
Comparison at a distance

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Abstract. The visual system is known to contain hard-wired mechanisms that compare the values of a given stimulus attribute at adjacent positions in the visual field; but how are comparisons performed when the stimuli are not adjacent? We ask empirically how well a human observer can compare two stimuli that are separated in the visual field. For the stimulus attributes of spatial frequency, contrast, and orientation, we have measured discrimination thresholds as a function of the spatial separation of the discriminanda. The three attributes were studied in separate experiments, but in all cases the target stimuli were briefly presented Gabor patches. The Gabor patches lay on an imaginary circle, which was centred on the fixation point and had a radius of 5 deg of visual angle. Our psychophysical procedures were designed to ensure that the subject actively compared the two stimuli on each presentation, rather than referring just one stimulus to a stored template or criterion. For the cases of spatial frequency and contrast, there was no systematic effect of spatial separation up to 10 deg. We conclude that the subject's judgment does not depend on discontinuity detectors in the early visual system but on more central codes that represent the two stimuli individually. In the case of orientation discrimination, two naïve subjects performed as in the cases of spatial frequency and contrast; but two highly trained subjects showed a systematic increase of threshold with spatial separation, suggesting that they were exploiting a distal mechanism designed to detect the parallelism or non-parallelism of contours.

1 Introduction

How precisely can the human observer compare stimuli that are well separated in the visual field? What are the cortical mechanisms that underlie such comparisons? These questions have been rather seldom addressed, either experimentally or theoretically.

There are numberless experiments in which discrimination thresholds are measured for juxtaposed or nearly juxtaposed stimuli of the kind used in traditional photometry and colorimetry (Wright 1941). And there are also experiments in which the discriminanda are presented in the same spatial position, and thus to the same pool of neurons, but are presented in two successive temporal intervals, as for example in some studies of spatial-frequency discrimination (Hirsch and Hylton 1982; Magnussen et al 1991; Regan 1985). But consider, by contrast, a task in which one stimulus is presented several degrees to one side of fixation and a second stimulus to the other side, so that they are presented to distinct pools of sensory neurons. Suppose that the observer is asked to compare these separated stimuli with respect to some sensory attribute such as spatial frequency, contrast, orientation, or hue. Will the observer's discrimination deteriorate as the separation of the two stimuli is increased (while their eccentricity is held constant)?

The issue derives interest from the traditional view that the visual system, and indeed all our senses, contain mechanisms that extract differences or ratios rather than the absolute values of stimulus attributes (Craik 1940; Kaplan et al 1988; Weber 1834).

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Both physiological and psychophysical evidence, however, might lead us to suspect that different mechanisms underlie the comparison of nearby stimuli, on the one hand, and the comparison of separated stimuli, on the other. In classical terminology, we are asking which comparisons are sensory and which are perceptual. In speaking of a *sensory comparison*, we mean that a neural signal representing the difference or ratio of the discriminanda is extracted early in the visual system (and indeed this signal may be available centrally with more precision than are the absolute values of the signals corresponding to the individual stimuli). By speaking of a *perceptual comparison*, we mean that attributes of the two stimuli are analysed independently in the early visual system and that what are compared centrally are symbolic representations of the individual stimuli. We cannot specify in detail the nature of these representations, for the code and the protocol by which the brain conducts its central operations remain completely unknown.

1.1 *The existence of local comparators*

A paradigmatic example of a distal comparator is a chromatically opponent ganglion cell, which draws inputs of opposite sign from different classes of cone. Over a range in which the quantum catches of the cones themselves may vary by several log units, a channel composed of such cells can detect a change of less than 1% in the ratio of the quantum catches of cones of different types (Chaparro et al 1993). Similarly, the centre-surround organisation of ganglion cells allows us to distinguish small differences in the illumination falling on adjacent retinal regions: the difference or ratio signal transmitted to the cortex represents local contrast (Kaplan et al 1988; Kuffler 1953). One might suppose that it is local contrast signals of this kind that are used when the observer equates the luminance of two abutting or interdigitated fields in a traditional visual photometer.

Clearly belonging to this large class of local neural comparators are directionally selective movement detectors, which make a spatiotemporal comparison of the illumination falling on adjacent retinal regions (Barlow and Levick 1965); and their auditory analogues, detectors specific to direction of change of pitch, which are effectively making a temporal comparison of the excitation at different points on the basilar membrane (Whitfield and Evans 1965). There is also evidence for relatively distal detectors that respond to discontinuities in the spatial features of the image. Recording from the lateral geniculate of the cat, Sillito and his colleagues have found cells that gave a stronger response if a central grating and a surrounding annular grating were of different orientation; the effect was shown to be mediated by efferent cortical signals (Sillito 1993). In the visual cortex of the macaque, Sillito et al (1995) found simple cells that gave no response to an annulus surrounding the classical receptive field but gave a supra-optimal response when the same annulus was concurrent with, and differently oriented from, a grating in the classical receptive field. These authors wrote: "The receptive field needs to be conceived in terms of the discontinuity rather than any arrangement that can be mapped with a single stimulus". Rather similar results were obtained by Knierim and Van Essen (1992): many cells in V1 of the macaque gave a reduced response to a bar in their classical receptive field when bars of the same orientation were present outside the field. Hammond and Mackay (1975) showed that complex cells in area 17 of the cat would respond to a boundary between a region of static visual noise and a region of moving noise of the same space-averaged flux.

Psychophysical studies similarly suggest the existence of mechanisms that detect discontinuities between areas of different texture. Rapid, pre-attentive segmentation of the visual field occurs if the sub-areas differ in the orientation, the spatial frequency, the size, or the colour of their elements (Beck 1983; Regan 2000; Sagi and Julesz 1987). Several authors have proposed a central representation of the visual field in which are

recorded local discontinuities, whether they are discontinuities in orientation, texture, colour, brightness, or some other primary attribute—the ‘common representation’ of Cavanagh et al (1990) or the ‘salience map’ of Lu and Sperling (1995). It is attractive to suppose it is cells of the type identified in visual cortex by Sillito and colleagues that mediate the detection of such local discontinuities and provide the input to pre-attentive mechanisms that segment the visual field and support parallel visual search. Sagi and Julesz (1987) have postulated “a generalised lateral inhibitory process between adjacent feature detectors that enhances feature gradients in the same way luminance gradients are enhanced” (page 47).

1.2 *Comparison at a distance*

It seems unlikely that the mechanisms that detect local discontinuities will subserve comparison of stimuli separated by many degrees of visual angle. It is true that lengthy lateral connections have been reported in the visual cortex, sometimes extending for several millimetres. In the case of the cat, examples of axons extending for as far as 6–8 mm are found (Alexeenko et al 1999; Gilbert and Wiesel 1989), while shorter lengths have been reported for monkeys (Amir et al 1993). Moreover, the axonal terminations may cluster in regions of cortex with the same preferred orientation and spatial frequency. Nonetheless, such lateral connections become systematically sparser with distance. Thus Bosking and his colleagues (1997) found that a doubling of distance from an injection site led to a threefold decrease in the number of labelled boutons.

If a subject is asked to compare two stimuli at different separations and if the comparison does depend on lateral connections in primary visual cortex, then we might certainly expect the precision of comparisons to deteriorate monotonically as separation increases. In a task that required the subject to detect an element of discrepant orientation in a background of homogeneously oriented elements, Sagi and Julesz (1987) indeed found that performance improved as the density of the background elements increased and thus the average separation of elements was reduced. It seems likely that direct signals of difference are available only for juxtaposed, or temporally substituted, stimuli, and that well separated stimuli are likely to be compared by means of symbolic descriptions. Neither the informational nor the neural nature of such descriptions is known (since the central codes of the brain are not known); but if stimulus descriptions *are* in a symbolic form, we might expect experimentally to find that the precision of comparison is unchanged over a wide range of separations.

