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One spatial filter limits speed of detecting low and middle frequency gratings

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Abstract

Reaction times for detecting sinusoidal gratings depend jointly on grating contrast and spatial frequency. We examine whether the effect of spatial frequency results from low-pass filtering in a single channel or reflects processing of different frequencies by two or more different processing streams. Observers performed a speeded two-alternative spatial forced-choice detection. Errors and reaction times were measured. Contrasts varied from 0.05 to 0.67, and spatial frequencies from 0.72 to 6.51 cpd. No effect of uncertainty about spatial frequency was found, arguing against multiple channels. The data are well fit by a single channel model driven by a low pass filter. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Reaction times for the detection of sinusoidal gratings are jointly determined by the contrasts and spatial frequencies of the gratings (Breitmeyer, 1975; Harwerth & Levi, 1978; Felipe, Buades & Artigas, 1993). The research reported here examines how spatial frequency exerts its effect. In particular, does this effect reflect the operation of multiple, parallel streams or channels or does it reflect a single channel? In this paper we use the term channel to refer to a mosaic of pathways which have identical temporal and spatial filtering properties except that their receptive fields are centered on different points in the visual field.

Because reaction times depend on contrast, any early filtering which differentially attenuates gratings of different spatial frequencies will cause reaction times to vary as a function of spatial frequency, as well as of contrast. The question addressed here is whether the observed effect of spatial frequency results, on the one hand, only from filtering within a single channel or whether, on the other hand, it also reflects the use of different channels to process different spatial frequencies.

It is well established that in unspeeded detection tasks, when contrast threshold rather than reaction time is the measure of performance, detection is mediated by multiple, parallel channels with band-pass selectivity in the frequency domain (Olzak & Thomas, 1986; De Valois & De Valois, 1988; Graham, 1989). However, the mechanisms which govern reaction times may be different. Reaction times increase as a function of spatial frequency even after grating contrasts have been adjusted for differences in contrast thresholds, i.e. even after the effects of different degrees of attenuation by different channels have been neutralized. This fact suggests that the mechanisms and/or processes which govern reaction times may differ from those which constrain contrast thresholds. Furthermore, this same fact suggests that the mechanisms which govern reaction times have a narrower overall bandwidth than those which govern contrast thresholds. Thus, it is reasonable to ask whether reaction time performance is mediated by a single channel or by multiple, parallel streams or channels.

Two different, but mutually compatible, types of multiple channel mechanisms have been proposed. One

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posits two different processing streams: a fast stream with low spatial resolution and a slower stream with higher spatial resolution (Breitmeyer, 1975; Tolhurst, 1975; Lupp, Hauske & Wolf, 1976; Harwerth & Levi, 1978; Felipe, Buades & Artigas, 1993; Breitmeyer & Breier, 1994). The fast stream, it is proposed, tends to dominate in the detection of low spatial frequency gratings and the slower stream tends to dominate at higher frequencies, although the balance between their roles may also be affected by stimulus contrast. The second proposal is that detection of gratings of different spatial frequencies is mediated by pathways driven by receptive fields of different sizes (low frequencies are detected with pathways having large receptive fields, high frequencies are detected with pathways having small receptive fields) and that large receptive fields lead to faster responses than small ones. Rudd (1988) quantified this proposal, deriving the differences in response speeds from considerations of quantum fluctuations. The basic idea is that the speed of detection is constrained in the first instance by quantum fluctuations: response is delayed until enough quanta have been captured to provide a critical level of reliability. Pathways which have larger receptive fields capture quanta at a faster rate and reach the critical level of reliability sooner.

Against these dual or multiple channel proposals, we may consider the possibility that, when rapid response is the goal, detection of gratings of all spatial frequencies is mediated by a single processing stream or channel, driven by a single class of receptive fields. According to this proposal, reaction times are longer for high frequency than for low frequency gratings because the filter properties of the receptive field attenuate the effective contrasts of high frequency stimuli by a greater factor, thus slowing response. Normalizing grating contrasts against observed contrast thresholds does not, according to this proposal, remove the effect of spatial frequency because the bandwidth of the single channel which controls reaction times is narrower than the combined bandwidths of the multiple channels which constrain contrast thresholds.

There are several experimental procedures for selecting between the multiple and single channel proposals. Our experiments use the uncertainty paradigm, which has provided key evidence for the role of multiple channels in mediating contrast thresholds for different frequencies (Davis, 1981; Davis & Graham, 1981; Davis, Kramer & Graham, 1983) and for distinguishing between single and multiple mechanism alternatives in suprathreshold discrimination tasks (Thomas & Olzak, 1996). Whenever the signals needed to perform a perceptual task come over one of two or more alternative channels, performance is better when the viewer knows what the stimulus is and which channel provides the relevant signal than when the stimulus and channel are unknown. No such effect is found when all information comes over only a single channel.

Our viewers performed a two-alternative spatial-forced choice detection task. On each trial, a patch of grating appeared either to the left or right of fixation. The subject responded as quickly as possible by indicating which side. We examined reaction times as a function of contrast and spatial frequency under conditions of certainty and uncertainty with respect to spatial frequency. Finding no evidence of an uncertainty effect, we fitted our data with a single channel model and estimated its sensitivity function with respect to spatial frequency.

