CHANNELS IN THE VISUAL NERVOUS SYSTEM: NEUROPHYSIOLOGY, PSYCHOPHYSICS AND MODELS

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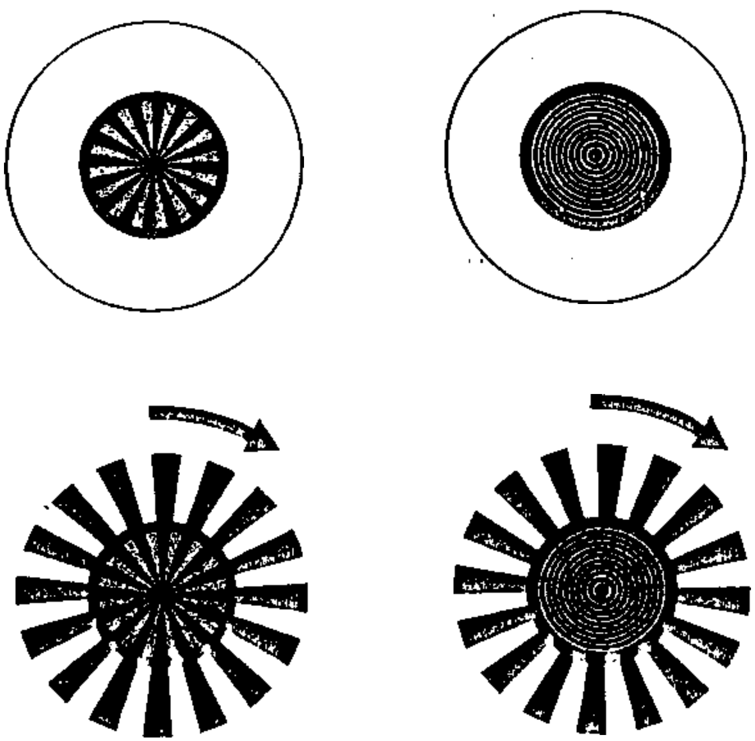

CHANNELS: BANDWIDTH, CHANNEL INDEPENDENCE, DETECTION VS. DISCRIMINATION

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Abstract

Spatial vision research during the 1970s was dominated by the spatial frequency channel paradigm of Campbell and Robson (1968). This article summarizes some research and current views on spatial frequency channels. By channels, we mean an array of medium bandwidth mechanisms, similar to the simple cells that are commonly found in the visual system. The viewpoint presented here provides a useful perspective, slightly different from that found in Graham's excellent book (1989).

Spatial frequency channels play a central role in enabling us to discriminate small, complex objects with our constantly moving eyes. Given an image that is constantly moving on the retina, it is of great value to recode the information from the position domain to the relative position (size) domain to remove the effects of image motion.

Keywords: channels; independence; spatial frequency; bandwidth; summation;detection;discrimination

Introduction

At the 1964 Optical Society Meeting, Campbell and Robson (1964) announced the following: "When a second harmonic was added to a sine-wave grating (in any phase relation), it appeared to be detected independently." In 1968, they published a paper (Campbell & Robson, 1968) called "Application of Fourier analysis to the visibility of gratings", which showed that a square wave grating above 4 c/deg could be detected when its fundamental became visible. This notion differed from the older concept that the higher harmonics should also contribute to the visibility. Campbell and Robson also showed that a square wave could be discriminated from its fundamental sinusoid when the third harmonic was at its independent threshold. In that single paper, they seemed to have a theory for detection (when any Fourier component is visible then the pattern is visible) and a theory for pattern discrimination (two suprathreshold patterns can be discriminated when the leading Fourier components that distinguish the two patterns are independently visible). The next year, Blakemore and Campbell (1969) published a psychophysics paper entitled, "On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images". They showed that after adapting to a grating, thresholds were elevated only for nearby sizes and orientations. Gilinsky (1968) and Pantle and Sekuler (1968) had previously shown similar results for the orientation and spatial frequency domains respectively. At about the same time, Thomas (1969; 1970) was reaching similar conclusions without using a single grating. The importance of these results is that they were exactly what would be expected from the orientation tuned mechanisms with deep lateral inhibition that were found by Hubel and Wiesel (1962; 1968).

