

THE CODING OF VELOCITY OF MOVEMENT IN THE HUMAN VISUAL SYSTEM

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Abstract—A very simple model of velocity perception which requires only 17 channels is outlined. The important points of the model are that: (1) in each direction of movement just two temporal frequency channels are necessary at any spatial frequency, (2) at low temporal frequencies the spatial frequency domain is encoded by many channels, but only those at low spatial frequencies are direction-specific. Using a detection/discrimination technique the supposition that channels which detect high spatial, low temporal frequencies are not direction specific is investigated. Possible reasons for the apparent non-directional behaviour of these channels are investigated: the notion that non-directionality reflects a failure of the stimulus to travel some threshold distance across the retina is rejected, but the proposal that a velocity threshold must be exceeded before the direction of a grating may be identified at detection threshold remains a possibility.

INTRODUCTION

Over the past fifteen years, researchers in the field of spatial vision have provided good evidence that there exist within the human visual system many narrowly tuned spatial channels. However, in the same period our knowledge of the mechanisms underlying movement perception has not made such impressive progress. This paper seeks to review a little of the research on temporal tuning of channels, will propose a minimal model and will describe some experiments which test and refine the model.

It has long been known that the temporal tuning in the visual system does not share the same characteristics as spatial tuning. Whereas adapting to a stationary sinewave grating gives rise to threshold elevation which is narrowly tuned around the adaptation frequency, (Blakemore and Campbell, 1969), adapting to temporal flicker produces very broadly tuned threshold elevation, (Smith, 1970). Furthermore the tuning of the size aftereffect, (Blakemore and Sutton, 1969), is very different from the tuning of the velocity aftereffect, (Thompson, 1980); and while the spatial frequency of a grating does not alter during inspection, (Blakemore and Sutton 1969), the perceived rate of movement of a pattern decreases dramatically as it is inspected, (Wohlgemuth, 1911).

Although broadly tuned, channels for movement have been shown to be directionally specific by Levinson and Sekuler (1975) in a most elegant set of experiments. More recently Watson *et al.* (1980) have shown that the direction selectivity of these channels is not so simple; results of subthreshold summation experiments indicated that although low spatial frequency gratings moving at high temporal frequ-

encies did appear to be detected by direction-specific channels, slow-moving gratings of high spatial frequencies appeared to be detected by non-directional mechanisms. Examination by Watson *et al.* (1980) of the discriminability of moving gratings at detection threshold, the detection/discrimination difference, confirmed this view; the direction of movement of low temporal frequency gratings cannot be accurately determined at detection threshold whereas that of low spatial, high temporal frequency gratings can.

Watson and Robson (1981) have also used the discriminability of patterns at their detection thresholds to investigate the spatio-temporal tuning of channels. The logic of this technique is well known, see for example Nachmias and Weber (1975), Thomas (1982): if a stimulus at detection threshold is detected by the single channel which is most sensitive to it, and if the principle of univariance applies, then for two stimuli to be discriminated from one another at their respective detection thresholds, they must excite different "labelled" detectors. Watson and Robson took two slices through both the spatial and temporal dimensions, determining just noticeable differences of spatial and temporal modulation at detection threshold. For stationary gratings they found that 7 channels were needed to span the spatial domain, each separated from its neighbour by about 1 octave. At a high rate of counterphase modulation, 16 c/sec. discrimination performance fell, and just 3 channels were required. In the temporal domain they found that, both at low and high spatial frequencies just 2 channels were required.

We can now construct the crude model shown in Fig. 1. It portrays a spatio-temporal space incorporating a single meridian of movement, i.e. it applies only to one-dimensional patterns. The chan-

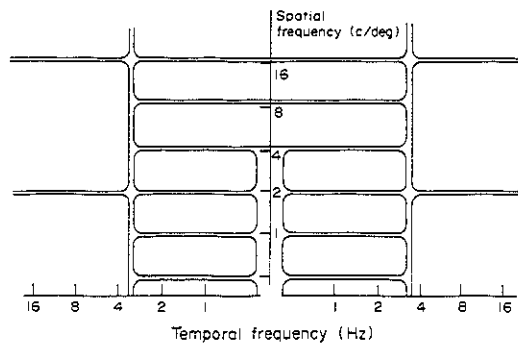


Fig. 1. A simple model of velocity coding. See text for details. Note that both axes are logarithmic in accord with the accepted representation of spatial and temporal frequency. Stationary stimuli are envisaged as lying along the central ordinate.

nels are shown to occupy the spatio-temporal area over which they are the most sensitive mechanism, the channel which will detect stimuli at contrast threshold. At suprathreshold levels the overlap in sensitivity of neighbouring channels will be considerable.

