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FACTORS INFLUENCING VELOCITY CODING IN THE HUMAN VISUAL SYSTEM

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Abstract—Differential velocity detection in the fovea was measured over a wide range of velocities (0.25–256°/sec). Differential thresholds were minimum (about 6%) for intermediate velocities (4–32°/sec). Velocity judgements were shown not to depend on duration judgements. The U-shaped curve relating differential velocity detection and velocity was preserved at different background levels and different contrasts. The physiological correlates of these observations are discussed.

INTRODUCTION

This paper is concerned with the ability to detect small differences in velocities of moving objects. In a recent study on differential velocity detection in the fovea, McKee (1981) showed that velocity detection is generally better than the ability to detect differences in the total duration a target takes to cross a fixed distance. She further showed that the differential velocity threshold expressed as fraction of the velocity at which the threshold was measured, decreased with increasing velocity (range explored 0.5 to 12°/sec). She concluded that there is a local mechanism detecting velocity and that this mechanism improves in performance with increasing velocity: for velocities over 2°/sec the differential thresholds were only 5%. Since McKee (1981) using an oscilloscope display could not investigate fast velocities, we measured differential velocity detection at velocities up to 256°/sec using a mirror system. Our experiments show that the differential velocity sensitivity is a U-shaped function of velocity. In order to test to what extent the shape of this function depends on other stimulus variables we have manipulated some of them. In particular we have measured differential velocity detection at reduced contrast levels. Under these circumstances we believe (see van der Glas *et al.*, 1981), that the number of active cells is reduced thereby unmasking the most sensitive part of the differential detection mechanism i.e. the parameter range in which most cells operate. This manipulation confirms that the differential velocity detection is most sensitive at medium velocities. The possible physiological correlates of these observations will be discussed.

METHODS

The moving stimulus in these experiments was a bright narrow (0.2°) vertical light slit, 7° long projected onto a polacoat screen. The standard background illumination was 0.03 cd/m^2 but could be reduced to 0.00003 cd/m^2. Standard stimulus luminance was 130 cd/m^2 so that with the standard background illumination contrast was very high ($\log \Delta I/I = 3$). The slit was moved by moving a mirror under control of a microprocessor. The mirror moved in discrete steps but the programmed steps were below the spatial and temporal resolution limits of the visual system (1 min arc and 10 msec). This processor also controlled a shutter allowing presentation of a stationary slit for different durations. To avoid that sounds associated with opening or closing of the shutter would provide duration information we used masking with acoustical white noise. For a given velocity the stimulus duration (Table 1) was determined in two ways. For velocities of 4°/sec and more the window width was actually 0.2° narrower than indicated in Table 1 so as to limit exposition time of a slit 0.2° wide to the durations listed in Table 1. For slower velocities this would have resulted in a too narrow window and for velocities of 2°/sec or slower the stimulus duration was set by closing of the shutter. The velocities and durations were checked by photocell-oscilloscope measurements and the light levels by photomultiplier measurements. Subjects viewed the stimuli appearing

Table 1. Stimulus conditions

Velocity (deg/sec)	Distance (m)	Window width (deg)	Duration (msec)
0.25	3.42	0.1	400
0.5	3.42	0.2	400
0.5	3.42	0.1	200
1	3.42	0.2	200
2	3.42	0.4	200
4	1.71	0.6	200
8	1.71	1.4	200
16	1.71	3.0	200
32	0.57	6.2	200
64	0.57	12.5	200
128	0.57	12.5	100
256	0.57	12.5	50

in a window binocularly with natural pupils at a distance ranging from 0.6 to 3.4 m depending on the requirements of the experiments (Table 1). Four subjects participated in this study: J.D.W. had normal vision, E.F., H.J. and F.V.C. were corrected myopes. Attempts were made to reduce the eye movements. Slits moved horizontally either left- or rightwards in random order so that predictive eye movements were unlikely. The subjects fixated a fixation spot before presentation of the moving target. For most stimulus conditions the movement duration was 200 msec or shorter. This is roughly the latency of eye movement (Westheimer, 1954) so that one can assume that slit motion is about equal to retinal image motion for most movements.