The channel approach gained a rapid following among vision researchers because of surprising results in the psychophysical experiments attempting to determine the bandwidth of the underlying mechanisms. This idea was a straightforward extension of Campbell and Robson's experiments (1964; 1968). Graham and Nachmias (1971) showed that there was no subthreshold summation between a fundamental and its third harmonic. This implied that the underlying mechanisms must have a bandwidth that was narrower than 1.5 octaves. The next experiment was done by Sachs, Nachmias and Robson (1971) who did subthreshold summation experiments with grating pairs of a wide range of spatial frequency separations. They found the very surprising result that two gratings with a 20% difference in spatial frequency did not summate. This seemed to imply the underlying mechanisms must have incredibly narrow tuning, just like true Fourier analyzers.

In the last 20 years many advances have been made in our understanding of the properties of channels. I am concerned here with three aspects of these advances: 1) the bandwidth of the underlying channels, 2) channels' independence, and 3) efforts to connect the channels to suprathreshold discriminations.

As stated above, the findings of Campbell and Robson (1968), Blakemore and Campbell (1969), Graham and Nachmias (1971), and Thomas (1970) were compatible with the bandwidths found in cat simple cells by Cooper and Robson (1968). The real problem came with explaining the findings of Sachs et al. (1971). In order to achieve the narrow bandwidths suggested by their results, there must be summation over many cycles. Stromeyer and I suggested that this summation need not be done by a single mechanism, but rather by a pooled summation over many mechanisms (Stromeyer & Klein, 1974). The idea is that the visibility of a grating is not based on the peak contrast, but rather on an average, spatially pooled contrast. In this view, the reason that the 4 plus 5 c/deg gratings did not summate well is because the sum of the two gratings produces beats that reduce the pooled contrast. The amount of reduction in visibility due to the beats was a technical question that was based on assumptions on how to do the pooling. Quick (1974) suggested a simple way to do pooling based on probability summation and we applied his formalism to the grating summation - bandwidth problem (Stromeyer & Klein, 1975). Granger (1973) used a similar approach to account for Sachs' data.

It is not fully apparent that the amount of spatial summation could really be quantitatively explained by probability summation rather than by some more active "complex cell" type of summation. The problem (Stromeyer & Klein, 1975) was that the psychometric function seemed to be too steep to allow much probability summation. Probably the cleanest study of two-component summation was done by Graham and Robson (1987). They conclude that the spatial summation data is compatible with probability summation (based on the shape of the psychometric function). This conclusion is questionable. Their peripheral data (Fig. 4) show that the sum of a 6 c/deg plus a 6.3 c/deg grating is slightly less than 1.4 times as visible as each grating alone. The 1.4 factor is what one would have expected from a pooling exponent of *[3 = 2* (Stromeyer & Klein, 1975). The value of *(3* from the steepness of the psychometric function is higher. Three methods have been used to determine the steepness (slope) of the psychometric function:

Method 1 - 2AFC data

When gratings are detected using the two-alternative forced choice (2AFC) method and the data are fitted to a Weibull function (Quick, 1974), one typically finds that the Weibull exponent β is between 3 and 4. Nachmias, for example, found β 3 (Nachmias, 1981). A value of β 3 is not that different from β 2, which is needed to account for spatial summation as discussed in the preceding paragraph. The problem with this approach is that the theory connecting the 2AFC task to probability summation is not convincing. Nachmias (1981) points out that there is no obvious connection between probability summation and the psychometric function of a 2AFC task.

Method 2 - "Yes-no" data

Contrary to the 2AFC situation, the connection between probability summation and the β from a "yes-no" task is straightforward. The problem here is that the values of β obtained using the "yes-no" method are always higher than the 2AFC values. Nachmias (1981) found β_{y-n} 4.2 and β_{2AFC} 3.0. Thus the values of β from the psychometric function seem larger than the exponent needed (β 2) to account for the 2-grating summation data (Sachs et al., 1971; Graham & Robson, 1987). This difficulty results from ignoring criterion effects. A proper treatment needs signal detection analysis.