In this paper we consider in turn three basic spatial attributes of visual stimuli: spatial frequency, contrast, and orientation; and we measure the difference threshold for adjacent stimuli and for stimuli separated by up to 10 deg of visual angle. Similar stimuli—Gabor patches—and similar procedures were used in all three experiments.

1.3 *Ensuring that the stimuli are actively compared*

Our experiments require us to ensure that the subject actively compares the sensory properties of the two stimuli presented. This is not something that can be taken for granted, as can be seen by considering the temporal analogue of our own experiments. Studies by Magnussen and colleagues appeared to show that subjects could discriminate spatial frequencies with the same precision whether the reference and variable stimuli were presented simultaneously or were separated in time by many seconds, minutes, or hours (Magnussen and Dyrnes 1994). In the case of such experiments, Lages and Treisman (1998) have suggested that the subject does not perform a true comparison between the two stimuli presented but, instead, judges the target stimulus against an internal criterion. According to Lages and Treisman, subjects are able to set and retain in memory “a specification for modifying the criterion used in later decisions” (page 559). In a variant form of this account, one could suppose that the subject, over many trials, constructs an internal template, a neural representation of

the average stimulus; and that it is against this template that the target is judged, rather than against an external reference stimulus. Such strategies might paradoxically be the more efficient, since the subject's judgment would then depend on only one sample of external noise rather than the two samples of external noise that are introduced if the external reference stimulus is used.

In the present experiments, we adopted arrangements that allowed us to establish that our subjects did compare one external stimulus against a second.

On each trial, two stimuli were presented on an imaginary circle (figure 1), one being a referent stimulus and the other the test stimulus. The subject was asked to report whether the more clockwise stimulus was, say, of higher or lower spatial frequency than the less clockwise. The program randomly assigned the reference stimulus to the more clockwise or the less clockwise position. Within an experimental run, an ascending and a descending staircase were randomly interleaved. Thus, on a given trial, the subject did not know in advance which was the referent stimulus and did not know the direction in which the test stimulus differed from the referent. Therefore, if then he were to adopt the strategy of considering only one of the two stimuli (say, the more clockwise), he could never score better than 75% correct. Even if absolute judgments of the single stimulus allowed him to be correct on all of those trials (50% of the total) when the test was the more clockwise, he could score only at chance on the remaining half of the trials, when the referent stimulus was the more clockwise. Reconstructions of psychometric functions from our staircases show that subjects were readily able to exceed this upper limit of performance that would be allowed by absolute judgments of a single stimulus. Moreover, we have shown in earlier experiments that symmetrical psychometric functions of similar slopes can be reconstructed for trials on which the referent is the more clockwise and for those on which the test is the more clockwise (Danilova and Mollon 1999).

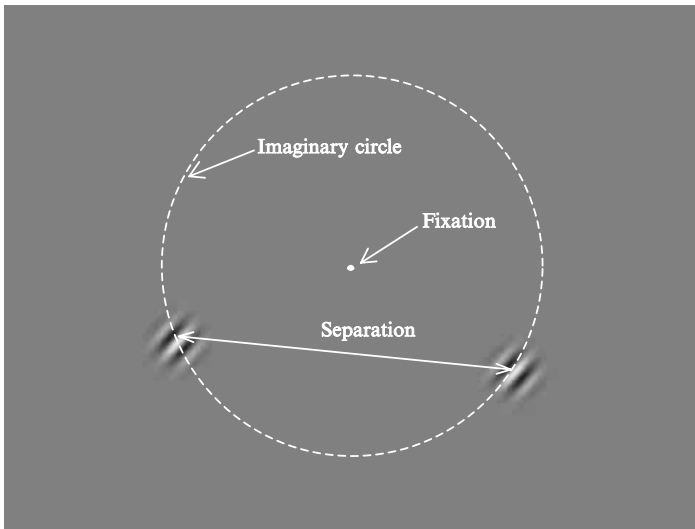


Figure 1. Example of the stimuli used in experiments 1 and 2. The case illustrated is one where the separation is intermediate.

In the present experiment, we took the additional step of jittering the notional referent from trial to trial, allowing it to take on any of 25 closely spaced values. Suppose nevertheless that the subject constructs a template that corresponded to the time-weighted average of all stimuli presented on recent trials, and that he judges just one of the two stimuli against the template. Even on the 50% of trials where it is

the notional test stimulus that he judges against the template, he will be in error whenever the test value lies between the stimulus values of the referent and the template. On this account, his performance should deteriorate the further the notional referent lies from the middle of the range. Our data allow us to test this prediction of the hypothesis that the subject compares just one stimulus to an internal template (see section 2.2.1).

2 Experiment 1. Discrimination of spatial frequency

For the case of spatial frequency, we centred our range of reference frequencies on a value of 2 cycles deg^{-1} . In this range, the Weber fraction for discrimination of frequency is almost constant (Campbell et al 1970); and thus we were able to use a psychophysical method in which the ratio of test to reference frequency was adjusted from trial to trial while yet the value of the reference frequency was randomly chosen from a range of 25 closely spaced frequencies.

It was important for our purpose to define with some precision the positions of our stimuli within the visual field. We therefore chose to use Gabor patches, as a conventional compromise between precision of specifying spatial frequency and precision of specifying spatial position.

2.1 Method

2.1.1 *Apparatus and stimuli.* The experiments were carried out in Cambridge, UK, and St Petersburg, Russia, with similar apparatus and programs, and with common calibration equipment.

The stimuli were pairs of vertical Gabor patches presented on a calibrated monitor screen (Sony Trinitron 21 inch with a refresh rate of 60 Hz and a resolution of 1280×960 pixels). All parameters of the stimuli were controlled by a VSG 2/2 (St Petersburg) or 2/3 (Cambridge) graphics board (Cambridge Research Systems). The average luminance of the display was 7.6 cd m^{-2} . Calibrations of both monitors were performed with the same Spectrascan 650 spectroradiometer.

At the viewing distance of 114 cm, each Gabor patch subtended 2 deg and its standard deviation was equal to 30 min of arc. An example of the stimuli is given in figure 1. In order not to confound the separation and the retinal eccentricity of the stimuli, the Gabor patches were always centred on an imaginary circle of 5 deg radius. A fixation point was always present at the centre of the circle, both between presentations and during the presentation of the stimuli. The separations between the two Gabors were measured as the separations of the centres of the two patches. Thus, when the separation was 2 deg, the two patches were juxtaposed, and when their separation was 10 deg they lay on a diameter of the imaginary circle. The contrast of the reference stimulus was always 0.3, but the contrast of the target stimulus was jittered in the range ± 0.03 . All stimuli were in cosine phase. Stimulus duration was 100 ms for the practised subjects MD and JM, and 150 ms for the naïve subjects.

2.1.2 *Procedure.* Within a single block of trials, the separation of the targets was held constant and their midpoint lay on a radius that had a random angle chosen in steps of 5° from 12 o'clock. The subject's task was to report whether the more clockwise stimulus was of higher or lower spatial frequency than the less clockwise stimulus. Feedback was not given. Discrimination thresholds were measured by a staircase procedure. Ascending and descending thresholds were measured separately by two randomly interleaved staircases.