The psychophysical testing is very similar to that described by McKee (1981). The basic procedure is a variation of the method of constant stimuli in which seven velocities, equally spaced in a small range around the reference velocity, were presented to the subject. The subject had to judge the stimuli as faster or slower than the mean of the seven velocities. Each experimental run was a block of 280 trials and each threshold is based on two experimental runs corresponding to the same condition. Before each experimental run training was given in which only 2 velocities, symmetrical around the reference velocity, were presented. The interval between those 2 velocities was reduced until the performance of the subject fell below 90% correct responses. The narrowest interval for which the subject reached 90% correct responses was used as range for the testing in the experimental run. For the second experimental run of the same condition the same interval was used and training was only given with the two extreme velocities of that interval. Conditions of one curve or one set of curves were counterbalanced by testing the first experimental run of all conditions in random order before testing the second run of the same conditions again in random order. Subjects were given considerable training in velocity detection before they were allowed to participate in these experiments. Each threshold is based on 560 responses and its defined as the velocity increment corresponding to a difference between 50% and 75% response levels, estimated from the normal cumulative curve fitted to the psychometric functions by probit analysis.

RESULTS

Velocity detection for a high contrast slit at mesopic background levels

As in McKee (1981) we disentangle the contribution of timing to velocity judgements by measuring differential thresholds for both. Both differential thresholds are expressed as Weber fraction of the reference velocities ($\Delta\omega/\omega$) or durations ($\Delta t/t$). Figure 1 shows these Weber fractions of velocity plotted as a function of increasing reference velocity under our standard experimental conditions (see Methods). For reference velocities between 0.5 and 64°/sec the duration of movement remained constant (200 msec) as window width was increased with increasing velocity (Table 1). Despite this constant duration, velocity thresholds decreased from 11% or 15% for a velocity of 0.5°/sec to a constant value between 5 and 7% for velocities over 4°/sec. Over 2°/sec differential velocity thresholds are much lower than the differential duration threshold which was 16%, 22% and 23% for F.V.C., J.D.W. and H.J.

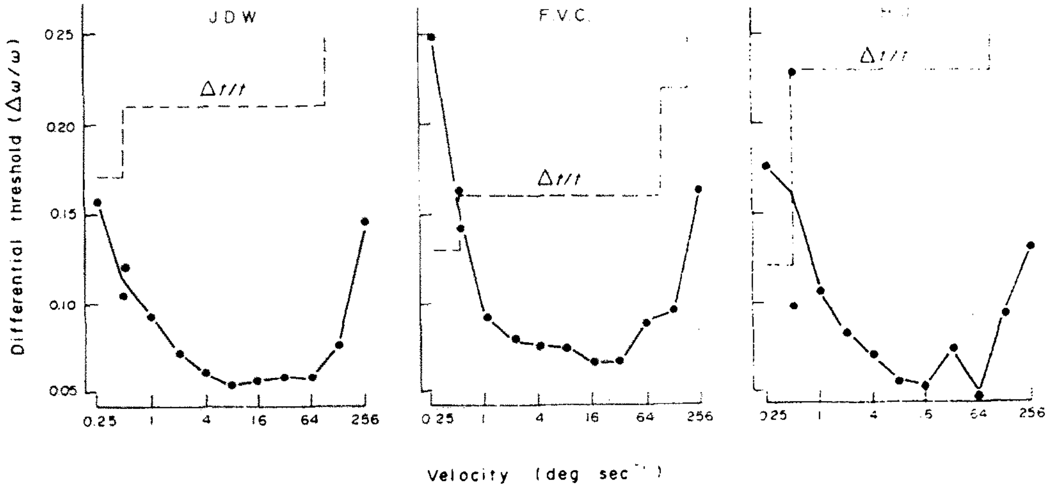

Fig. 1. Just noticeable differences in velocity, expressed as Weber ratios and plotted as a function of stimulus velocity. Standard conditions (see Methods). The differential threshold at 0.5°/sec was measured for two durations: 200 msec (upper datapoints) and 400 msec (lower datapoints. The differential duration thresholds for durations used in velocity judgement experiments are given in Fig. 7 (curve $\log \Delta I/I = 3$). Those below 0.25 are indicated by the stippled lines in this figure.