2. Stimulus uncertainty and reaction times

Stimulus uncertainty exists when some parameter of the stimulus (such as its location, direction of motion or spatial frequency) is unknown prior to the performance of a perceptual judgment (such as detection or discrimination) about the stimulus. Any decrease in the quality of performance which accompanies the introduction of uncertainty is called an uncertainty effect. Several authors have reviewed uncertainty effects and their various possible causes (Ball & Sekuler, 1980; Sperling & Dosher, 1986; Palmer, 1994). In some cases, the effects may stem from an inability of the observer to fully monitor multiple sources of information and/or the use of sub-optimal decision strategies. However, as Tanner (1961) pointed out, even an ideal observer using an optimal decision strategy will show uncertainty effects. That is, an uncertainty effect must be observed whenever stimuli with different parameter values are processed by different, stochastically independent sensory channels. When the value of the parameter is unknown, the observer must monitor all of the potentially relevant channels. Because each additional channel which is monitored contributes additional noise to the judgment process, performance must suffer, even for an ideal observer. Thus, the presence or absence of an uncertainty effect provides critical evidence about whether or not stimuli which differ along a particular dimension are processed by different sensory channels. Uncertainty effects have been empirically demonstrated for stimuli which differ with respect to spatial location (Cohn & Lasley, 1974; Palmer, 1994), direction of motion (Sekuler & Ball, 1977; Ball & Sekuler, 1980), speed of motion (Ball & Sekuler, 1980), as well as spatial frequency (Davis, 1981; Davis & Graham, 1981; Davis, Kramer & Graham, 1983).

The uncertainty studies which support the existence of multiple spatial frequency channels have used contrast thresholds as the measure of performance. For the purposes of the present study, it is important to establish that uncertainty effects must also occur when reaction time is the measure of performance and stimulus contrast is above the contrast threshold. Stone (1960) provides an ideal observer analysis that reaction times must rise with stimulus uncertainty, provided that error rates do not increase. Ball and Sekuler (1980) extend this analysis to show that two non-optimal decision strategies also lead to increased reaction times. On the empirical side, Ball and Sekuler (Sekuler & Ball, 1977; Ball & Sekuler, 1980) measured reaction times for detection of the onset of motion of high contrast random dots. They found that reaction times increased when there was uncertainty about either the direction or velocity of the motion. Most important, Ball and Sekuler compared uncertainty effects obtained with reaction times to effects obtained using a two-alternative forced-choice detection task and found good agreement between the two types of measures. Thus, there is good reason to believe that the reaction time data of the present study will show uncertainty effects if more than a single channel is used to perform the reaction time task.

Stimulus uncertainty may affect performance in a reaction time task in one or more of three different ways. First, reaction times will increase, as found in the studies cited in the previous paragraph. Second, error rates may also increase (Stone, 1960; Ball & Sekuler, 1980). As always, there is the possibility of speed-accuracy trade-off, i.e. the subject may limit any increase in reaction time by relaxing the response criterion, thus permitting more errors to occur. Finally, because monitoring more channels adds noise to the decision process, the variability of reaction times may also increase. If the subject monitors only a subset of relevant channels on each trial and changes the subset from trial to trial, there will be a large increase in variability (Ball & Sekuler, 1980). The relative magnitudes of these three possible effects depends upon the decision strategy and criterion adopted by the subject. Consequently, in our uncertainty analyses we test the data for all three types of effects.

3. Method

3.1. Stimuli

Stimuli were generated using a Cambridge Research Systems VSG Graphics Board (version 4.02). Each stimulus was a horizontal sinusoidal grating, spatially windowed by a two-dimensional Gaussian with a standard deviation on the horizontal axis of 1.09°. The standard deviation on the vertical axis was either 1.09° or 0.67 cycles of the grating, depending upon the experimental condition. In both conditions, the grating was in cosine phase with respect to the window. The center of the window was 3° to the left or right of fixation. Exposure duration was 160 ms, with abrupt onset and offset. The stimuli were presented on a monochrome monitor with mean luminance of 11.3 cd/m^2. Fixation was controlled by a fixation point in the center of the illuminated area of the screen, which measured 17° high × 22° wide. The surround was dark. Viewing distance was 0.85 m.

Five grating contrasts (measured before windowing) were used: 0.054, 0.131, 0.240, 0.436 and 0.673. There were five spatial frequencies: 0.72, 1.08, 1.81, 3.25 and 6.51 cpd. Trials were run in blocks of 200. All five contrasts, randomly varied from trial to trial, were used in each block. In some experimental conditions, all five spatial frequencies, randomly varied from trial to trial, were used in each block. In other conditions, only a single frequency was used in each block.

3.2. Procedure

Subjects adapted to the screen luminance for several minutes before trials began. The beginning of each trial was signaled by a beep. After a brief delay, varying from 500–1000 ms, the stimulus appeared either to the left or right of the fixation point and the subject responded by indicating which side. The response was made by using the left and right forefingers respectively, to press one of two keys on the computer keyboard. Both the side selected and the reaction time, measured in ms from stimulus onset, were recorded. If the reaction time was longer than 1000 ms, the results were discarded and the trial was repeated at the end of the block. Subjects ordinarily completed four blocks of 200 trials each, per day, with rests between blocks.