On any trial, one stimulus was conceptually the reference stimulus and the other was the variable stimulus. However, the spatial frequency of the reference stimulus took on a random value from a range of 25 values centred on 2 cycles deg^{-1} and differing

in steps of 1%. There were not separate staircases for each of the 25 possible reference stimuli. Rather, what was adjusted in each of the two staircases was a ratio (Δf), which related the frequency of the reference stimulus (f_{standard}) and the frequency of the variable stimulus (f_{test}). Initially,

$$\Delta f = \frac{|f_{\text{test}} - f_{\text{standard}}|}{f_{\text{standard}}} k = 0.1$$

and the factor k was 1.0. Thereafter k was multiplied by 0.9 after three correct responses and multiplied by 1.1 after one incorrect response. This three-to-one rule converges to 79.4% correct responses (Wetherill and Levitt 1965).

In each experimental session, eight different separations were tested in different, randomly ordered, blocks of trials. There was also a ninth condition in which only a single Gabor patch was presented and the subject was asked to indicate whether it was of higher or lower frequency than the average of the stimuli presented in the experiment. This ‘absolute judgment’ condition was randomly placed within a session with the restriction that it could not be the first block of the first session. In this condition, 35 different spatial frequencies were presented in random order, each repeated 5 times during the session; the 35 frequencies were centred on 2 cycles deg^{-1} and spaced at 1% intervals. The spatial position of the single Gabor was varied randomly as in the main conditions.

Each subject completed either six or eight experimental sessions.

Subjects were not required to respond as quickly as possible, but the program routinely recorded the interval between the offset of the stimulus and the moment when the subject pressed a button on the response box. We refer to this measure as ‘response time’. The naïve subjects were unaware that response time was recorded.

2.1.3 Subjects. There were four subjects, two female and two male. Two of them were the authors of the paper, and two (AM male, IB female) were naïve as to the purposes of the experiment. All had previous experience in psychophysical observations. MD and JM were tested in Cambridge, AM and IB in St Petersburg.

2.2 Results and discussion

In figures 2a–2d we show for each subject the Weber fraction as a function of the spatial separation of the two Gabor patches. Data are shown separately for ascending and descending staircases. Figure 2e shows the results averaged for ascending and descending staircases and for the four subjects.

The data for each subject were analysed by a two-way ANOVA, with the factors Separation and Ascending versus Descending Staircase. The separation of the targets had no significant effect for any subject ($F_7 = 1.74$, $p = 0.11$ for MD; $F_7 = 1.53$, $p = 0.16$ for IB; $F_7 = 1.57$, $p = 0.16$ for JM; $F_7 = 1.21$, $p = 0.31$ for AM). There was a significant difference between staircases only for subject AM ($F_1 = 6.74$, $p = 0.01$). There was no significant interaction between factors for any subject ($F_{1,7} = 1.95$, $p = 0.07$ for MD; $F_{1,7} = 1.02$, $p = 0.42$ for IB; $F_{1,7} = 0.87$, $p = 0.54$ for JM; $F_{1,7} = 0.52$, $p = 0.82$ for AM).

Our central conclusion from this experiment is that for separations up to 10 deg there is little or no change in the precision with which subjects discriminate the spatial frequency of separated patches. Individual subjects show particular trends or inflexions, but in all cases the threshold for adjacent Gabor patches is the same or higher than for the most separated: there is no evidence for the decline with separation that might be expected if the discrimination at short range was achieved by local discontinuity detectors. The present findings are similar to those of our earlier experiment on spatial frequency, in which only a single referent was used (Danilova and Mollon 1999).

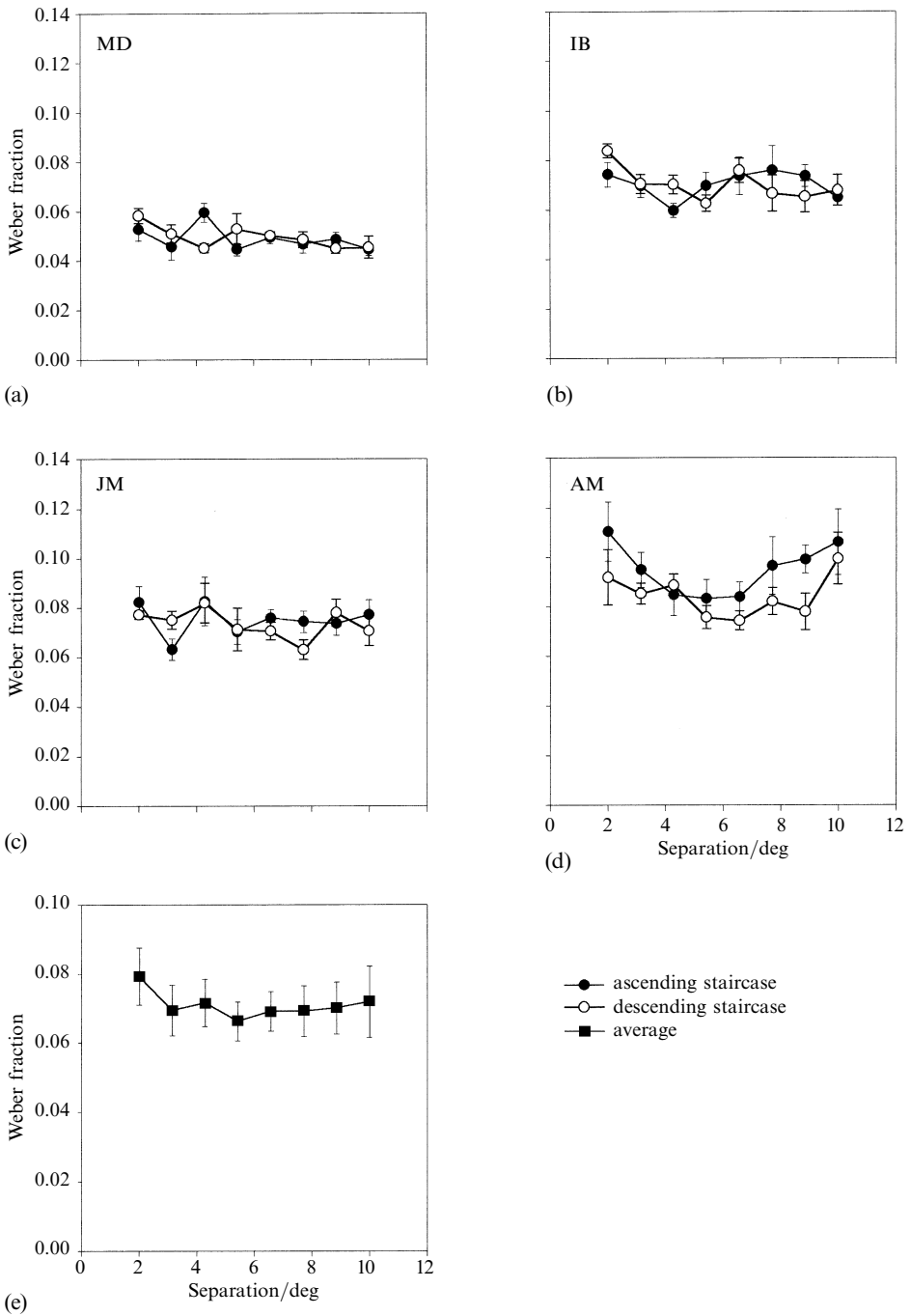


Figure 2. Panels (a)–(d) show for individual subjects the Weber fraction for discriminating spatial frequency as a function of the separation of the two Gabor patches (experiment 1). Data are shown separately for ascending and descending staircases. Error bars are ± 1 SEM, based on the between-session variance. Panel (e) shows the data averaged across staircases and across subjects; the error bars are based on the between-subjects variance and represent ± 1 SEM.