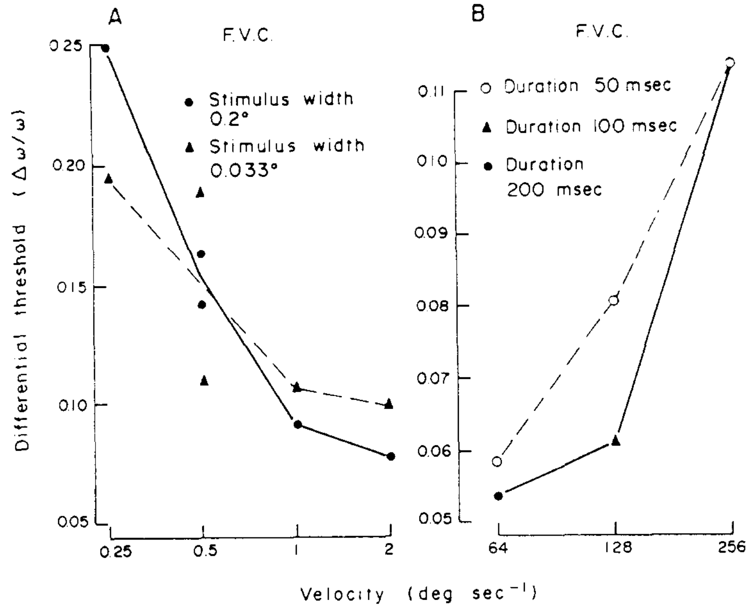

Fig. 2. (A) Just noticeable differences in velocities plotted as a function of velocity for 2 stimulus widths (0.2° is the standard width). (B) Just noticeable differences in velocity plotted as a function of velocity keeping either duration (stippled line) or length of movement (full line) constant. Same conditions as in Fig. 1.

respectively. These results are in full agreement with those of McKee (1981) and McKee and Nakayama (1982). At the lowest velocities tested, window width had to be reduced below the slit width to keep stimulus duration short enough (Table 1). Despite this, these velocities elicited a clear motion percept, but velocity judgements were poor (ratios of 10 to 25%). At the higher end of the velocity range, velocity judgements got worse again, the Weber fractions increasing from 5 to 7% to values of 10 to 15% at 256°/sec. Thus, under our basic experimental condition the differential velocity sensitivity is thus a U-shaped function of velocity with a minimum between 4 and 32°/sec.

At low velocities (1°/sec or less) given the slit width of 0.2° only the light edge crossed the window. At faster velocities both edges crossed the window. These differences may explain some of the increase in velocity JNDs with slower velocities. Therefore we performed a control experiment with a narrower slit (0.033°). As shown in Fig. 2(A) differential velocity sensitivity improved with increasing velocity both with the narrower slit and with the standard slit. Both Figs 1 and 2(A) show that at slow velocities longer durations improved the velocity judgements (compare the 2 durations at 0.5°/sec). The high velocities (128°/sec and 256°/sec) in Fig. 1 were obtained by reduction of duration (Table 1). The uprising of the JND-velocity curve could therefore be attributed to this reduction in duration. In a control experiment the differential velocity thresholds were measured at the three highest velocities 64, 128 and 256°/sec keeping either window width constant (12.5°) or duration constant (50 msec). As shown in Fig. 2(B) thresholds increases with velocity under both conditions. Thus differential velocity sensitivity decreases with velocity increasing over 64°/sec. In addition this control experiment confirms that longer stimulus duration at a given velocity improve the subjects performance especially at the extremes of the velocity range.