The main features of the model and the research which has promoted their inclusion in the scheme shown in Fig. 1 are:

(1) At all spatial frequencies just two temporal channels are proposed for each direction of movement. This follows the findings of Watson and Robson (1981) and Thompson (1982a, b; 1984). Rothblum (1982) has also provided strong evidence for a minimum of two spatio-temporal channels at any given spatial frequency.

(2) At low temporal frequencies there are many spatial channels as suggested by many studies, Blakemore and Campbell (1969), Graham and Nachmias (1971); the number shown is 7, in accord with the minimal requirements of Watson and Robson (1981). That the number of spatial channels is small is in accord with the work of Wilson, (see for example Wilson and Bergen 1979, Gelb and Wilson 1983), and is consistent with the "scalloping" found in spatial frequency discrimination reported by Hirsch and Hylton (1982a, b) and Yager and Richter (1982).

(3) At high temporal frequencies just 3 spatial channels are required, again from Watson and Robson (1981). That spatial tuning broadens at high temporal frequency is supported by Graham (1972).

(4) All the high temporal frequency channels are direction-selective. This notion has been suggested by Levinson and Sekuler (1975) and Watson *et al.* (1980).

(5) At high spatial frequencies the "slow" spatial channels are not directionally specific. The idea that some channels are non-directional is not new: it has been put forward by Levinson and Sekuler (1974), and Watson *et al.* (1980) obtained data which

suggested that slowly moving, high spatial frequency gratings are detected at threshold by non-directional channels. The division of the 7 spatial channels into 4 direction-specific and 3 non-specific channels is somewhat arbitrary. The rationale is that Watson *et al.* found that at low temporal frequency (1.5 Hz) the contrast sensitivity of counterphase gratings at a spatial frequency of 8 c/deg was approximately as predicted by channels non-selective for direction. At 4 c/deg their data fell almost exactly between the direction selective and non-selective predictions: (see Watson *et al.*, 1980, Fig. 3).

The present paper will examine one aspect of this model in more detail; namely the non-directional channels proposed to encode slow moving high spatial frequency gratings. Watson *et al.* (1980) examined detection/discrimination thresholds at just two spatial frequencies, 2 and 8 c/deg. Their stimuli were all of the same short duration, 410 msec, and there remains the possibility that direction specificity was not found because some threshold distance was not traversed by the slow-moving stimuli in such a brief presentation period.

Lennie (1980), who carried out a similar experiment to that of Watson *et al.* (1980), with similar results, makes a slightly different suggestion for the apparent non-directional nature of some channels; namely that it is the velocity of the grating which determines whether or not direction will be discernible at threshold. Lennie suggests that from his results, obtained at 3 spatial frequencies, it appears that at velocities greater than 0.4 deg/sec direction of movement can be discriminated at detection threshold.

METHODS

Sine wave gratings were generated by computer on the screen of a Joyce Electronics display with P4 phosphor. Details of the system software have been described elsewhere, Runciman (1981). All stimuli were shaped in space, with a gaussian profile along the X-axis and a raised cosine along the Y-axis. This shaping ensured that there were no edges to the stimuli which might have enabled their discrimination on the basis of some cue other than rate of movement. Stimuli were also shaped in time. "Short" stimuli were shaped by a temporal gaussian of 1.2 sec duration, 0.38 sec above half amplitude. "Long" stimuli were shaped by the same gaussian with a 1.0 sec plateau inserted at peak amplitude—therefore the long stimuli were 2.2 sec in duration, 1.38 sec above half amplitude. Subjects sat 263 cm from the screen with subtended 7×5 deg of visual angle. Subject PT used a bite bar to restrict head movement during the experiment, PS used a forehead rest. A small spot on the screen was provided for fixation. Viewing was binocular.

A detection/discrimination procedure was used to determine whether opposite directions of movement

were detected by independent mechanisms at detection threshold.

Detection thresholds for oppositely moving gratings were established using a two-interval forced choice procedure. A staircase, modelled on that described by Graham *et al.* (1978) determined thresholds. Once detection thresholds have been established, the method of constant stimuli was employed, 4 contrast levels of each of the opposite directions of movement being chosen to span their detection thresholds. Again a two-interval forced choice procedure was used, the subject having to determine the interval containing the stimulus, the detection task, and to identify the direction of movement, the discrimination task. In each experimental session each stimulus was presented at each of its 4 contrast levels 50 times. From the subject's responses frequency of detection and frequency of discrimination curves were plotted, the curves through the data being optimised by a maximum likelihood method described by Watson (1979). The contrasts which yielded 82% detection and 82% discrimination were chosen as detection and discrimination thresholds.