We show in figure 3 the averaged response times for each subject as a function of the separation of the patches. A one-way ANOVA showed no significant effect of spatial separation for three of the subjects (MD: $F_7 = 0.99$, $p = 0.45$; JM: $F_7 = 1.29$, $p = 0.28$; AM: $F_7 = 0.58$, $p = 0.77$). This was also true of subject IB if all the experimental runs were included ($F_7 = 0.95$, $p = 0.47$); but if the first of the eight runs (where her responses were systematically slower) was removed, the upward trend in her data (see figure 3, open circles) was statistically significant ($F_7 = 3.03$, $p = 0.01$). With this exception, the subjects do not appear to gain precision of judgment at large separations by an increase in processing time.

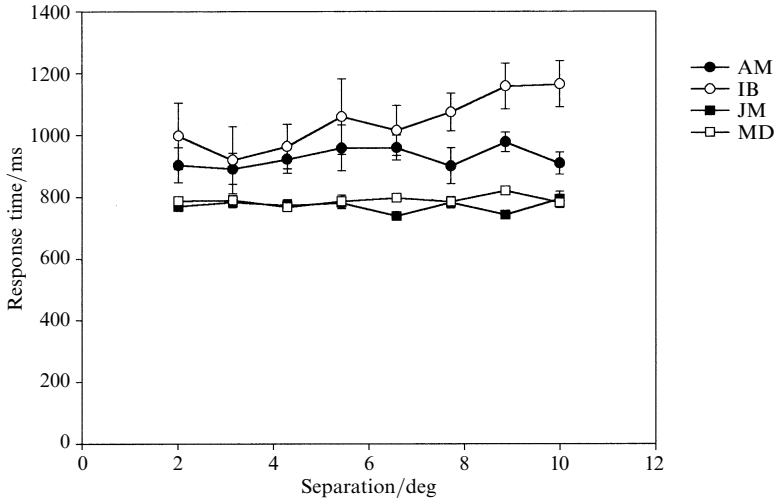


Figure 3. Response times in experiment 1 for each subject as a function of the spatial separation of the Gabor patches.

2.2.1 Absolute judgments. Figure 4 shows for each subject the psychometric functions constructed for the absolute judgment condition, in which only a single Gabor patch was presented on each trial. The data points have been fitted with the sigmoid function:

$$y = y_0 + \frac{a}{1 + \exp\left(-\frac{x - x_0}{b}\right)}.$$

One way to conceptualise this experiment is to consider that the subject compares the single Gabor with an internal standard in the way that he or she compares the more clockwise Gabor to the other external stimulus in the main conditions. If then we take as the difference threshold the interval between (i) the spatial frequency at which the responses “higher” and “lower” are equally probable and (ii) the spatial frequency at which the subject responded 79.4% “higher”, then the thresholds are of the same order of magnitude, but somewhat larger, than those found in the main conditions of the experiment. The thresholds for absolute judgments range from 122% (MD) to 150% (AM) of the values for direct comparisons.

Thus the subject can compare a single stimulus to an internal standard with a precision of the same order as he or she can compare one external stimulus to a second, although the threshold is always larger in the absolute-judgment case. Since performance is not so very different in the two cases, it is important to eliminate the possibility that has been discussed in the case of comparison of temporally separated stimuli (Lages and Treisman 1998): could it be that in our primary conditions one stimulus is being compared to a single internal template rather than to the other external stimulus? An analysis of the data from our primary task shows convincingly that the

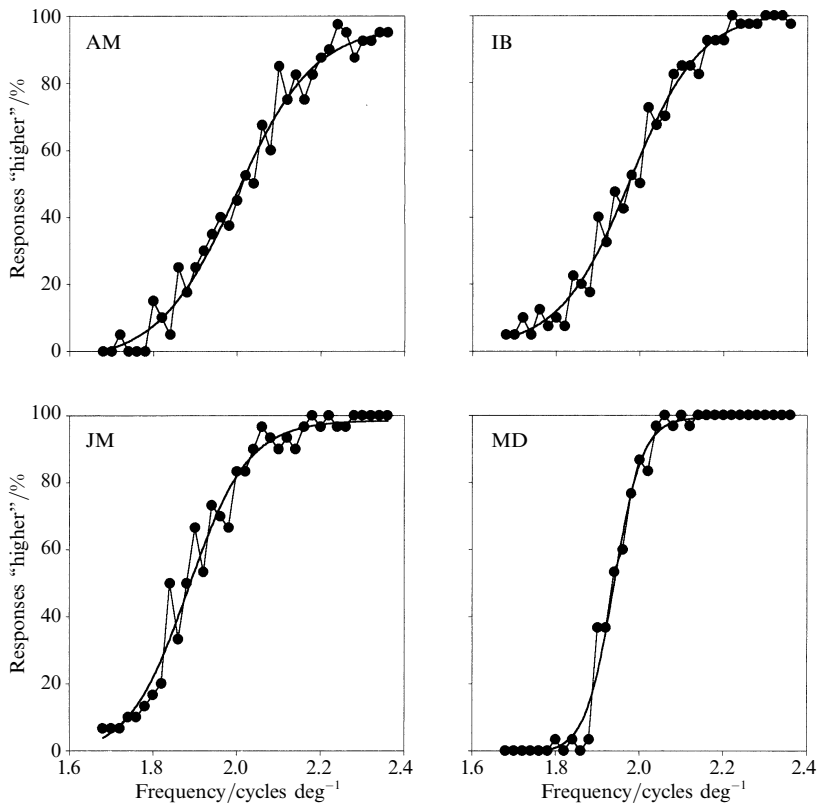


Figure 4. Psychometric functions reconstructed for the absolute-judgment condition of experiment 1, when only a single Gabor patch was presented. The ordinate represents the probability with which the subject indicated that the single Gabor patch was of higher spatial frequency than the average value presented during the experiment. Data are shown for individual subjects. The solid lines are fitted with a sigmoid function.

subject does compare the two external stimuli. For this analysis we have reconstructed psychometric functions for (i) the 5 lowest reference frequencies, (ii) the 5 frequencies in the middle of the range, and (iii) the 5 highest frequencies. In order to have enough trials in each of these sub-samples, we combined data from all separations for a given subject. Frequencies visited on fewer than 5 trials were excluded from the analysis.

Examples of psychometric functions reconstructed for different subsets of referents are shown in figure 5 for subject IB. The data are fitted with sigmoid functions (see above). Note first that the functions always approach 0% and 100%, indicating that subjects achieve better performance than the 75% correct that would be possible if they considered only one of the external targets (see section 1.3). Second, note that the slopes of the functions are similar for the three data sets, ie IB is able to achieve almost as good discrimination when the two external stimuli are drawn from the extremes of the range as when they lie near the centre of the distribution of referent frequencies. Equivalent analyses for the other subjects gave similar results. Thus it cannot be that the subjects are solving the task by referring just one of the external stimuli to a single internal template.