Since for a given reference velocity the movement amplitude was set by the window width, the small variations in velocity around the reference were obtained by small changes in duration around the mean duration. In order to test whether subjects could use this duration information in their velocity judgements one has to compare differential velocity thresholds with differential duration thresholds measured at the same duration and under similar experimental conditions. Differential duration thresholds increase monotonically with decreasing duration (Figs 1 and 6). Except for the thresholds at 0.25°/sec and 0.5°/sec all velocity thresholds are much lower than the differential duration thresholds. Since differential duration thresholds were measured with acoustic white noise masking we measured a number of velocity thresholds with this acoustic masking. This did not affect the velocity thresholds. Our results suggest that velocity judgements do not depend on duration of movement information since the levels of both differential thresholds are different and unrelated.

Influence of slit length and binocular vs monocular viewing

It has been shown that differential orientation detection depends on slit length (Vogels *et al.*, 1981).

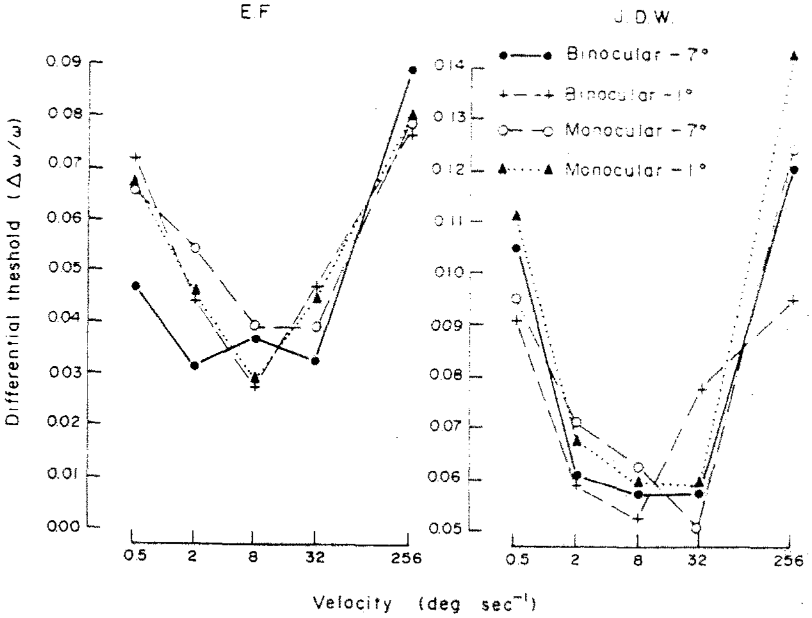

Fig. 3. Just noticeable differences in velocity plotted as a function of velocity for 4 experimental conditions combining long (7°) and short (1°) slits and binocular and monocular viewing.

Differential velocity detection was tested for two slit lengths 1° and 7° and for binocular versus monocular viewing. Neither of both changes affected velocity judgements to a great extent (Fig. 3). Differential velocity detection seems to depend on other neuronal mechanisms than differential orientation detection.

Influence of background illumination on differential velocity judgements

For one subject we have tested the influence of lower background illumination on differential velocity judgements. Three background illumination levels were tested in an interleaved fashion, keeping the contrast equally high ($\log \Delta I/I = 3$). The highest background illumination is our standard condition (0.03 cd/m^2) and corresponds to the middle of the mesopic range. The lowest level is 3×10^{-5} cd/m^2 which corresponds to scotopic vision. Figure 4 shows that over a wide range of background illuminations the basic U shape of differential velocity sensitivity curve is preserved. The reduction in background illumination decreases differential velocity detection but much more so at the low velocities than at the median or high velocities. Scotopic vision eliminates cone function and one can expect a sharp decrease in sensitivity to stimuli exactly restricted to the fovea. In fact at very low velocities the movement amplitudes, set by the window, were extremely small (Table 1) so that the stimulus center remained in the fovea. This could explain the strong increase in velocity threshold at low velocities. It should however be noted that the stimuli were 7° long so that retinal regions outside the fovea were stimulated at all velocities.