Method 3 - Signal detection

A signal detection method of constant stimuli is used to obtain a transducer function relating d' to contrast (d^1 c^n where n is the transducer exponent). We showed (Stromeyer & Klein, 1975) that the Quick pooling exponent, β, is twice the transducer exponent. The factor of 2 is present because the d' of independent mechanisms summate according to a Pythagorean rule. Since the transducer function was shown to be a strongly accelerating function with a transducer exponent of n 2 (Stromeyer & Klein, 1974; Nachmias & Sansbury, 1974), the corresponding Quick exponent is expected to be 2n = 4 (a very steep psychometric function). Thus our signal detection analysis agrees with the "yes-no" analysis that the psychometric function seems to be too steep to be able to account for the strong spatial pooling found in summation experiments. One explanation of the discrepancy is that the noise in the different mechanisms is not independent, but rather it is correlated. In that case, the d^1 of the mechanisms might summate linearly and the pooling exponent might be 2, in agreement with the spatial summation data. See Stromeyer and Klein (1975) for further discussion of this issue. Klein and Tyler (1991) argue that if the psychometric function is dominated by uncertainty effects, then the connection between summation and the psychometric function is similar to what has been discussed so far. The interrelationships between mechanism bandwidth, amount of summation, amount of uncertainty, and nonlinearity of the transducer function are difficult to untangle, but progress is slowly being made.

Before leaving bandwidth, two items should be pointed out: First, very few people actually ever believed that *very* narrow channels were used to take a local Fourier transformation, or that much of early visual processing was done in the Fourier domain. However, many people *thought* that there were many people who believed in narrow channels. So there never really was much of a debate. Secondly, physiological studies show that a very wide range of bandwidths are present in visual cortex (DeValois & DeValois, 1988). Psychophysical models do not deal with a multiplicity of bandwidths since that would provide too much freedom to the models and make it difficult to make predictions. We should learn how to place constraints on multiple bandwidth theories.

Recently, I have come back to the question of calculating the underlying bandwidths (Klein, 1989; Klein et al., 1990). The new approach is to compare thresholds for multipoles (derivatives of edges: edge, line, dipole, quadrupole) to thresholds for extended sinusoids. In this approach an edge is detected by mechanisms near the peak (4 c/deg) of the contrast sensitivity function (CSF), a line is detected by mechanisms where the CSF has a slope (on log-log axes) of -1 (10 c/deg) and dipole and quadrupole detection are based on mechanisms where the slope is -2 (16 c/deg) or -3 (22 c/deg). The idea is that a narrow bandwidth will reduce thresholds for sinusoids while a broad bandwidth will reduce thresholds for the local multipoles. The ratio of sinusoid sensitivity to multipole sensitivity should thus be directly proportional to the mechanism bandwidth. Details are to be found in Klein (1989) and in a detailed forthcoming paper .(Klein, 1991). One equation from Klein (1989) is $BW_c = (\pi/2)^{0.5}\ S_s/S_e$, where BW_c is the effective bandwidth of the mechanisms near the peak of the CSF, S_s is sinusoid sensitivity (the CSF) at its peak, and S_e is edge sensitivity (the reciprocal of the edge contrast at threshold, where edge contrast is twice the Michelson definition). This equation for bandwidth makes a peak detector assumption that the pattern will be detected when the most sensitive mechanism reaches threshold. The effective bandwidth differs slightly from the true bandwidth because of effects of probability summation. In order to make the connection between multipoles and sinusoids rigorous, our definition of bandwidth is based on the area under the normalized mechanism tuning function plotted on log axes. The $(\pi/2)^{0.5}$ factor is included to make our definition equal to the mechanism's standard deviation divided by its peak frequency in the limit of narrow bandwidth. Our finding was that the bandwidth of the edge detecting mechanism near the CSF peak is slightly broader than the Blakemore-Campbell bandwidth ($BW_{edge} \sim 0.7$) and the bandwidths for line, dipole and quadrupole gradually decrease to values slightly lower than the Blakemore-Campbell bandwidths (BW_{quad} 0.25). Blakemore and Campbell (1969) also found a decrease in bandwidth as spatial frequency increased, but their decrease was not as strong as that which we found. We believe that the difference is due to the effects of probability summation (Klein, 1991).

In a related approach, Campbell, Carpenter and Levinson (1969) used a single mechanism that had the bandwidth of the full CSF instead of using the multiple mechanisms of the channel model. Because of this broad bandwidth their predictions for the dipole and quadrupole thresholds would have been too high.