2.2.2 Same versus different hemifields. Of interest is the special case where the two Gabor patches fall on opposite sides of the vertical midline of the visual field. In this case they will be projected to opposite hemispheres and therefore any comparison must depend on transmission of information across the corpus callosum. We have analysed

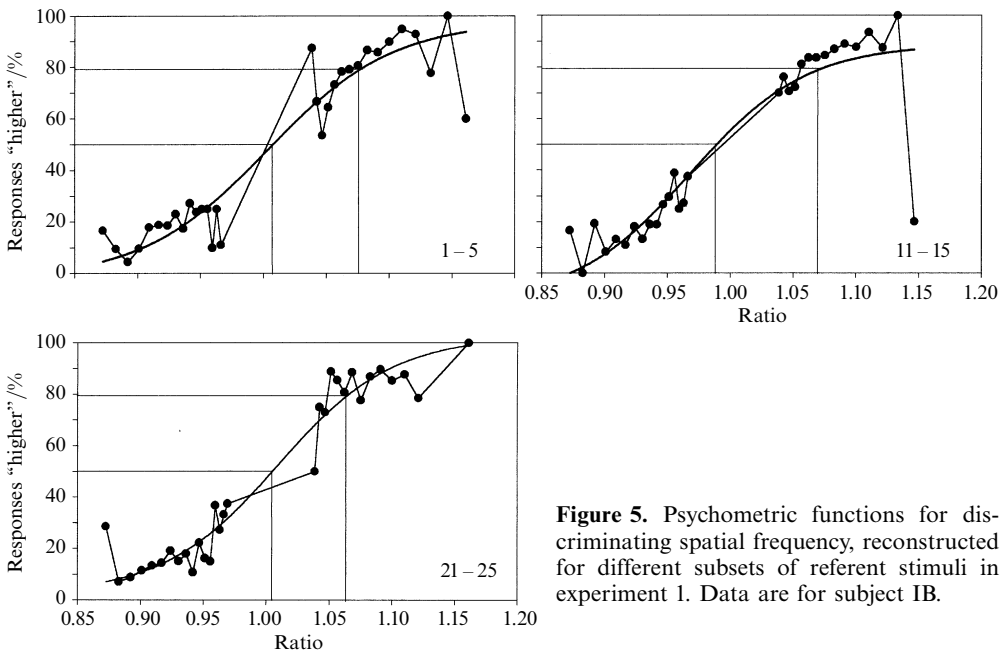


Figure 5. Psychometric functions for discriminating spatial frequency, reconstructed for different subsets of referent stimuli in experiment 1. Data are for subject IB.

the data of experiment 1 to contrast such trials with trials on which both Gabor patches fell within one hemifield. Trials were excluded from the analysis if the centre of the Gabor patch fell within two standard deviations (ie 1 deg) of the vertical midline. This rule eliminates the smallest separation from the analysis. Additionally the largest separation was eliminated, since there are then no cases where the Gabor stimuli fall completely within one hemifield. In the case of the remaining separations, the data were collapsed across sessions, and psychometric functions were constructed showing, for a given separation, the percent of responses “higher” as a function of the ratio of the test and standard frequencies. This was done separately for the case of stimuli falling in the same hemifield and for the case of stimuli falling in opposite hemifields. The psychometric functions were fitted with a sigmoidal curve, and thresholds were estimated by taking the difference between the ratios that gave 50% and 79.4% “higher” responses.

For each subject, a *t*-test was used to compare the resulting thresholds for stimuli falling in same and different hemifields. In no case was there a significant difference between the case where the comparison can potentially be completed within one hemisphere and the case where information must be transmitted across the corpus callosum.

3 Experiment 2. Contrast discrimination

In a second experiment we used vertical Gabor patches identical to those used in experiment 1, but now we held constant the spatial frequency of the patch and required the subject to discriminate its contrast.

3.1 Method

The apparatus, the spatial arrangement of the stimuli, and the calibration procedure were as for experiment 1. The spatial frequency of the Gabor patches was fixed at 2 cycles deg^{-1} and they were in cosine phase. The Michelson contrast of the referent stimulus could take one of 25 values, centred on 0.3 and varying by steps of 0.003. The subject was required to judge whether the more clockwise Gabor patch was of greater or lesser contrast than the second patch. Ascending and descending staircases

were randomly interleaved as in experiment 1. The ratio (ΔC) now related the contrast of the reference (C_{standard}) and the contrast of the variable stimulus (C_{test}). Initially,

$$\Delta C = \frac{|C_{\text{test}} - C_{\text{standard}}|}{C_{\text{standard}}} k = 0.1$$

and the factor k was 1.0. Thereafter k was multiplied by 0.9 after three correct responses and multiplied by 1.1 after one incorrect response.

Eight spatial separations, in the range 2–10 deg, were tested in random order in each experimental session. We did not include an absolute-judgment condition in this experiment. MD completed five experimental sessions, AM six, and JM seven.

The subjects were the authors (who were tested in Cambridge) and a naïve male subject, AM (who was tested in St Petersburg).

3.2 Results and discussion

In figures 6a–6c we show for each subject the Weber fraction (ΔC) as a function of the spatial separation of the two Gabor patches. Data are shown separately for ascending and descending staircases. Figure 6d shows the results averaged for ascending and descending staircases and for the three subjects.

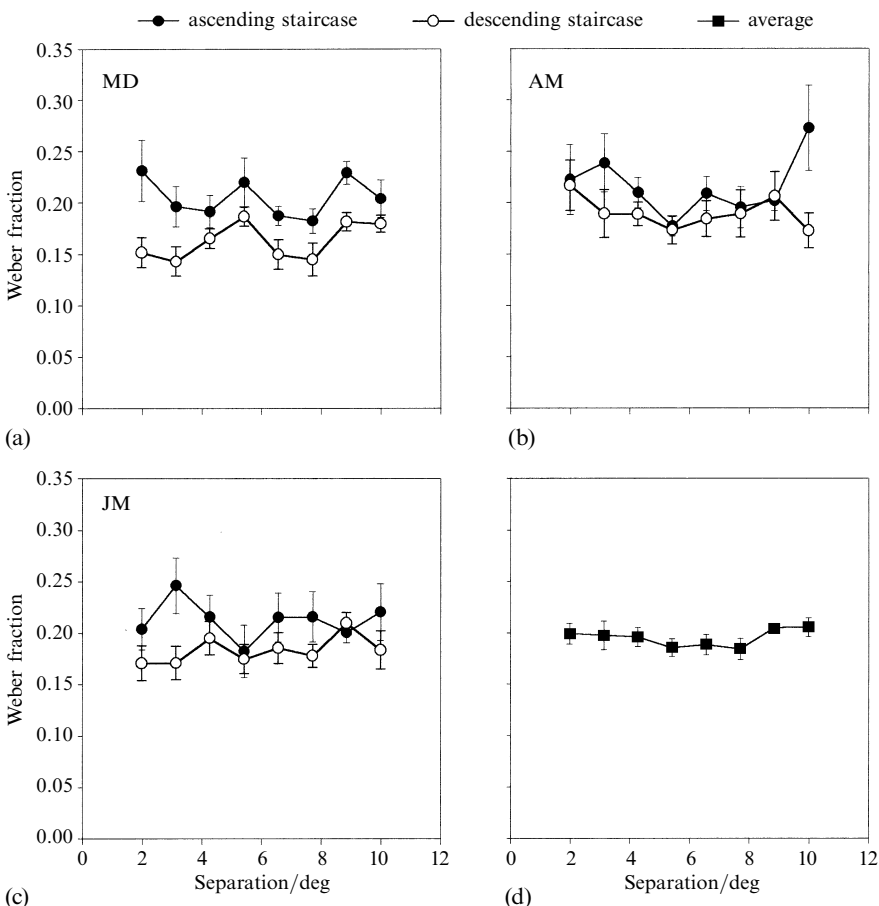


Figure 6. Panels (a)–(c) show for individual subjects the Weber fraction for discriminating the contrast as a function of the spatial separation of the two Gabor patches (experiment 2). Data are shown separately for ascending and descending staircases. Error bars are ± 1 SEM, based on the between-session variance. Panel (d) shows results averaged across staircases and across subjects; the error bars are based on the between-subjects variance and represent ± 1 SEM.