Under these different background illumination levels the differential duration threshold increased with decreasing duration (Fig. 5) and differential velocity sensitivity at least at medium and high velocities remained far better than duration judgements. It should also be noted that changes in velocity and duration judgements induced by the change in background illumination were unrelated. The reduction of background illumination to 0.00003 cd/m^2 hardly affected the differential dur-

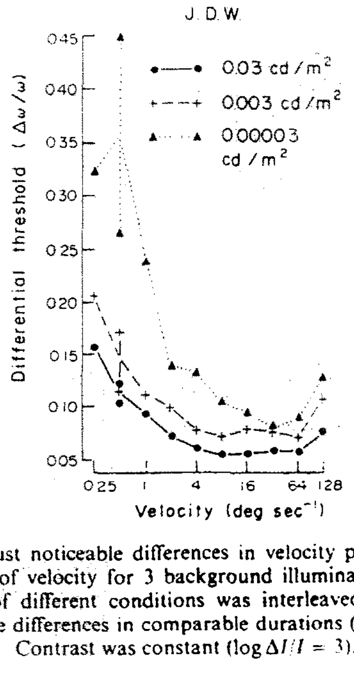

Fig. 4. Just noticeable differences in velocity plotted as a function of velocity for 3 background illumination levels. Testing of different conditions was interleaved. For just noticeable differences in comparable durations (see Fig. 5). Contrast was constant ($\log \Delta I/I = 3$).

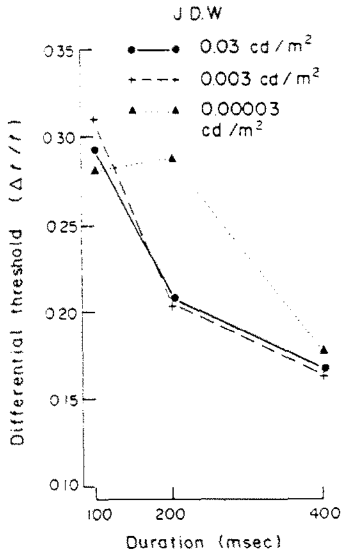

Fig. 5. Just noticeable differences in duration expressed as Weber ratios and plotted as a function of duration for 3 background illuminations.

ation threshold at 400 msec, yet it strongly increased the differential velocity threshold at 0.25°/sec measured for the same duration.

Influence of contrast on differential velocity judgements.

Different contrast levels, $\log \Delta I/I$ ranging from 3 to -0.65, have been tested in an interleaved way for three subjects (Fig. 6). Reducing the contrast decreases the differential velocity sensitivity but more so at the lower and upper ends of the velocity range than at the medium velocities. There is some individual variability, since at a $\log \Delta I/I$ of -0.65 subject J.D.W. had a strongly reduced sensivitity while the other subjects (F.V.C. and H.J.) still had thresholds below 10% for velocities between 8 and 64°/sec. For these different contrast levels the differential velocity sensitivity plotted as a function of velocity remained U-shaped, while differential duration thresholds still increased monotonically with decreasing duration (Fig. 7). As observed for different background illuminations, the changes in velocity sensitivity at different contrasts seem not related to the changes in duration judgements. For example a reduction of $\log \Delta I/I$ to -0.65 had little effect on the differential duration thresholds of F.V.C. at 200 and 400 msec. Yet velocity judgements at low velocities were severely impaired. This further confirms that velocity judgements do not depend on duration judgements.

DISCUSSION

Our experiments confirm McKee's (1981) conclusion that velocity judgements depend on a genuine response to movement rather than on some indirect inference from distance traversed by the stimulus or the total duration. Indeed differential velocity judgements seem to be independent of duration judgements. Both judgements have different and unrelated levels, whether one considers the range of durations (50–400 msec) used in the velocity testing or the changes induced by different background illuminations or contrasts. Since for a given differential velocity threshold the distance was fixed the later