Channel independence

Of greater importance to models of spatial vision than the precise value of the underlying bandwidths is the notion that the underlying channels are independent. Independence of channels was the main message of the Campbell and Robson (1964, 1968) papers. Independence meant that a suprathreshold square wave could be discriminated from a suprathreshold sine wave when the third harmonic of the square wave reached its independent threshold. Stromeyer and Klein (1974) showed that the Campbell and Robson finding was not really correct. We found that the visibility of a third harmonic was *not* independent of the presence of a fundamental but could be strongly facilitated by the fundamental. Since this facilitation seemed to be taking place between well-separated spatial frequency channels our data seemed to spell the end of the independent channel

theory. Lange, Sigel and Stecher (1973) and Stecher, Sigel and Lange (1973) were also pushing the notion that the underlying channels were not independent. However, in a theoretical calculation (Stromeyer & Klein, 1974), we showed that a mechanism whose peak frequency was between the first and third harmonic was ideally situated to be just sensitive enough to both the suprathreshold fundamental and the subthreshold third harmonic to be able to account for our data. This notion of searching for the optimal mechanism is the basis of our viewprint approach (Klein & Levi, 1985) that will be discussed later. Our message was that one must be careful before jumping to the conclusion that channels are interacting. We showed that independent channels were able to produce data that looked like interactions. A result that would have shown a violation of independence is to have found that a fundamental facilitates a *fifth* harmonic. However, Stromeyer and Klein (1974) showed that whereas there was a strong facilitation between first and third harmonics, there was no interaction between a first and fifth. The data agreed with our theory.

A recent contribution to the Campbell and Robson story is the finding of Greenlee and Magnussen (1988) who did the square-wave, sine-wave discrimination after adapting to the third harmonic. They reasoned that if it was the third harmonic that did the discrimination (as suggested by Campbell & Robson) then the threshold for doing , the discrimination should be elevated. The results were opposite. There was no threshold elevation for the discrimination task, although there was a large threshold elevation for simply detecting the third harmonic. Greenlee and Magnussen's result is in agreement with what was discussed in the preceding paragraph, that instead of the third harmonic being responsible for discriminating a square wave from a sinusoid, a mechanism tuned to a frequency near the second harmonic is responsible. I conjecture that, after adaptation to the third harmonic, the optimal mechanism for the discrimination task will have a slightly reduced spatial frequency, but the discrimination threshold will hardly be changed at all. Verification of this conjecture by a calculation similar to that described by Stromeyer and Klein (1974) would provide further evidence that the standard channel model is valid, even in the face of results that at first seem contrary to its spirit. There are other instances of masking. Thomas (1989), for example, showed that a suprathreshold mask interfered with frequency discrimination at the second and third harmonic. A similar result using adaptation rather than masking was found by Regan and modeled by Wilson (Wilson & Regen, 1984) and will be discussed later. When one looks at the profile of these masked stimuli it is not at all surprising that their spatial frequency is difficult to discern. The high contrast lower frequency mask nearly obliterates the "character" of the test pattern. In a square wave one does not "see" the third harmonic. In terms of the channel story, the masking may not be surprising. Frequency discrimination would be accomplished by mechanisms about an octave below the test frequency, at the point where the tuning slope is steep. The presence of a lower harmonic would interfere with the steep descent of the tuning function. However, in a similar masking experiment, Regan (1985) found that the threshold elevation pattern was hugely affected by whether the mask was jittered. It looks like more data will be needed to pin down the effect of masking on frequency discrimination. These are important experiments since they provide important insights into the basis of suprathreshold perception.

In most examples of interaction between channels, the interaction falls off when the components are separated by more than two octaves. A striking exception to this rule was found by Henning, Hertz and Broadbent (Henning et al., 1975) and Nachmias and Rogowitz (1983). The beats produced by the amplitude modulated grating consisting of 8 + 10 + 12 c/deg components masked the fundamental at 2 c/deg. The effect spans more than two octaves, and it could undoubtedly be extended to a fundamental at 1 c/deg and masks at 9 + 10 + 11 c/deg which spans more than three octaves. It is easy to say that nonlinearities acting on the high contrast mask could turn the beat into a real grating. However, it is much more difficult to account for the specific phase effects that are found (Nachmias & Rogowitz, 1983). These results are still mysterious and are deserving of more study. They do not violate the independence assumption, since that assumption is only expected to hold for very weak stimuli (near threshold).