The data for each subject were analysed by a two-way ANOVA, with the factors Separation and Ascending versus Descending Staircase. For two subjects, JM and AM, the separation of the targets had no significant effect ($F_7 = 0.68$, $p = 0.69$ for JM; $F_7 = 1.01$, $p = 0.43$ for AM). For MD there was a marginally significant effect ($F_7 = 2.21$, $p = 0.04$), although inspection of the data (figure 6a) suggests that this reflects inflexions in the function rather than a systematic upward trend with separation. All subjects showed a significant difference between staircases ($F_1 = 34.56$, $p = 1.63 \times 10^{-7}$ for MD; $F_1 = 15.5$, $p = 0.0002$ for JM; $F_1 = 5.38$, $p = 0.02$ for AM). This latter result is probably a by-product of the way thresholds are calculated: although from a subject's point of view the test and reference stimuli cannot be distinguished, in the calculation of the threshold (see section 3.1), the threshold is expressed as a percentage of the larger contrast in the case of the descending staircase and as a percentage of the smaller contrast in the case of the ascending staircase. There was no significant interaction between factors ($F_{1,7} = 0.57$, $p = 0.78$ for MD; $F_{1,7} = 0.44$, $p = 0.87$ for JM; $F_{1,7} = 1.2$, $p = 0.31$ for AM).

Our main conclusion, as in the case of spatial frequency, is that for separations up to 10 deg there is little systematic change in the precision with which subjects discriminate separated patches. The absolute values of the Weber fractions are larger than in the case of spatial frequency, but are comparable with those in the literature (Barlow et al 1987).

In figure 7 we show the response times for each subject as a function of separation. Two-way ANOVAs showed that separation was a significant factor for each subject ($F_7 = 2.46$, $p = 0.03$ for MD; $F_7 = 2.43$, $p = 0.025$ for JM; $F_7 = 2.62$, $p = 0.02$ for MD). However, inspection of figure 7 shows that response times actually decrease with separation in the case of JM and AM, while the significance for MD derives from an inflexion at a separation near 8 deg. So subjects do not maintain constant thresholds at large separations by increasing their response times. A particularly interesting result is that two of the subjects show a significant effect of staircase: for MD the response times, averaged across separations, were 50 ms shorter in the case of the descending staircase ($F_1 = 12.8$, $p = 0.0007$), while for AM response times were 40 ms shorter for the descending staircase ($F_1 = 3.96$, $p = 0.05$). JM showed a non-significant difference of 17 ms in the same direction ($F_1 = 1.54$, $p = 0.22$). Since the Weber fraction for contrast proved to be large, contrasts on the ascending staircase would on average be

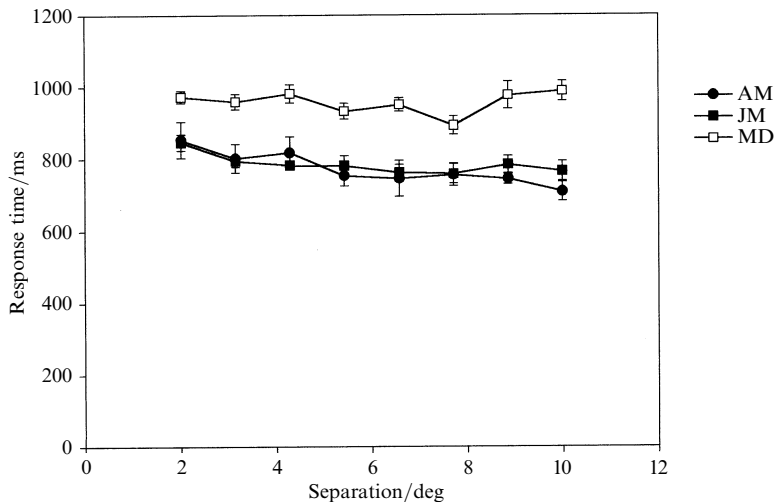


Figure 7. Response times for the discrimination of contrast as a function of the spatial separation of the Gabor patches (experiment 2).

significantly higher than on the descending. So our finding might hint that high contrasts produce initially saturating signals, and that the two signals are more discriminable at some later instant during recovery from saturation.

4 Experiment 3. Orientation discrimination

In a third experiment we used Gabor patches identical to those used in experiments 1 and 2, but now we held constant the spatial frequency and contrast of the patch and required the subject to discriminate its orientation. We centred the discrimination on a tilt of 45° , in order to avoid the enhanced discrimination that occurs near the vertical and horizontal.

4.1 Method

The apparatus, the spatial arrangement of the stimuli, and the calibration procedure were as for experiments 1 and 2. The spatial frequency of the Gabor patches was fixed at 2 cycles deg^{-1} and the Michelson contrast was fixed at 0.3. There were 25 possible referent orientations, centred at 45° clockwise from the vertical and spaced by 1° . The subject was required to judge whether the more clockwise Gabor patch was more tilted than the less clockwise patch. Ascending and descending staircases were randomly interleaved as in experiments 1 and 2. The difference in orientation for each staircase was initially 10° and it was multiplied by 0.9 after three consecutive correct responses and by 1.1 after one incorrect response.

To eliminate the possibility that the subject would relate the test stimuli to the vertical or horizontal edges of the screen, a circular mask was placed over the screen, giving an illuminated aperture of 14.4° .

The subjects were the authors MD and JM, who already had extensive practice in orientation discrimination, and two female naïve subjects, NL and IB. The subjects MD, JM, and NL completed 8 sessions, testing 8 separations per session; IB completed 6 sessions, testing 6 separations.

4.2 Results and discussion

In figures 8a–8d we show for each subject the threshold as a function of the spatial separation of the two Gabor patches. Data are shown separately for ascending and descending staircases. Figure 8e shows the results averaged for ascending and descending staircases and for the four subjects.

The data for each subject were analysed by a two-way ANOVA, with the factors Separation and Ascending versus Descending Staircase. The two naïve subjects exhibit the behaviour that we have seen for spatial frequency and for contrast: there was no significant effect of the spatial separation of the two Gabor patches ($F_7 = 0.7$, $p = 0.63$ for IB; $F_7 = 0.92$, $p = 0.5$ for NL). However, in this experiment we see the first example where discrimination deteriorates with separation: for adjacent stimuli, the two very experienced subjects, MD and JM, have thresholds of 4° – 6° , about half those of the naïve subjects, but their thresholds increase with separation ($F_7 = 3.09$, $p = 0.005$ for MD; $F_7 = 3.1$, $p = 0.005$ for JM). For these subjects, our findings are analogous to those found for *temporal* separation, where orientation thresholds, but not those for spatial frequency, increase with the delay between stimulus presentations (Magnussen 2000; Vogels and Orban 1986).

The case of orientation discrimination illustrates well the central issue that we raised in section 1. Does the subject (a) rely on dedicated comparators that are designed to recognise directly the parallelism or non-parallelism of separated contours; or does he or she (b) extract two independent orientation signals, relate each of them to a framework supplied by visual or vestibular or somatosensory signals, and finally compare the results of the two earlier comparisons?

