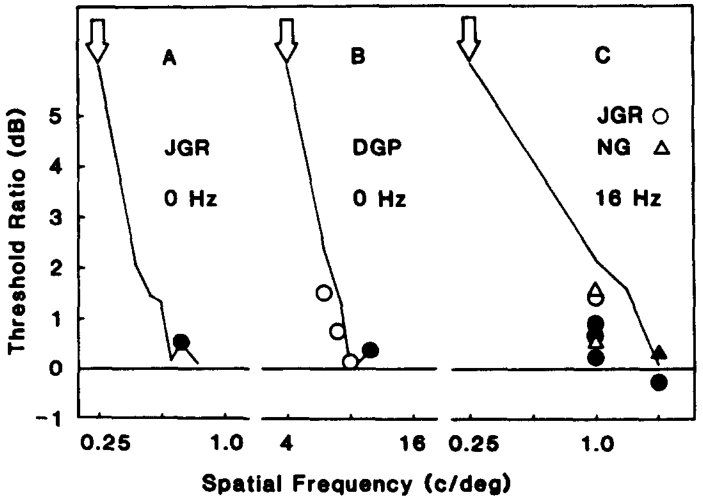

Fig. 4. Spatial discriminations of other observers. The observer and temporal modulation are indicated in each panel. The curves are reproduced from the comparable data of observer A.B.W.

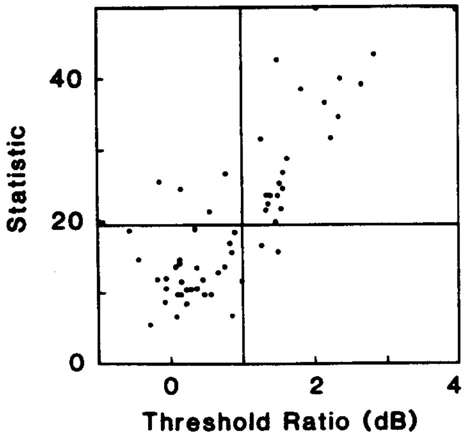

Fig. 5. Relation between detection-to-identification threshold ratios and values of the statistic which tests the perfect discrimination hypothesis. The horizontal line is at 19.5, the critical value of the statistics ($P < 0.05$), and the vertical line is at 1 dB.

comparison of the responses of several detectors, while we suppose they may be based only on the identity of a single detector. However, in the model we are considering, each detector has a threshold, and a threshold response in one detector is sufficient to detect the stimulus. A simple probability calculation shows that at threshold contrast (82% correct in a 2AFC experiment), about 60% or more of all detections involve only a single detector. Thus on most occasions, no comparisons among detector responses are possible, as only one detector is above threshold. Under these conditions, identification of the set to which the detector belongs is the only available technique, and stimuli will be perfectly discriminated only if they excite different labelled detectors.

From this argument, it might seem that each pair of perfectly discriminated stimuli implies precisely two different labelled detectors. In the absence of noise, this would be so, since each stimulus would always be detected by the same detector. But the detectors in our model are noisy, so that, from trial to trial, a given stimulus may be detected by any of a set of different detectors. For two stimuli to be perfectly discriminated, the model only requires that the two sets should not overlap. The detectors within a set may be few or many, heterogeneous or all alike, but this cannot be determined from our data without additional assumptions. We can only say that each pair of perfectly discriminated stimuli is consistent with two mutually exclusive sets of detectors. But since each set must contain at least one member, the number of mutally exclusive sets of detectors is a lower bound on the number of different labeled detectors.

In this light, the results in Fig. 2 are consistent with two sets of labelled detectors, one selective for high temporal frequencies, the other for low. The similarity of the results at 0.25 and 16 c/deg suggests that this partition into these two sets is appropriate at both high and low spatial frequencies.

The data in the upper panel of Fig. 3, which show spatial discriminations at a low temporal frequency, are consistent with seven distinct sets of spatial frequency selective labelled detectors. At a high temporal frequency, as shown in the lower panel of Fig. 3, only 3 distinct sets are required. It is interesting that these two very different patterns of spatial discrimination are obtained with two varieties of temporal modulation which are themselves perfectly discriminated. It is tempting to suppose that the set of low temporal frequency detectors is partitioned into seven distinct spatial frequency selective sets, but that the high temporal frequency set is much more coarsely divided.

We can compare these estimates of detector selectivity to those obtained by other methods. When modulated at 0 Hz, two spatial frequencies an octave apart are perfectely discriminated. Such frequencies also fail to summate, as though detected by independent detectors (Sachs *et al.*, 1971). Recently, one of us has shown (Watson, 1980) that summation between patches of grating modulated at 0 Hz is explained by detectors with spatial frequency bandwidths of less than one octave. Our stimuli have bandwidths of one half octave or less. Under these conditions, two stimuli an octave apart are very likely to be detected by non-overlapping sets of detectors. There is thus a good qualitative agreement between these different estimates of detector selectivity. A quantitative comparison requires additional assumptions, for example, those which predict discrimination performance when the two sets of detectors overlap. We are now investigating various alternative assumptions.

The much poorer spatial frequency discrimination found at 16 Hz may be a consequence of broader spatial frequency bandwidths among the detectors of high temporal frequencies. Arend and Lange (1979) report little effect of exposure duration (and hence, to an extent, temporal frequency) on summation bandwidth, but Pantle (1973) reports larger summation bandwidths at higher temporal frequencies. We are now making our own measurements. It should be emphasized, however, that a failure to distinguish two stimuli implies only the absence of labelled detectors, not the absence of selective detectors *per se*.