Strong interactions between spatial frequency channels have also been found in adaptation studies. Blakemore and Campbell (1970) reported that adapting to a square wave grating caused a threshold elevation at the third harmonic, as would be expected from independent channels. However, when examined closely their data show that the threshold elevation is less than would be expected from independent channels. Tolhurst (1972), and Nachmias, Sansbury, Vassilev and Weber (1973) found that the presence of the fundamental strongly suppressed the adapting power of the third harmonic. Stecher, Sigel and Lange (1973) also found strong finely tuned interactions between adapting frequencies. Klein and Stromeyer (1980) showed that what was going on wasn't simply

inhibition between spatial frequency channels. They showed that the inhibition only occurred when the relative phase between the first and third was fixed. When the phase was decoupled by jittering or moving one of the harmonics, then the full strength of the third harmonic's adapting power came back. Also, when the adapting pattern consisted of a first and fifth harmonic, the first did *not* inhibit the fifth (contrary to first plus third). A summary of their data was that whenever the third harmonic "appeared" as a separate grating, then its adapting power was strong. Klein and Stromeyer pointed out that a model involving inhibition between different *phases*, rather than different frequencies, could account for all of the data. A different hint of possible inhibition between spatial frequency channels is the finding by Tolhurst and Barfield (1978) and DeValois (1977) that, after adapting to a simple fundamental, the third or fourth harmonic is *facilitated* (this is in the opposite direction to Olzak's [1985] finding). Klein and Stromeyer (1980) looked for this facilitation using a signal detection methodology but were unable to find a significant effect. Greenlee (1990) also failed to find any facilitation. This failure to find a facilitation effect provides support for a simple fatigue explanation of selective adaptation.

Many of these interaction effects were summarized in a review article by Kelly and Burbeck (1984). The naive reader of the Kelly and Burbeck review would probably be left with the belief that the independent spatial frequency channel story was in a state of shambles. The real message should have been that at suprathreshold levels nonlinearities are present that produce interactions. The real test for the independent channels conjecture is in the case where all components are near threshold.

The one contender for a violation of independence *at threshold* is the results of Olzak (Olzak & Wickens, 1983; Olzak, 1985) and Hirsch (Hirsch et al., 1982). They found that the presence of a *threshold* fourth harmonic reduced the visibility of the fundamental. This experiment was run using a variety of methodologies and the surprising results were consistent across methods. However, Klein (1985) offered a critique of all the methodologies that were used and showed that cognitive factors could have produced results that looked like interactions between spatial frequency channels. This is a very important subject that needs to be clarified. Unfortunately, it is difficult to think of clear-cut experiments that would do the job.

In summary, I know of no evidence in which the independence hypothesis breaks down for stimuli near threshold. For suprathreshold stimuli the story is complicated. It might be that the only interaction between channels is a simple gain control. It is also possible that for suprathreshold stimuli the interactions are so involved that the channel concept loses meaning. This latter possibility is what one would suspect; however, our adaptation studies (Klein & Stromeyer, 1980) and our masking studies (Stromeyer & Klein, 1974) with first and fifth harmonics provide evidence that the independent channel concept is still useful for suprathreshold stimuli. Further studies are still needed to clarify the suprathreshold interactions.