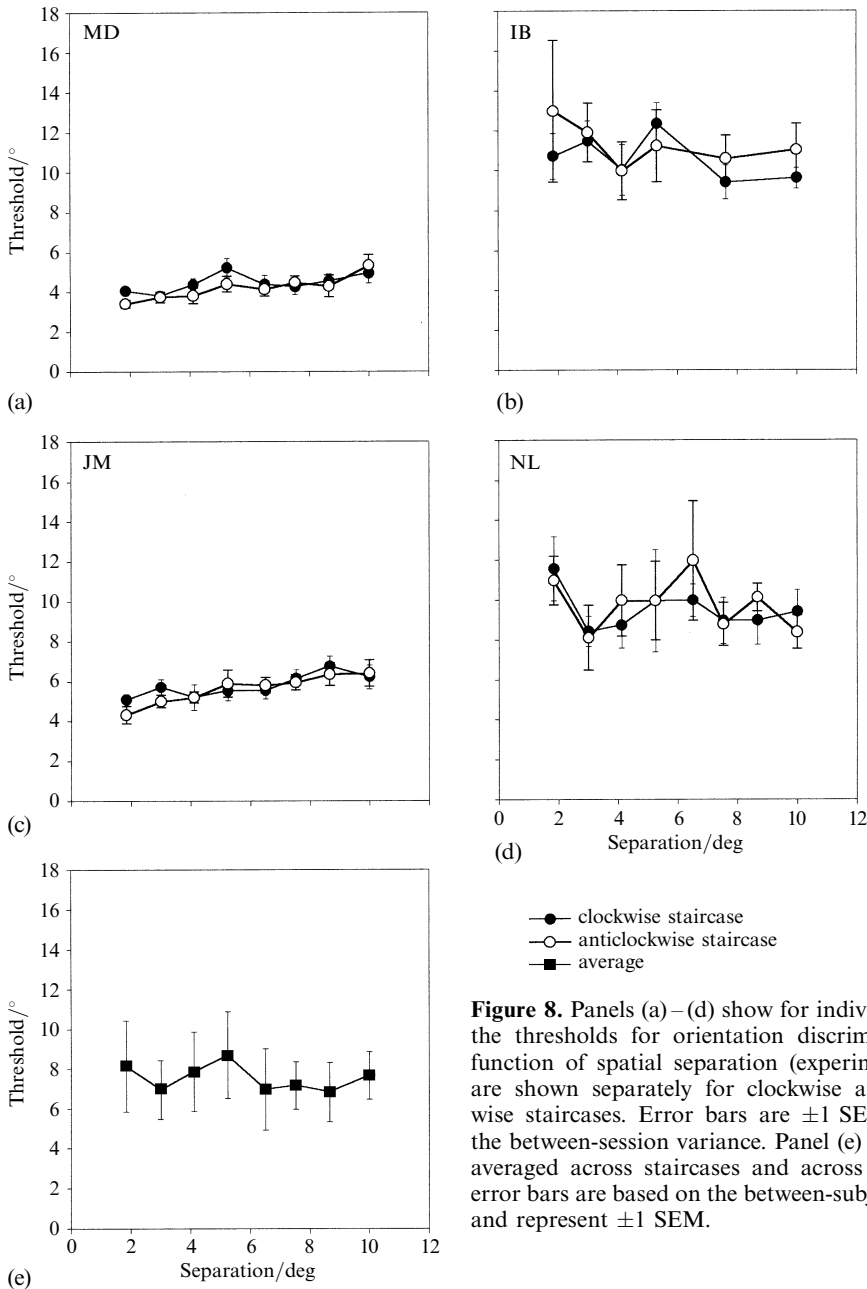


Figure 8. Panels (a)–(d) show for individual subjects the thresholds for orientation discrimination as a function of spatial separation (experiment 3). Data are shown separately for clockwise and anticlockwise staircases. Error bars are ± 1 SEM, based on the between-session variance. Panel (e) shows results averaged across staircases and across subjects; the error bars are based on the between-subjects variance and represent ± 1 SEM.

In support of possibility (a) we can note that cells are found in area 17 of the monkey that give an enhanced response if a grating of a different orientation lies outside the classical receptive field of the cell (Sillito et al 1995); and that cells of the class that Hubel and Wiesel called higher-order hypercomplex are sensitive to the presence of contours that are not collinear (Hubel and Wiesel 1965; Shevelev et al 1999). Several findings in the psychophysical literature (Heeley and Buchanan-Smith 1996; Regan et al 1996) support the existence of dedicated filters for the estimation of angle—that is to say, detectors that directly signal the relationship between two intersecting contours.

In support of possibility (b) we can turn to the classical perceptual tradition that shows how judgments of orientation are influenced by the framework of the visual field and by vestibular and somatosensory information (Howard and Templeton 1966). There is an interesting difference here between orientation and spatial frequency: in the case of orientation the subject has available a long-term external reference that is independent of the particular sequence of exemplars that is presented in the experiment.

In the present experiment, subjects IB and NL show little effect of the separation of the Gabors over a range of 10 deg. We may suppose that they conform to strategy (b), extracting the local orientation signals for the two Gabors independently, perhaps referring each to an external frame, and then performing a central comparison. Subjects MD and JM, on the other hand, whose thresholds are lower and increase with separation, may have gained access to cortical mechanisms that directly relate paired orientation signals over several degrees. Since orientationally selective cells tuned to higher spatial frequencies have smaller receptive fields, it would be instructive to test whether thresholds would rise more quickly with separation if subjects such as MD and JM were tested with higher spatial frequencies, and whether thresholds would rise if the two Gabor patches were of different spatial frequency. Such predictions are suggested by the results of Dakin and Hess (1998), who studied subjects' ability to detect collinear strings of Gabor patches. Our own task differs from that of Dakin and Hess, in that our stimuli are near-collinear on only a minority of trials (when one Gabor patch is to the lower left of the other), but it is instructive that Dakin and Hess found that the performance of their subjects deteriorated above 6 cycles deg^{-1} or when two different spatial frequencies were alternated in the string.

Response times for the four subjects are shown in figure 9 as a function of the separation of the Gabor patches. A two-way ANOVA performed for each subject showed that there was a significant effect of separation for all subjects ($F_7 = 5.35$, $p = 2.6 \times 10^{-5}$ for MD; $F_7 = 3.28$, $p = 0.003$ for JM; $F_7 = 4.11$, $p = 0.003$ for IB; $F_7 = 2.23$, $p = 0.04$ for NL). However, the trends are different for different subjects, and it is interesting that a given subject's response times to some degree reflect the trend in his or her thresholds: thus MD and JM become slower at large separations, whereas IB becomes faster.

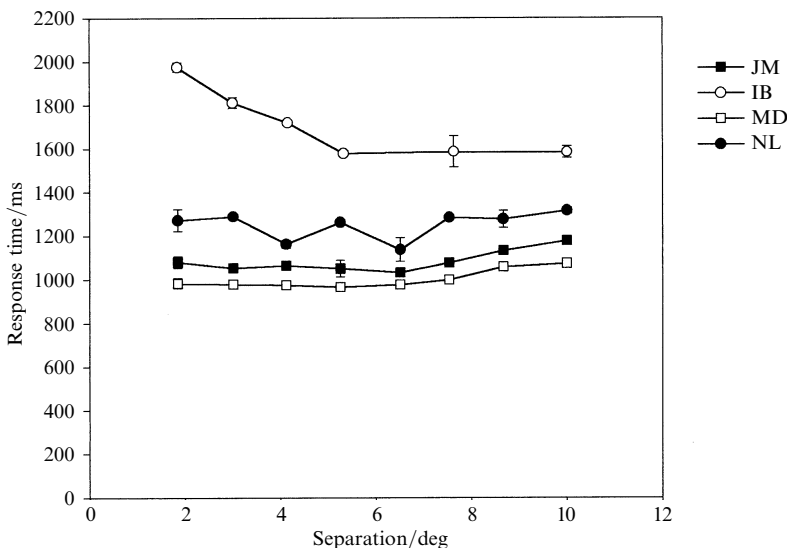


Figure 9. Response times for orientation discrimination as a function of the spatial separation of the Gabor patches (experiment 3).