RESULTS

Gratings of 5 different spatial frequencies, 1, 2, 4, 8 and 16 c/deg and 4 different temporal frequencies, 1, 2, 4 and 8 c/sec were investigated, although not all possible combinations were pursued. The difference between detection and discrimination thresholds, the sensitivity difference, has been plotted against spatial frequency in Fig. 2. Sensitivity differences approaching zero indicated that independent mechanisms for opposite directions of movement are responsible for detecting the stimuli; Watson and Robson (1981) reported that a sensitivity difference of 1 dB or less coincided, on nearly all occasions, with a failure to reject the hypothesis that different labelled detectors were responsible for the detection.

The results show that for both the short and the long stimuli the sensitivity difference increases with increasing spatial frequency and falls with increasing temporal frequency. There is, however, no statistically significant difference between short and long stimulus duration. These results dismiss the possibility that the reason for the lack of direction selectivity found in slow moving stimuli is the failure of the stimuli to move a sufficient distance during the presentation interval. Lennie's proposal that some velocity threshold marks the divide between directional and non-directional behaviour remains a possibility. It is certainly true that as velocity drops direction selectivity disappears, but it is less clear that velocity is the only critical variable. This is demonstrated by Fig. 3 which plots the detection/discrimination differences as a function of temporal frequency. The temporal frequency at which the function drops below 1 dB does increase

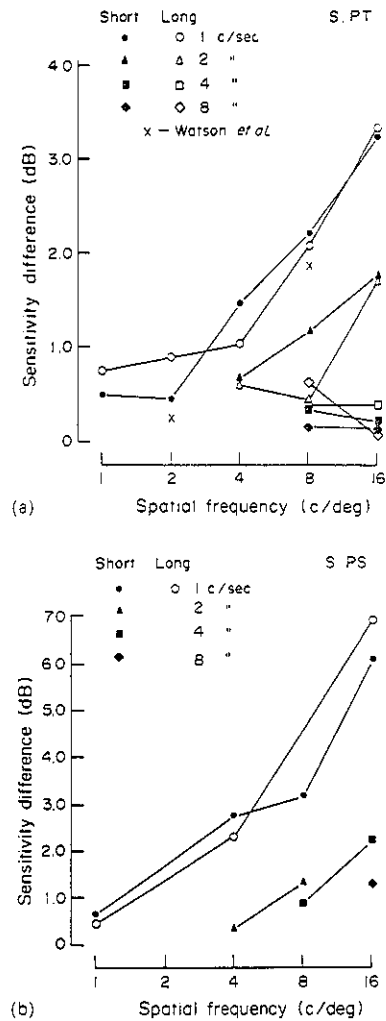


Fig. 2. Detection/discrimination threshold differences as a function of spatial frequency. Short stimuli were 1.2 sec, 0.38 sec above half amplitude; long stimuli were 2.2 sec, 1.38 sec above half amplitude—see method for further details. The data from Watson *et al.* (1980) were collected in a similar experiment on subject P.T. Their gratings were moving at 1.5 c/sec and were presented for 410 msec.

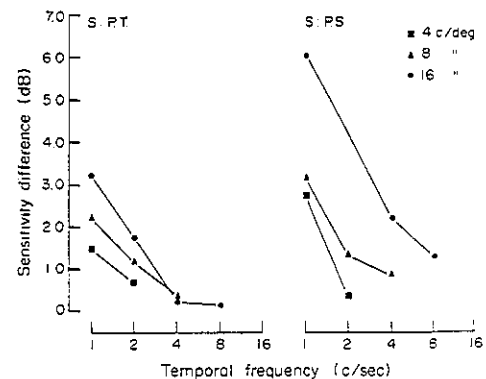


Fig. 3. Detection/discrimination threshold differences as a function of temporal frequency. Some of the "short" data from Fig. 2 replotted to show that the temporal frequency at which discrimination may be made at threshold increases with increasing spatial frequency.

with increasing spatial frequency, but it may not occur at constant velocity. For subject P.T. the detection/discrimination difference is 1 dB for a velocity of 0.38 deg/sec at 4 c/deg, 0.29 deg/sec at 8 c/deg and 0.18 deg/sec at 16 c/deg. For subject P.S. the results show the 1 dB difference occurring near 0.4 deg/sec at 4 and 8 c/deg; at 16 c/deg data were not obtained indicating discrimination at threshold, but extrapolating from the results available it appears that the 1 dB difference would occur around 0.6 deg/sec. Lennie reported a significant difference in this detection and discrimination thresholds at about 0.4 deg/sec for 0.5, 2 and 8 c/deg.