Connection between the detection channels and suprathreshold discriminations

Spatial frequency channels were not only supposed to account for the visibility of spatial patterns, they were also supposed to explain the appearance of patterns. An example is perceived spatial frequency. Blakemore, Nachmias and Sutton (1970) found that after adapting to a sinusoid, a subsequently presented sinusoid had an apparent spatial frequency that was shifted away from the adapting pattern. They explained this change in appearance as being due to fatigue of the size-selective Blakemore-Campbell channels (1969). Klein, Stromeyer and Ganz (1974) replaced the adaptation paradigm with a simultaneous center-surround stimulus in which the surround grating induced a spatial frequency shift in the center grating. However, the surround did not affect the detection threshold of the center. This decoupling between threshold elevation and frequency shift threw cold water on any simple connection between the underlying mechanisms and judged size. An equally important complication was that in the adaptation case (as well as the center-surround case) the spatial frequency range of the shift effect was larger (about 2 octaves from the adapting pattern) than the range of the threshold elevation effect (about 1 octave from the adapting pattern). This discrepancy is also present in the attempt by Wilson and Regan (1984) to predict the shift in a "blind" application of Wilson's model (the data had a broader extent than the "blind" prediction). Even though the "blind" calculation did not get the bandwidth right it was a pretty good attempt. Also, it might not be fair to test the channel model on a perceived size paradigm, since we know that the judgement of perceived size is a very complicated affair, influenced by cognitive factors, such as size constancy. It seems clear that the judgement of perceived spatial frequency requires a second stage of pooling (Klein et al., 1974) across spatial frequencies following the stage based on the

Blakemore-Campbell channels. Rather than applying the channel model to the appearance of patterns, it is sounder to ask whether independent channels might account for the *discrimination* of suprathreshold patterns, as considered next.

We would like to determine whether the detection channels can account for suprathreshold discriminations. It seems reasonable to try to predict a task for which the human visual system is performing at its best. The task I would like to consider is bisection. The bisection threshold is better than 1 part in 60, so that for line separations of about 1.5 min, thresholds are better than 1.5 sec (Klein & Levi, 1985). This is close to the best spatial discrimination that can be performed by the visual system, so we wondered whether Campbell's spatial frequency channels , can be used to predict these hyperacuity thresholds. The one encouraging factor is that many hyperacuity tasks show that thresholds are proportional to the separation of the features. This "Weber's Law" for separation does not seem natural for a model based on the positions of the features, but it does seem reasonable for a model based on the size of the pattern (the distance between features). Klein and Levi (1985) showed that their "viewprint" model based on spatial frequency channels has just the right properties to be able to account for the data. We now present the highlights of the viewprint model since we believe it embodies the essence of Campbell's insight that started the spatial frequency approach.

The essence of the viewprint approach is that there are lots of mechanisms with different spatial positions and sizes. In addition the eyes are jiggling, so the absolute position of any feature cannot be accurately specified. In the viewprint model, absolute position is lost while relative position is maintained by having the mechanisms come in quadrature pairs (officially called Hilbert pairs). The Pythagorean sum of the output of the pair eliminates phase and maintains intensity just as does the Pythagorean sum of a cosine plus a sine. We developed the Cauchy functions (Klein & Levi, 1985; Klein, 1989) to simplify the Pythagorean sums. It is possible to do viewprint calculations with functions other than Cauchy functions as was shown by Stromeyer and Klein (1975).

A viewprint is familiar to anyone who reads music. The standard 5-line music notation with open and filled ovals is a temporal viewprint and it applies equally well to the spatial domain (Klein & Levi. 1985). Frequency is plotted along the vertical axis and position along the horizontal. This representation is useful because a musician can accurately choose the frequency of a note but not its phase. Local phase is ignored in this representation. Coarse phase is preserved by the sequence of notes. The same representation is called a voiceprint or a spectrograph and is used to show the formants of human speech and to describe birdsong. Details are presented elsewhere (Klein & Levi, 1985). The main point of this approach is that, in order to predict threshold for suprathreshold discriminations, there are many mechanisms that must be checked to determine which is optimally positioned to be most sensitive for doing the discrimination. For the task of judging the interval between two closely spaced lines (say 5 min apart), the optimal mechanism is probably a symmetric mechanism located halfway between the two lines. The size of the optimal mechanism would be such that the lines fall on the mechanism's zero crossings (a pair of zero crossings spaced at 5 min corresponds to a peak spatial frequency of about 6 c/deg). The Pythagorean sum of this mechanism and its antisymmetric partner would be zero since neither mechanism would be stimulated. A small shift in the positions of the two lines, keeping the separation fixed, would not cause a big change in the output. However, the slightest change in the line spacing would cause the output to be nonzero. This "nullpoint" mechanism seems able to account for the exquisite hyperacuity thresholds (Klein & Levi, 1985) even while the eye may be shifting its direction of gaze. Exactly this same strategy of examining a range of mechanisms to find the one that is optimal was used by Stromeyer and Klein (1974) to account for the facilitation of a third harmonic by the first. The process of predicting thresholds based on the *optimal* mechanism is a highly nonlinear process, so it is easy to be surprised and discover that independent channels are capable of sophisticated discriminations. Before eliminating the independence hypothesis one must examine the possibility that there exists a mechanism with just the right tuning properties to be able to account for the task without interactions between separate channels.