3.3. Conditions

Data were gathered under two main conditions: constant window size and variable window size. The two conditions were run sequentially, rather than intermixed. Subject PF ran the variable condition first and the constant condition second. Subject JPT ran the conditions in the reverse order.

3.3.1. Constant window size

In this condition, the same Gaussian window was used for stimuli of all spatial frequencies. The standard deviation of the window was 1.09° on both vertical and horizontal axes. There were two sub-conditions. In the mixed condition, all five spatial frequencies were used in each block of 200 trials. Frequency was randomly varied from trial to trial. In the blocked condition, only one spatial frequency was used in each block of trials. Only three of the spatial frequencies (0.72, 1.81 and 6.25 cpd) were run in the blocked condition. The order in which the frequencies were tested was independently randomized from one replication to another and one subject to another. Each subject ran a total of 20 blocks of trials under the mixed condition and 12 under the blocked condition, yielding a total of 160 trials for each combination of contrast and spatial frequency under each condition. Blocks of trials from the mixed and blocked sub-conditions were randomly interleaved.

3.3.2. Variable window size

In this condition, the standard deviation of the Gaussian window on the vertical axis varied inversely with the spatial frequency of the grating, such that the standard deviation was 0.67 cycles of the grating. Only the blocked subcondition was used, and all five spatial frequencies were run under the blocked condition. The order in which the frequencies were tested was independently randomized from replication to replication and subject to subject. Each subject ran a total of 20 blocks of 200 trials, yielding a total of 160 trials for each combination of contrast and spatial frequency.

3.4. Subjects

The subjects, PF and JPT, are two of the authors. PF was a 25 year old female who was emmetropic in one eye and amblyopic in the other. She viewed the stimuli monocularly, the amblyopic eye being patched. JPT was a 64 year old male presbyope who wore corrective lenses for the viewing distance used. He viewed the stimuli binocularly.

4. Results

The raw data consist of 130 distributions of 160 reaction times each, one distribution for each combination of contrast and spatial frequency under each condition and subcondition for each subject. The individual distributions are unimodal. Although the distributions show slight positive skewing, means and medians agree closely.

Fig. 1(a)–(f) show mean reaction times for the two subjects under the different conditions. Means were calculated from all trials, regardless of whether the response was correct or incorrect. (Statistical analysis failed to find a significant difference in reaction times between correct and incorrect trials.) Each error bar shows ±1 S.E. of the mean. Table 1 summarizes the error rates for the two subjects under the different conditions.

The data replicate previous findings: reaction time decreases as contrast increases and, at every contrast, is longer for high spatial frequencies than for low frequencies. Except for fluctuations which are consistent with error of measurement, the decrease in reaction time as contrast increases is smooth and without 'breaks' which might indicate a transition from one mechanism to another (Harwerth & Levi, 1978; Felipe, Buades & Artigas, 1993). The reaction times for PF are consistently shorter than those for JPT. This difference probably reflects the difference in their error rates, although the difference in their ages may also be a factor. However, despite the overall differences in speed and error rates, their data are otherwise in close agreement.

5. Uncertainty analysis

As indicated in Section 1, one way to distinguish between the single and multiple channel alternatives is to look for an effect of stimulus uncertainty. If detection of gratings of different spatial frequencies is mediated by different channels, then performance should be better in the blocked condition, in which the spatial frequency of the grating to be detected is known before its presentation, than in the mixed condition, in which frequency varies from trial to trial and is unknown before presentation. If the frequency is known, the viewer need monitor only those channels which are important for detection of that frequency. However, if the frequency is unknown all of the possibly relevant channels must be monitored and, as described in the introduction, there will be some combination of increased error rates, increased variability of reaction times, and/or longer reaction times. On the other hand, if detection of all spatial frequencies is mediated by a single channel, only this channel will be monitored in any case and performance should not be affected by whether the frequency is known (blocked condition) or unknown (mixed condition).

The comparison between performances in blocked and mixed conditions was made for the three spatial frequencies (0.72, 1.81 and 6.25 cpd) which were run in both blocked and mixed conditions, in interleaved blocks of trials, under the constant window condition. Blocked performances from the variable window condition were not compared with the mixed performances from the constant window condition because these two data sets were gathered sequentially, at well separated periods of time, rather than concurrently.

Table 1 gives error rates for the blocked and mixed conditions. The differences between the two conditions are small and go in opposite directions for the two subjects. Chi-square tests comparing the number of errors at each combination of contrast and spatial frequency indicate that the difference for neither subject approaches significance (PF: Chi-square $= 12.4$, $df = 15$, $P > 0.5$; JPT: Chi-square $= 10.8$, $df = 15$, $P > 0.5$). Thus, there is no evidence of increased errors in the mixed or frequency-uncertain case.