For orientation discrimination, there was no significant effect of staircase on threshold or on response time for any subject. This might be expected, since there is no reason to expect an asymmetry of discriminability for orientations on the two sides of 45° .

5 General discussion

We set out to ask how accurately subjects can compare stimuli presented at different separations in the visual field. In the case of spatial frequency and contrast we found little systematic increase in the discrimination threshold as the two Gabor patches were separated by distances of up to 10 deg. For two subjects this was also true for discrimination of orientation.

In cases where the threshold remains constant over separations of up to 10 deg, we suggest that it is unlikely that the comparison depends on dedicated local comparators.

5.1 *An implausible model*

There is extensive evidence elsewhere that visual discrimination cannot be explained simply by first-stage cortical filters that are sensitive to both orientation and spatial frequency at a particular point in the visual field (eg Olzak and Thomas 1999). However, many models then postulate higher-order neurons or dedicated circuits that act as collector units or comparators units. We doubt whether the present results can plausibly be explained in such terms.

In figure 10, for the case of spatial frequency, we illustrate the class of model that we wish to reject. At the lowest level of the model is represented an array of primary units tuned to different spatial frequencies and specific to small patches of retina: there is good evidence that each local retinal region is sampled in this way by several spatial-frequency analysers in parallel (De Valois et al 1982; Glezer et al 1973). We draw here only four out of six of the neural filters that Wilson and Gelb (1984) postulate to account for the discrimination of spatial frequency and of width.

Whether or not the number of primary analysers is limited to six for each position, it is unlikely that there are as many analysers at each position as there are JNDs in a psychophysical task. So at the next stage (in the middle of figure 10) we postulate local comparators that extract the ratio of activity in the primary analysers and so support psychophysical thresholds of a few percent.

In order to explain the results of the present experiment, we should then be obliged to postulate a third level (represented at the top of figure 10) in which, for every possible pairing over the central 10 deg, there exists a second-order comparator connected to two first-order comparators. Moreover, at this level or at an earlier level, the number of connections in the model would need to be multiplied to account for the fact that subjects in a forced-choice task can judge spatial frequency with the same accuracy whether the two targets are of the same or of different orientation (Burbeck and Regan 1983).

A model of this kind appears to us implausible. First, the number of second-order comparators must be very large and proportional to the square of the number of first-order comparators. Second, and perhaps more importantly, a large part of the cortical mass would be given over to long axons.

Wilson (1991) has advanced an analogous 'combinatorial argument' against Morgan and Regan's (1987) model of line-interval discrimination. In order to account for the ability of subjects to estimate distances in the visual field, Morgan and Regan's model postulates 'a plurality of coincidence detectors', each of which pairs one retinal location with a second. Additional 'opponent elements' then compare the outputs of particular pairs of coincidence detectors. In response to the combinatorial argument, Kohly and Regan (2000), however, have suggested that the coincidence detectors and opponent

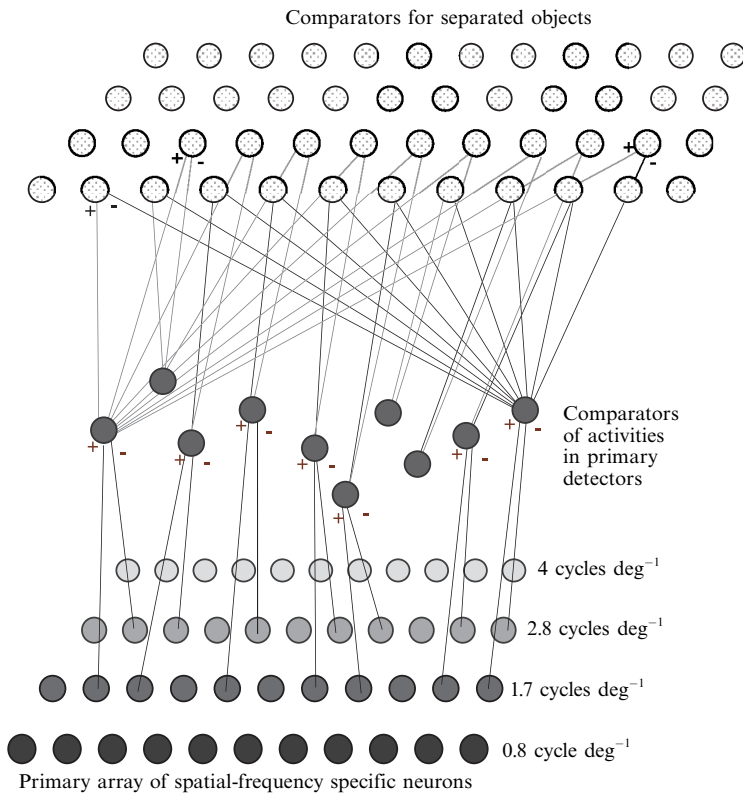


Figure 10. An implausible model for the discrimination of the spatial frequencies of separated objects. At the base of the model is an array of primary neurons specific for different spatial frequencies at different positions in the visual field. To account for the small JNDs found psychophysically, an array of comparator units is postulated, each comparator drawing inputs of opposite sign from two primary analysers that are tuned to adjacent spatial frequencies and have receptive fields in the same local region of the visual field. To explain the results of experiment 1, we must then postulate second-order comparator units, which draw inputs of opposite sign from the first-order comparators for two different positions in the visual field.

elements of their psychophysical model should not be identified with single neurons. We should make clear, therefore, that our criticism of models resembling that of figure 10 is explicitly a criticism of models in which the comparison of separated stimuli is carried out by dedicated individual neurons.

5.2 *A cerebral bus?*

We favour an alternative hypothesis that is not often considered in current neuroscience. Beyond the cortical stage where local stimulus features are represented by the activity of single units, there may be a radical transformation, so that stimulus attributes are represented in an abstract code that can run on a cerebral bus in the way that a computer bus or an Internet link carries different messages for different destinations. The essential feature of the Internet is that it eliminates the need for a dedicated cable between any particular pair of computers that need to communicate. Communication is by packets of data that carry with them, in an agreed code, the identity of the sender and that of the addressee. In the brain, as on the Internet, the information available at a local site may be required from time to time at many different sites: it is possible that the brain too has side-stepped the proliferation of dedicated lines and has evolved a means of representing stimulus attributes—as well as objects, words, and concepts—that does not depend on the activity of single cells.

5.3 *The role of iconic storage and selective attention*

Our stimulus presentations in these experiments were deliberately short (100–150 ms), in order to ensure that subjects could not make an eye movement from one Gabor patch to the other. A traditional reason for choosing presentations of this duration is that they resemble a single fixation pause between saccades.

Our subjects' performance is likely to be limited by the briefness of the stimulus and its short-lived iconic trace, but this limitation appears to be independent of separation, at least in the case of spatial frequency and contrast. Several authors have suggested that selective attention takes time to travel across the representation of the visual field or within the visuospatial sketch-pad; and that the time required is a positive function of the distance in the external field or in the internally represented image (Kosslyn et al 1978). If this were a general property of selective attention and if our subjects were processing the two stimuli successively, then we might expect performance to deteriorate as the separation of the Gabor patches increases: at large separations, the representation of the second stimulus would have decayed further before the translation of attention was complete. In the particular case of the two subjects who show an increase in threshold for orientation discrimination as separation increases, it is possible that performance is limited by the rate of displacement of attention across the field. However, in all the remaining conditions where our subjects show no elevation in threshold as separation increases, we can exclude models in which the two stimuli are analysed serially and performance is limited by the rate at which attention is displaced across the field.

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