Our finding that only high and low temporal frequencies are perfectly discriminated is consistent with previous proposals that this dimension is served by two distinct sets of mechanisms, one selective for high temporal frequencies, the other for low. Probably the evidence most frequently cited for these mechanisms are the different thresholds sensations reported at high and low temporal frequencies (Kulikowski and Tolhurst, 1973). The results in Fig. 2 are an objective documentation of this claim, as distinct from the descriptive (and occasionally contradictory) reports of observers. It has also been argued that the high temporal frequency mechanisms provide information only about motion or temporal change. To the contrary, we find that these detectors provide enough spatial information to permit perfect discriminations between at least three spatial patterns. But we do find the high temporal frequency set to be much poorer at spatial discriminations than are the detectors of low temporal frequencies. If the two sets of temporal detectors demonstrated here are identified as transient and sustained, then we have shown the transient system to be remarkably poor at spatial discriminations.

Our derivation of the number of distinct sets of detectors serving a dimension depends upon the assumptions of our model, most notably, our assumption that each detector has a threshold, and that the response of one detector is sufficient to detect the stimulus. But though some other model may show that somewhat fewer or more detectors are required, it is difficult to escape the conclusion that errorless identification of stimuli at threshold requires the existence of distinct labelled detectors. This in itself is exiciting as it suggests a mechanism by which the process of visual recognition may proceed, and a method by which it may be explored.

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APPENDIX

Here we derive a statistical test of whether two stimuli are perfectly discriminated. We adopt the following notation:

i—Index of stimulus ($i = 1,2$)
j—Index of contrast level ($j = 1,2,\ldots J_i$).
J_i—Number of contrasts for stimulus i.
k—Index of response category ($k = 1, 2, 3, 4$)
n_{ij}—Number of trials of stimulus i at contrast j.
m_{ijk}—Number of responses in category k for stimulus i at contrast level j.
p_{ij}—Detection probability for stimulus i at contrast level j.
r_{ijk}—Probability of response in category k for stimulus i at contrast level j.
b_i—Bias (probability of guessing stimulus i when no detection has occurred).
g—Probability of guessing correct interval when no detection has occurred.

We treat the outcome of each 2 × 2FC trial as a multinomial random variable. There are four possible responses, indexed by k:

$k = 1$—Correct interval, correct identity.
2—Correct interval, incorrect identity.
3—Incorrect interval, correct identity.
4—Incorrect interval, incorrect identity.

Each response has a probability r_{ijk}. Suppose that n_{ij} trials of stimulus i are performed at contrast j, and that the number of responses in each category is m_{ijk}. The likelihood of this outcome is

$$L_{ij} = n_{ij}!/\prod_k (m_{ijk}!) \prod_k r_{ijk} m_{ijk} \tag{A4}$$

The likelihood of the whole data set is then

$$L = \prod_i \prod_j L_{ij}. \tag{A5}$$

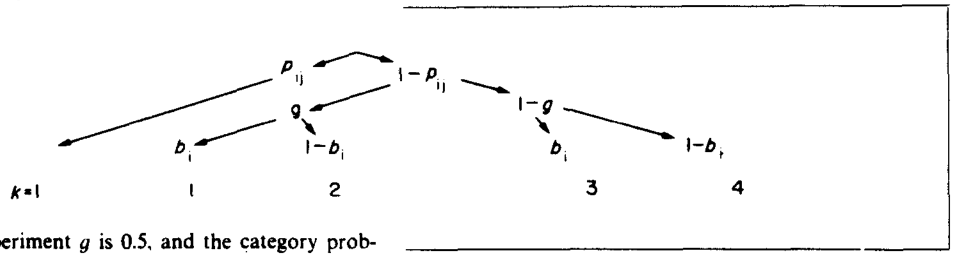
We consider this likelihood under two hypotheses. In the first, H_0, we assume nothing about the category probabilities. This hypothesis has one parameter, r_{ijk}, for each category of response to each stimulus at each contrast. However, since

$$\sum_k r_{ijk} = 1,$$

only three of each set of four are considered. The number of parameters is thus

$$3\sum_i J_i.$$

The second hypothesis assumes that detection implies correct identification. In this case, the response probabilities are easily derived from the detection probabilities, p_{ij}, and the guessing parameters b_i and g. The following tree diagram indicates the possible routes to each response, and their probabilities.



In a 2 × 2FC experiment g is 0.5, and the category probabilities must sum to 1, so we arrive at

$$r_{ij1} = 1 - r_{ij2} - r_{ij3} - r_{ij4} \tag{A1}$$

$$r_{ij2} = 0.5\,(1 - b_i)\,(1 - p_{ij}) \tag{A2}$$

$$r_{ij3} = 0.5b_i(1 - p_{ij}) \tag{A3}$$

$$r_{ij4} = r_{ij2} \tag{A4}$$

The number of parameters in this hypothesis is

$$\sum_i J_i + 1.$$

For both hypotheses, the maximum likelihood estimates of the parameters are those which maximize L, or equivalently its natural logarithm. For H_0, these estimates are given by the obtained category proportions, m_{ijk}/n_{ij}. For H_1, the estimates were obtained by means of STEPIT, a general minimization routine (Chandler, 1965). A test between the two hypotheses is given by the statistic $-2ln(\hat{L}_1/\hat{L}_0)$ where $\hat{L}$ indicates the maximum likelihood of the relevant hypothesis. This statistic is asymptotically Chi-square with degrees of freedom equal to the difference in the number of parameters in H_1 and H_0 (Hoel *et al.*, 1971). This difference is

$$2\sum_i J_i - 1.$$

In most sessions, three contrasts were used for each stimulus, giving 11 deg of freedom and a critical value at the 0.05 level of 19.5. In Fig. 4, the statistics from those sessions using 4 contrasts (15 deg of freedom) have been multiplied by 11/15 to make them approximately comparable.