An omnibus Chi-square test was conducted to test for any differences in distributions of reaction times

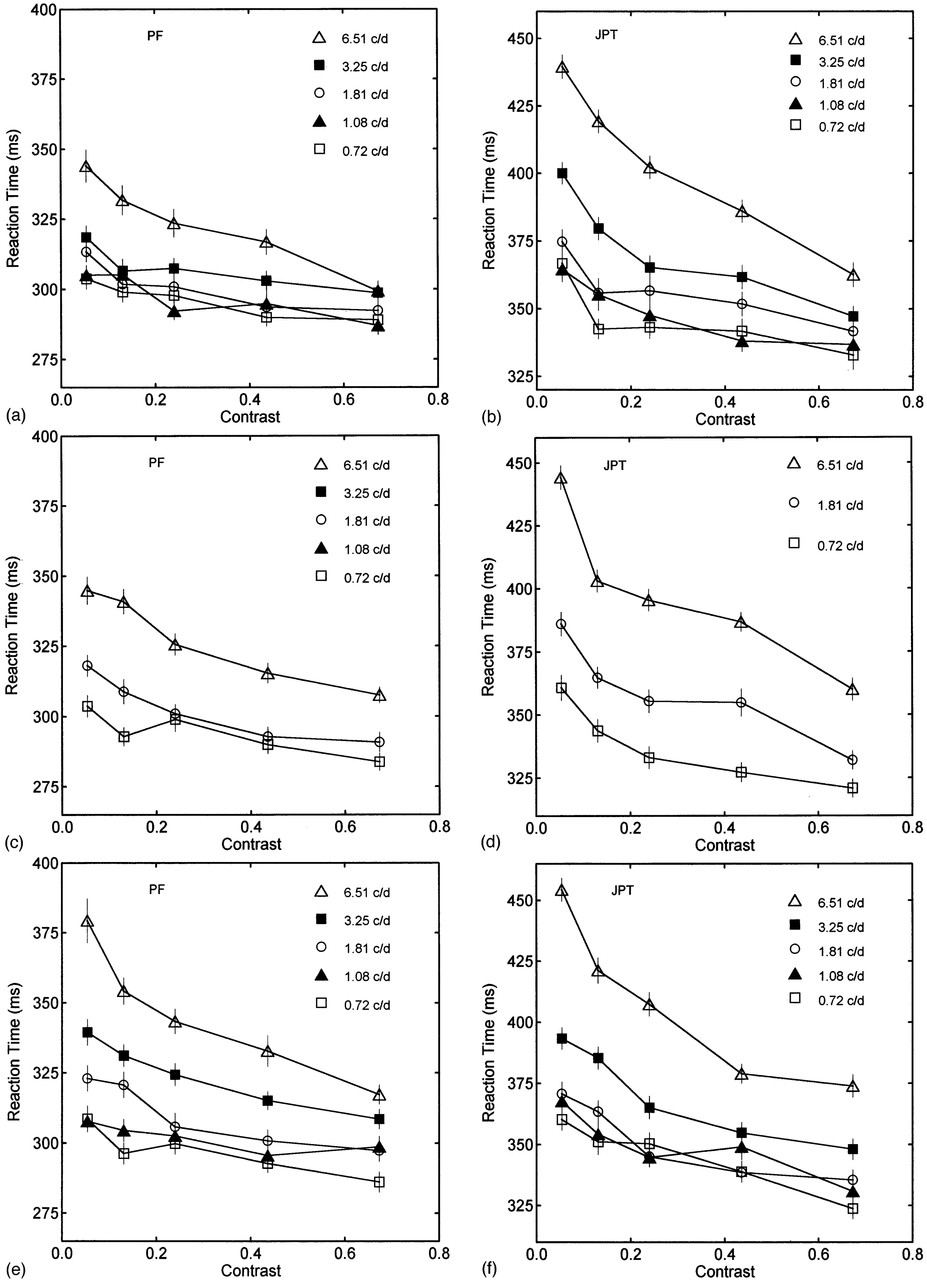

Fig. 1. Reaction times as a function of grating contrast. Each data point is the mean reaction time for one spatial frequency at one contrast: parts (a) and (b), constant window mixed condition; parts (c) and (d), constant window blocked condition; and parts (e) and (f), variable window condition.

Table 1
Error rates (%)

Subject	Constant window blocked	Constant window mixed	Variable window
PF	12.7	13.6	9.1
JPT	1.71	1.67	1.2

between the blocked and mixed conditions. For each combination of contrast and spatial frequency, two histograms were constructed, one for the blocked reaction times and one for the mixed reaction times. The histograms were constructed using the same five bins for each of the two distributions. A Chi-square was computed to test for a difference in the distribution of reaction times across the bins. Fifteen such Chi-squares were computed for each subject (five contrasts × three spatial frequencies) and summed to test for any systematic difference between reaction times in the two conditions. This test failed to show any difference between the two conditions with respect to reaction times (PF: Chi-square = 77.7, $df = 75$, $P = 0.39$; JPT: Chi-square = 79.5, $df = 75$, $P = 0.34$).

Figs. 2 and 3 further document the lack of an uncertainty effect on reaction times. Fig. 2 compares the variabilities of reaction times in the blocked and mixed conditions. Each data point shows the standard deviation of reaction times for a given combination of contrast and spatial frequency. The x-coordinate is the standard deviation in the blocked condition, the y-coordinate is the standard deviation in the mixed condition. Fig. 3 compares mean reaction times. Each data point shows the mean for a given contrast and spatial frequency. The x-coordinate is the mean in the blocked condition, the y-coordinate is the mean in the mixed condition. In both figures, an uncertainty effect would manifest itself as a tendency for the data points to fall above the diagonal line representing equality between the two conditions. There is no such tendency: In both figures, just as many data points fall below the line as above.