DISCUSSION

Increasing stimulus duration does not affect the detection/discrimination difference of gratings moving in opposite directions. This rejects the idea that the direction of some moving stimuli cannot be discriminated at detection threshold because they fail to traverse some threshold distance across the retina. For if this explanation were correct, then increasing stimulus duration should improve direction discrimination, and this result was not found. It is, of course, still possible that there is some threshold distance to be exceeded before directionally selective channels operate, but the present findings demand that any such threshold must occur at shorter distances than those involved in this experiment and therefore cannot be responsible for the non-directional behaviour observed.

It should be noted that the long stimuli were easier to detect than the short stimuli, typically by about 2 dB. The contrasts at which direction discriminations were made were therefore lower for the long stimuli than for the short. Presumably probability summation over time, (Watson, 1979; Burr, 1981), is responsible for this increased detectability. It might be argued that the detection/discrimination difference of the long stimuli was equal to that of the short simply because in each duration of exposure the stimulus exceeded threshold for some short period of time. However this seems unlikely as both subjects reported that even at detection threshold the perceived duration of the long stimuli was far greater than that of the short stimuli.

From the data reported here it may still be unnecessary to postulate functionally different channels at low and high temporal frequencies, even though the latter appear to be non-directional at threshold. There are several possible reasons for this behaviour: Lennie suggests that "... this happens simply because their velocities are generally too low". (Lennie, 1981, p. 33), but it is not clear how simple this possibility is. If the detecting channel is "labelled" as a directional channel, then the velocity of the stimulus is immaterial; if the suggestion is that at detection threshold the detecting channel is non-

directional at some velocities and directional at others, then a more complex model of the detection and discrimination of stimuli is required.

Some evidence against a simple velocity threshold for direction discrimination at threshold has come from Nachmias *et al.* (1978) who investigated the consequences for detection/discrimination differences of reducing stimulus duration. They found that at very short exposures, some as brief as 10 msec, the detection/discrimination differences did suffer: this is not surprising for in the limiting case of a single frame exposure the discrimination task must become impossible. However stimulus velocity was not the only crucial variable; when examining gratings moving with constant velocity, 0.75 deg/sec, it was found that reducing exposure duration impaired the discriminability of 2 c/deg gratings at threshold far more than those of 8 c/deg.

A second possibility, that eyemovements are responsible for the apparent non-directionality of some channels has been tackled by Mansfield and Nachmias (1981) who were able to replicate the findings of Watson *et al.* (1980) under conditions of stabilisation with an SRI Dual Purkinje-Image Eyetracker. They concluded that it was unlikely that eyemovements were responsible for the non-directional behaviour of channels detecting slow-moving gratings.

A different proposal might be that at all spatial frequencies the low temporal frequency channels have a direction preference but that they respond, to some extent, to slow movement in the opposite direction. If the limit of this sensitivity to the "null" direction were some constant velocity then, in temporal frequency terms, the overlap of sensitivity of oppositely tuned slow channels would be small at low spatial frequencies and large at high spatial frequencies, see Fig. 4. For example, suppose all low temporal frequency channels were sensitive to their null direction at velocities below 0.3 deg/sec, then at 0.5 c/deg the temporal frequency limit would be 0.15 c/sec whereas at 16 c/deg the limit would be

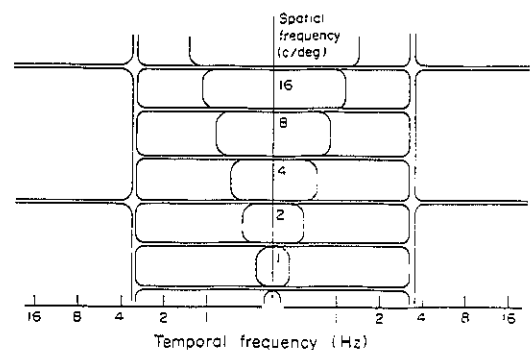


Fig. 4. A modified model of velocity perception. The non-directional channels of Fig. 1 are replaced with pairs of direction-labelled channels with similar sensitivities at low velocities.

4.8 c/sec. These channels could remain as directionally labelled channels: at high spatial frequencies however, slow-moving stimuli at threshold could be detected by either of two different channels labelled for opposite directions of motion, and their direction would not be discernable. Clearly the differences between the type of model illustrated in Fig. 4 and one including non-directional channels, as in Fig. 1, need to be explored.

In conclusion, the present paper provides some data to modify the simple model described in Fig. 1; further experiments are in progress to ascertain the nature of channels detecting slow moving high spatial frequency gratings and it is to be hoped that additional refinements to the model will be forthcoming.

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