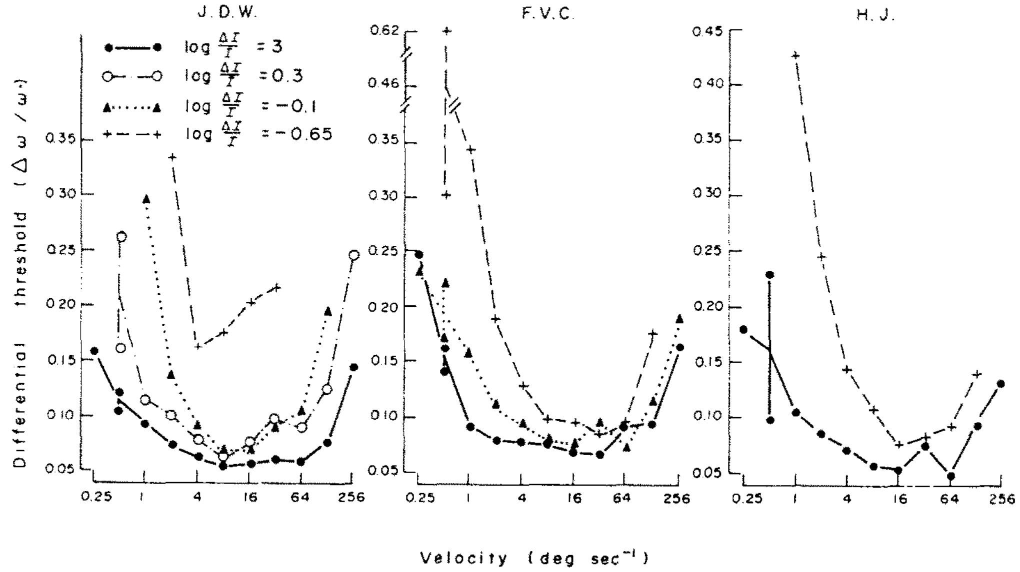

Fig. 6. Just noticeable differences in velocity plotted as a function of velocity for different contrast levels. Testing of different conditions was interleaved. For just noticeable differences in comparable duration see Fig. 7. Background illumination constant at 0.03 cd/m^2. At the lowest contrast, targets were invisible at fast velocities (over 64°/sec for J.D.W. and over 128°/sec for F.V.C. and H.J.) and low velocities (below 2°/sec for J.D.W., 0.5°/sec for F.V.C. and 1°/sec for H.J.).

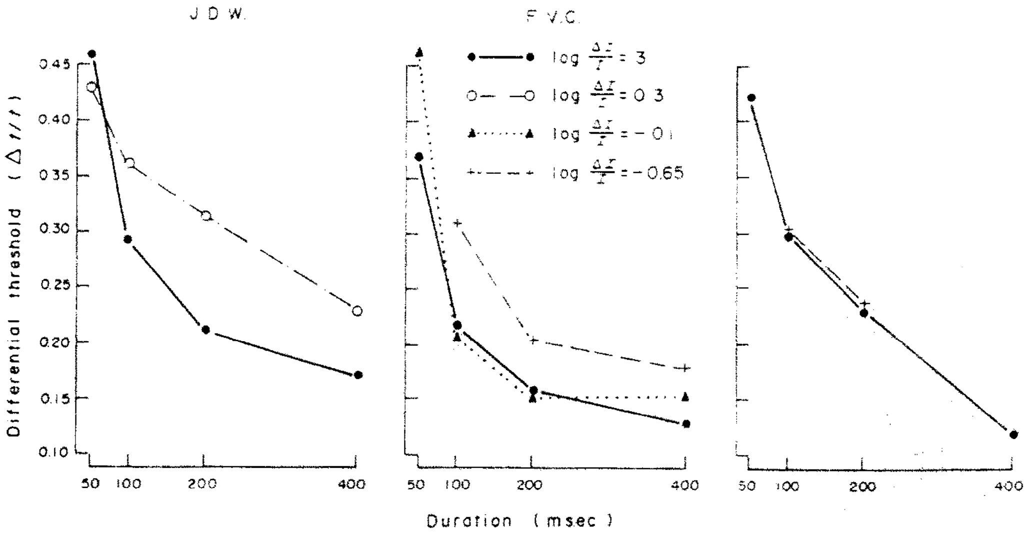

Fig. 7. Just noticeable differences in duration plotted as a function of duration for different contrast levels.

could be no cue for the velocity judgement at one reference velocity. On the other hand between reference velocities, distance traverse by the target changes (Table 1). But it is unlikely that this change explains the changes in velocity judgement. Indeed for reference velocities between 2 and 64°/sec, the distance traversed increased 25 times yet the velocity judgements remained at the same level of 5–7%.