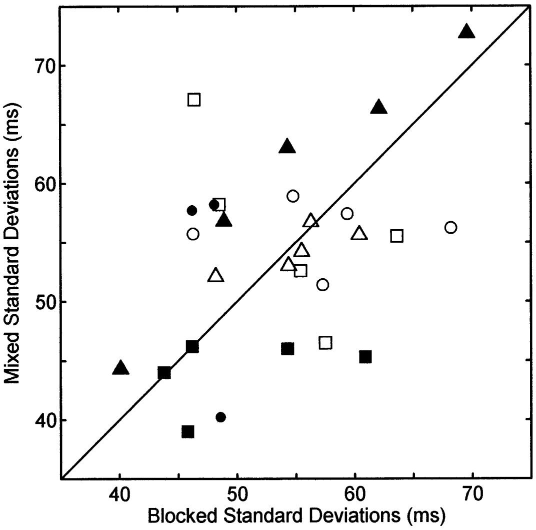

Fig. 2. Standard deviations of reaction times in the blocked and mixed conditions: squares, 0.72 cpd; circles, 1.81 cpd; triangles, 6.25 cpd; subject PF, filled symbols; subject JPT, open symbols.

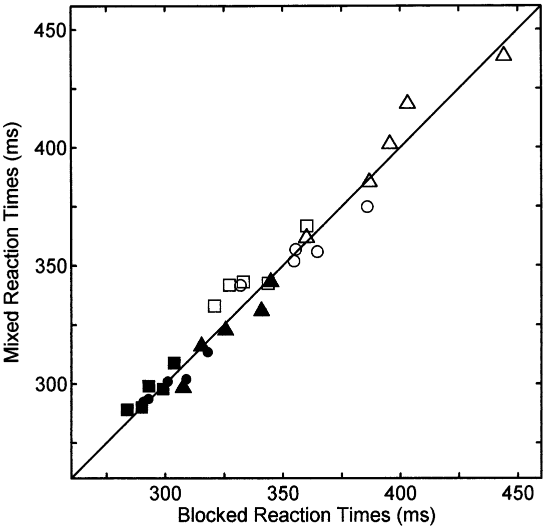

Fig. 3. Mean reaction times in the blocked and mixed conditions. Symbols have the same meaning as in Fig. 2.

To summarize, analyses of error rates and reaction time distributions yield no evidence of a stimulus uncertainty effect with respect to spatial frequency. The findings are consistent with the single channel hypothesis and must be considered as evidence against the multiple channel hypothesis.

6. Fitting a single channel model

To further evaluate the single channel hypothesis, a single channel model was fitted to the sets of reaction times for the constant- and variable-window conditions. In the model chosen, the stimulus passes through a filter which attenuates the stimulus contrast by a factor which depends upon spatial frequency. The output of the filter is accumulated over time until a critical level is reached, at which time the response is triggered. The only part of the process which depends upon spatial frequency is the action of the initial filter; the remainder of the process is independent of frequency. Thus, the essential prediction of the model is that when reaction time is plotted against the output of the filter, the reaction times for all spatial frequencies will fall on a single function.

Eq. (1) states the model in general terms:

$$RT(f, c) = g(cs(f)) \tag{1}$$

the reaction time, RT, to a grating of a given spatial frequency, f, and contrast, c, is a function, g, of the output of the filter, which is given by the product of the grating contrast, c, and the filter's sensitivity, s, which varies as a function of spatial frequency, f. For the function g, we have chosen a three parameter function used by Piéron (1952), Mansfield (1973), Pins and Bonnet (1996, 1997) to describe the relationship between reaction time and stimulus intensity. Eq. (2) states the model with this function incorporated.

$$RT(f, c) = a(cs(f))^p + b \tag{2}$$

where b is a component of the reaction time which does not depend on either stimulus contrast or spatial frequency, and the remainder of the right-hand term represents a component which is inversely related to the effective contrast of the stimulus, i.e. the filter output. The relationship is inverse because the exponent p takes a negative value. Note that only the weighting function $s(f)$, which describes the action of the filter, depends on spatial frequency.

Eq. (2) was fitted to the data sets by the procedure described in Appendix A. Because of the failure to find any difference between reaction times under the blocked and mixed sub-conditions of the constant window condition, the model was fit simultaneously to both sets of data. Table 2 gives the estimated values of the parameters a, b and p, as well the proportion of observed variance which the model accounts for (r^2) and the degrees of freedom (df) (number of data points minus the number of parameters estimated). Table 3 gives estimated values of the weighting function $s(f)$.