Unfortunately, the model of Klein and Levi (1985) is too simple. The following gedanken experiment shows the problem. Consider what should happen to thresholds in the bisection task as a function of contrast (line luminance). At high contrast the optimal mechanism will be positioned near the null point where it is barely stimulated, so that it is operating at its most sensitive point such that the slightest change in the line separation will cause the mechanism to be strongly stimulated. If the line contrast is doubled by increasing the line luminance then the bisection threshold should be halved. Based on linearity, a half-sized shift of a double strength line should produce the same differential response in the optimal mechanism. This gedanken

experiment shows that bisection thresholds should be inversely proportional to the line strength. The data disagree. Interval discrimination thresholds are relatively independent of contrast (Morgan & Regan, 1987) (contrary to vernier acuity). In the Klein and Levi (1985) paper, the problem of bisection predictions being too good was prevented by introducing a blurring stage at the output of the viewprint so that nonoptimal mechanisms would contribute to the pooled response. I suspect that a better way to deal with this problem is to introduce a nonlinear gain control for the mechanism sensitivity, in which the gain would depend on the activity of neighboring mechanisms with different sizes and positions.

We have recently been pursuing a new approach for predicting spatial discriminations based on detection data. Rather than using sinusoids to set the sensitivity of the underlying mechanisms, we avoid many of the modeling assumptions by using detection stimuli that are similar to the stimuli used in the discrimination task. For example, vernier acuity of an edge can be thought of as the detection of a line superimposed on the edge. The addition of the properly placed line will shift the edge. Similarly, vernier acuity of a line can be produced by adding a dipole to the line. Our hypothesis is that the vernier threshold of an edge can be predicted from the detection threshold of the line and the line vernier can be predicted from dipole detection. We found (Klein et al., 1990) that at low pedestal strengths (edge contrast) the hypothesis is pretty good, and at higher pedestals the vernier threshold is elevated, as might be expected from the gain control mechanism discussed in the preceding paragraph. Very recently we found a violation of this hypothesis. We found that for very short lines (3' and 6') the vernier thresholds are lower than the dipole detection threshold. We suspect that in these cases of short lines, vernier acuity might be limited by contrast discrimination rather than contrast detection. The dipper function allows contrast discrimination to be better than contrast detection.

The final example on spatial discrimination clarifies the domain in which spatial frequency channels are used. As mentioned earlier, bisection thresholds are proportional to the dot separation. Two hypotheses for this result are: 1) Relative positions are judged using spatial frequency channels. Widely separated dots would involve the larger filters whose large size makes them less sensitive to small changes in, the dot separation. 2) Rather than the judgement being based on the relative position of the dots, it might be based on the absolute position with the separation judgement being done at a later stage. The decrease in interval discrimination for large separations would be due to the outside dot being in the periphery where spatial sampling, and thus position judgements, are poorer. In a series of studies (Klein & Levi, 1987; Levi & Klein, 1990) we showed that, for separations that are less than about half of the eccentricity of the outside dots, the relative position determines threshold (hypothesis #1 - the filter regime), while for larger separations the position threshold is determined by the eccentricity (hypothesis #2 - the local sign regime). Some of our experiments were done on an iso-eccentric arc to separate the two regimes and the results clearly showed the two regimes.

Our present models are good to about a factor of 3 in predicting thresholds. We need to do much better. When our predictions are consistently within 50% of the data we will begin to have confidence that we understand what is going on. Although more work is needed on the quantitative details, the general channels approach and the viewprint representation of visual images seems on the right track. The viewprint representation is ideal for preserving high quality information about relative position without needing an accurate representation for absolute position. I believe that the spatial frequency channels proposed by Campbell and Robson, which enable our visual system to recognize small objects in the presence of eye movements, will continue to play a central role in our modeling.

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