Our experiments further show that the local mechanism on which velocity judgements depend is most sensitive (under our experimental conditions) at intermediate velocities (4–64°/sec). Indeed the U-shaped curve relating differential velocity detection and velocity is minimum at those velocities. Also at these velocities, velocity judgements are the least impaired by strong reduction in contrast. The observed change of velocity judgements as a function of velocity confirms McKee's (1981) and McKee and Nakayama's (1982) observations for velocities ranging from 0.5 to 30°/sec. In addition our data show a further increase of the differential velocity threshold for velocities between 64 and 256°/sec, a range unexplored by previous authors. The level of performance of our subjects at medium velocities is comparable to those reported by McKee. Thresholds at low velocities (0.5 and 1°/sec) were slightly higher than those reported by McKee (1981). This could be due to the lower background illumination used in our experimental set-up.

Finally results show that the U shape of the curve relating just noticeable difference in velocity and velocity is preserved over a wide range of stimulus conditions. The curve is hardly affected by changes in slit length or changes from binocular to monocular viewing. Furthermore reduction in background ilumination or contrast affect mainly the ends of the curve making the branches of U steeper.

Orban *et al.* (1981a) in a report on the influence of stimulus velocity on visual cortical cells of the cat have described 4 types of velocity-response curves. They suggested that one of these types, the velocity-tuned curves, could represent the neuronal mechanism underlying velocity judgements. They further reported that the range of optimal velocity of velocity-tuned cells was limited between 3 and 80°/sec. These physiological observations suggest a local velocity detection mechanism of which the performance should be optimal at medium velocities. The present results showing that human differential velocity sensitivity is optimal between 4 and 64°/sec, are in agreement with the hypothesis that a set of neurons similar to velocity-tuned visual cortical cells of the cat underly human velocity judgements. Two other observations further support this hypothesis. Firstly, velocity-tuned cells have been described in area MT of the monkey (Van Essen 1982, this symposium), secondly according to McKee (1981) velocity judgements are not affected by a change from continuous movement to apparent movement using fast temporal rates (over 25 Hz). Indeed Cremieux *et al.* (1984) have shown that velocity tuning is preserved under conditions of stroboscopic illuminations at high rates. It remains however to be shown that with respect to differential velocity judgements, cat, monkey and human perception are similar.

It is worth comparing the influence of velocity on differential velocity sensitivity, with the effect on direction discrimination and on acuity. There seems to be a sharp distinction between acuity on the one hand and direction and velocity discrimination on the other. Indeed acuity decreases sharply for velocities over 3°/sec (Westheimer and McKee, 1975) while direction discrimination judgements have been shown to be optimal at medium velocities (van der Glas *et al.*, 1981) as are velocity judgements. Thus the statement that visual perception is impaired by faster stimulus movements is only true for acuity and vision of high spatial frequencies (Burr and Ross, 1982). Again the physiological observations of the properties of cat visual cortical cells can help explain these differences under the proviso that cat and human perception use similar mechanisms. Indeed Orban *et al.* (1981b) have shown that cells sensitive to the slowest velocities (velocity low-pass cells) have the narrowst receptive fields (see also Duysens *et al.*, 1984 this issue). If acuity is based on the activity of cortical cells with the narrowest receptive fields, one can expect acuity to be a low-pass function of velocity. On the other hand Orban *et al.* (1981) have shown that direction selective cells in the cat have a weakly tuned velocity profile and one can expect that direction discriminations are most sensitive at medium velocities. This convergence between physiological observations and psychophysical measurements suggests that indeed electrophysiology and psychophysics are the twin means of investigation into sensory processes (Westheimer, 1981).

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