The high values of r^2 indicate a good fit between the model and the observed data. This fit is further illustrated in Fig. 4(a)–(d). Each data point in the figures plots the observed mean reaction time for a particular contrast and spatial frequency against the product of the stimulus contrast and the value of the weighting function $s(f)$ for that particular frequency. That is, the observed reaction time is plotted against the estimated output of the putative filter. The solid curves are the predictions of the model. The agreement between the data and predictions supports two conclusions. First, as predicted by the single channel model, when reaction times are plotted against the estimated filter output, the data for all spatial frequencies define a single, smooth function. This finding argues against the proposition that two (or more) processing streams with different temporal characteristics follow the initial filtering action. Second, this single, smooth function is accurately described by the three parameter function proposed by Piéron. Whether this same function would continue to fit the data as contrasts decreased to detection thresholds is an open question. Similarly, we do not know if the fit would break down at spatial frequencies significantly higher than those tested here.

Table 3 shows estimated values of $s(f)$ for the various conditions. These values describe how the initial filtering stage attenuates stimulus contrast by a factor which depends upon spatial frequency. They describe the sensitivity function of the filtering and are comparable to contrast sensitivity as defined by the reciprocal of the contrast threshold for detection. That is, at threshold, the product of contrast and contrast sensitivity is constant (by definition) across spatial frequencies. Similarly, as demonstrated by the data of Fig. 4, the product of $s(f)$ and contrast is constant across spatial frequencies for any given reaction time within the range measured.

Fig. 5 plots, the obtained values of $s(f)$ as a function of grating spatial frequency. Open and filled symbols show data from the constant and variable window conditions, respectively. The values from the two conditions are largely overlapping. In log-log coordinates, $s(f)$ declines as a nearly linear function of spatial frequency throughout the range tested. To estimate the rate of decline, the linear regression of log $s(f)$ on log spatial frequency was computed and a slope of -1.44 obtained. That is, over the frequency range examined, $s(f)$ decreases by a factor of 2.7 for each octave increase in spatial frequency.

It should be emphasized that these sensitivity values are for the putative channel as a whole, rather than for individual pathways comprising the channel. The effects of probability summation across pathways might cause the values for the channel to differ from those of individual pathways. However, the agreement between values of $s(f)$ obtained in the two window conditions suggests that probability summation has a limited effect and that the sensitivity functions of the channel and individual pathways are quite similar. The argument is

Table 2
Parameters of the fitted single channel model

Subject	Condition	a	b (ms)	p	r^2	df
PF	Constant window	21.6	270	−0.28	0.95	29
	Variable window	22.8	275	−0.29	0.97	17
JPT	Constant window	37.9	300	−0.29	0.97	29
	Variable window	47.6	290	−0.25	0.97	17

Table 3
Values of $s(f)$

Subject	Condition		f				
			0.72	1.08	1.81	3.25	6.51
PF	Constant	Mixed	2.58	2.37	1.47	0.70	0.21
		Blocked	3.75		1.27		0.16
	Variable		6.78	2.76	1.30	0.37	0.11
JPT	Constant	Mixed	2.70	2.12	1.24	0.58	0.17
		Blocked	6.27		1.19		0.19
	Variable		2.92	2.05	1.92	0.64	0.14

as follows: At the lowest frequency examined, 0.72 cpd, the constant and variable window conditions used identical stimuli. In the constant window condition, the same overall stimulus size was used for all frequencies and the number of grating cycles presented increased in proportion to spatial frequency. In the variable window condition, the number of cycles was held constant and the overall size of the stimulus decreased as frequency increased. Regardless of whether the magnitude of summation effects is determined by area, number of cycles, or some combination of both, the potential basis for probability summation is greater in the constant window condition and is increasingly so as grating frequency increases. Thus, if probability summation were important, the values of $s(f)$ obtained in the two window conditions would diverge as grating frequency increases. The lack of such divergence indicates: (1) a minor role for probability summation in the present task; and (2) that the sensitivity functions of the channel and its individual pathways are probably similar.

7. Discussion

Reaction times for the detection of sinusoidal gratings increase as a function of spatial frequency, even when grating contrasts are normalized against contrast thresholds. The experiments reported here were designed to distinguish between single and multiple channel explanations of the dependence on spatial frequency. Our basic finding is that uncertainty with respect to the spatial frequency of the grating to be detected has no effect on either error rates or reaction times. This finding argues against both of the multiple channel hypotheses described in the introduction: that low spatial frequencies are detected by a fast processing stream with low spatial resolution and that higher frequencies are detected by a slower stream with higher spatial resolution; and/or that the different pathways which mediate detection of different spatial frequencies are driven by receptive fields of different sizes and different rates of quantum capture.

A confirming analysis showed that a single channel model fits the reaction time data well. In this model, only the contrast attenuation exerted by an initial filtering process varies with spatial frequency. The other parameters of the model, which reflect the temporal dynamics of the pathways involved, are the same for all spatial frequencies. If pathways with different temporal properties, such as transient and sustained pathways (Breitmeyer, 1975; Harwerth & Levi, 1978), were involved, it would not be possible to fit the data for all spatial frequencies with a single set of parameters.

As shown in Fig. 5, the contrast sensitivity function of the putative single channel falls off rapidly as spatial frequency increases: sensitivity drops by a factor of 2.7 per octave over the frequency range examined. This rate of decline is much steeper than that found, using similar stimulus configurations at the same eccentricity, for contrast thresholds when the task is conventional detection (Robson & Graham, 1981; Johnston, 1987). The steeper decline in sensitivity means that the neural network which mediates reaction time performance has a bandwidth which is narrower (as measured by the fall from peak sensitivity) than the overall bandwidth of the multiple, parallel channels which mediate conventional detection. Thus, this difference provides further support for the conclusion that, while contrast thresholds for detection are determined by multiple, parallel channels, reaction times for the eccentricity and frequencies we tested are determined by a single channel.

What can be said about the identity of the neural pathways which constitute this single channel? A priori, magnocellular neurons would seem likely candidates because of their larger axons and faster conductance rates. The steep decline in sensitivity as spatial frequency increases indicates substantial receptor-to-neuron and/or neuron-to-neuron convergence, which also points to magnocellular neurons as likely candidates. However, there is reason for caution in pursuing this quest further. The reaction time response is probably triggered by the earliest parts of the neural response, whereas most of our characterizations of different types neurons (with respect to such properties as functionally defined receptive fields, contrast sensitivity functions, etc.) are heavily influenced or even totally determined by later portions of the response. Many of the processes which shape the later stages of response, such as gain control and lateral inhibitory interactions, may have a greatly reduced effect on the early stages. For example, as discussed in the next paragraph, the results of this and other reaction times studies suggest that observer responses may be triggered before the effects of receptive field surrounds are fully developed.

Most experiments, including the present ones, have found that for a given contrast reaction time increases as a monotonic function of spatial frequency. Felipe, Buades and Artigas (1993) observed a non-monotonic relationship when contrast was less than ten times the contrast threshold. However, their finding is atypical, possibly because of the small field (0.88°) which they used. Assuming that reaction times are mediated by a single channel, the monotonic relationship between reaction times and spatial frequency implies that the channel is driven by a low-pass filter and that the receptive fields which drive the individual pathways comprising the channel lack significant inhibitory surrounds. The apparent lack of inhibitory surrounds might result from the longer latency of surround effects, compared to the responses to central stimulation (Derrington & Lennie, 1984). That is, it might be that it is the leading edge of neural reaction which triggers the behavioral response, and this leading edge may be transmitted before the surrounds can exert their effects. In this respect, it should be noted that the primary effect of an inhibitory surround would be to reduce sensitivity to the lowest frequency stimuli and that it is these stimuli which have the shortest reaction times and provide the least opportunity for surround effects to become manifest.

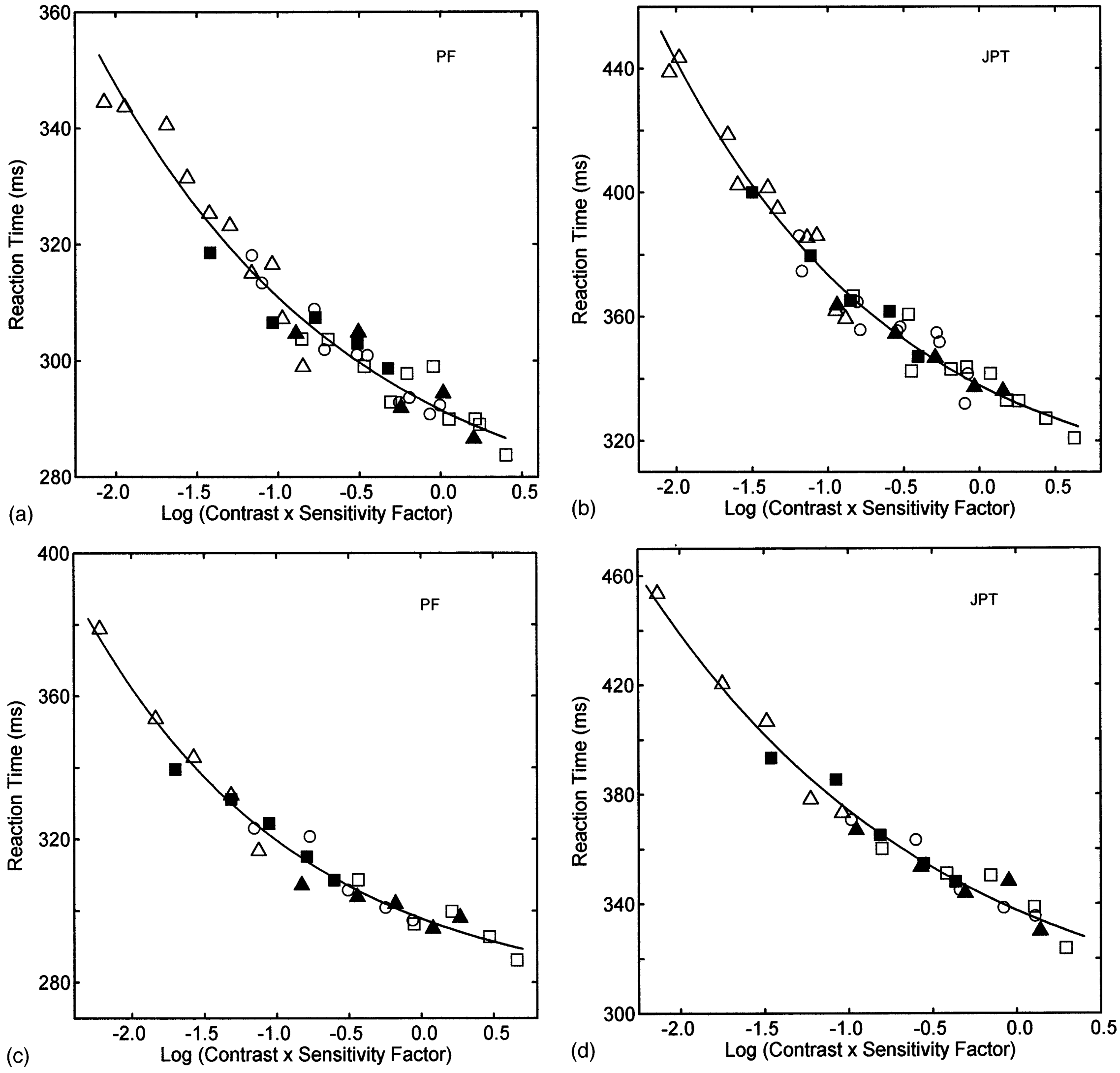

Fig. 4. Fit of single channel model to mean reaction times: parts (a) and (b), constant window condition, blocked and mixed; and parts (c) and (d), variable window condition.

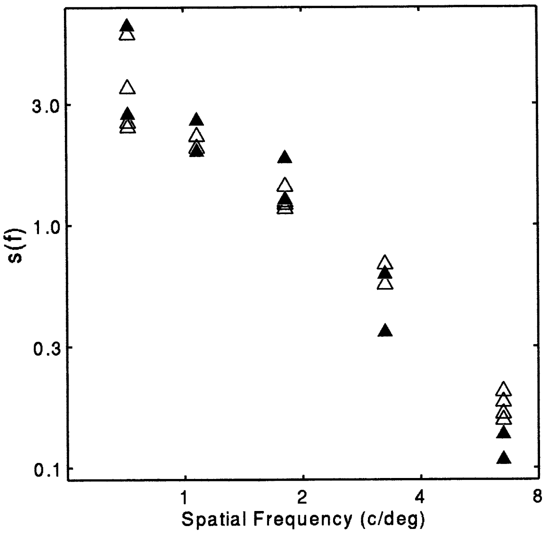

Fig. 5. Values of $s(f)$ obtained by fitting the single channel model: open triangles, data from the constant window condition; and filled triangles, data from the variable window condition.

Harwerth and Levi (1978) and Felipe, Buades and Artigas (1993) observed inflections for some spatial frequencies and/or subjects in the functions relating reaction time to stimulus contrast, which these authors interpreted as reflecting possible transitions between transient and sustained channels. We did not observe any evidence of such transitions, either in our raw data or in fitting the single channel model. However, it should be noted that the eccentricity of the stimuli may be a factor. Harwerth and Levi observed the inflections when stimuli were centered at 0 and 2.5° eccentricity, but not when stimuli were at 5° eccentricity. Our stimuli were centered at 3° eccentricity.

In summary, when the task is to detect a grating at the lowest possible contrast, performance is mediated by multiple, parallel band-pass channels. However, the results of the experiments and analyses presented here argue that the situation is different when the task is to detect a grating of a given suprathreshold contrast as rapidly as possible. That is, performance of the reaction time task appears to be mediated by a single, low-pass channel when the gratings have the low and intermediate spatial frequencies examined here.

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These experiments were performed while JPT was a Visiting Professor in the Laboratoire de Psychophysique Sensorielle, Université Louis Pasteur, Strasbourg. Preliminary reports were presented at the 1996 European Conference on Visual Perception and the 1997 ARVO meetings.

Appendix A. Fitting the single channel model

We use a procedure similar to one used by Mansfield (1973), but which differs by exploiting our use of several spatial frequencies to obtain a separate estimate of the constant b. The model is fitted to the means for each combination of contrast and spatial frequency. Although these means are perturbed by error, reference to error components is suppressed in the following for the sake of simplicity. Eq. (2) can be rewritten as

$$\log(RT(f, c) - b) = \log(a) + p(\log(c) + \log(s(f))) \quad \text{(A1)}$$

First, the value of b is estimated by a systematic evaluation of values between zero and the minimum observed reaction time. For each candidate value of b, the linear regression of $\log(RT(f,c)-b)$ on $\log(c)$ is computed separately for each spatial frequency. Given that the model is accurate, the slope of the regression will decrease (become more steeply negative) as spatial frequency increases if b is underestimated, will increase with spatial frequency if b is overestimated, and be independent of spatial frequency when b is correctly estimated. For each of the data sets, this procedure yielded a unique and unambiguous value for b.

Next, the values $\log(RT(f,c)-b)$ are entered in the cells of a matrix in which grating contrast varies across columns and grating frequency varies across rows. The slope of the linear regression of the column means on $\log(c)$ estimates the value of p. The difference between each row mean and the grand mean estimates the product of p and $\log(s(f))$. Finally, $\log(a)$ is given by the difference between the intercept of the regression of the cell entries on $\log(c)$ and the product of p and the mean value of $\log(s(f))$.

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