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On the shifter hypothesis for the elimination of motion blur

Manfred Fahle

Abstract

Objects moving at even moderate speeds stimulate many retinal photoreceptors within the integration time of the receptors, yet usually, no motion blur is experienced. An elegant model for the elimination of motion blur was proposed by Anderson and vanEssen (1987) who suggested that the neuronal representation of the retinal image is shifted on its way to the cortex, in an opposite direction to the motion. Thus, the cortical representation of objects would be stationary at least during short periods of time. I have measured thresholds for two vernier stimuli, moving simultaneously into opposite directions over identical parts of the retina. Motion blur for these stimuli is not stronger than with a single moving stimulus, and thresholds can be below a photoreceptor diameter. This result cannot be easily reconciled with the hypothesis of 'shifter circuits'.

This report describes research done within the Artificial Intelligence Laboratory and the Center for Biological Information Processing (Whitaker College) at the Massachusetts Institute of Technology E25-201 Cambridge, Massachusetts 02139, USA and at the Department of Neuroophthalmology of the University Eye Clinic in D7400 Tübingen, West Germany. Support for the A.I. Laboratory's artificial intelligence research is provided in part by the Advanced Research Projects Agency of the Department of Defense under Office of Naval Research contract N00014-85-K-0124. Support for this research is also provided by a grant from the Office of Naval Research, Engineering Psychology Division. Dr. M. Fahle holds a Heisenberg Stipend from the Deutsche Forschungsgemeinschaft (Fa 119/5-1 and Fa 119/3-2).

Introduction

The subjective sharpness of moving objects and the lack of motion blur with stimulus velocities up to around 4°/sec have long been a puzzle for researchers of vision. At 4°/sec, the retinal image of an object moves across almost 500 photoreceptors within one second. Within the integration time of the photoreceptors (at least 20 to 100 msec; Barlow, 1958; Ross & Hogben, 1974; Burr 1981a), 10 to 50 photoreceptors are stimulated, leading to a pronounced motion smear in any camera-like device that integrates over time. But most observers do not experience motion blur under these conditions.

Several possible mechanisms have been proposed for the subjective sharpness of moving contours (e.g., Burr, 1981b). An elegant alternative to these models is the suggestion by Anderson and vanEssen (1987) that 'shifter circuits' move the cortical position of visual inputs by controlling the mapping of retinal images onto the visual cortex. The shifting is assumed to take place in the monocular portions of the visual pathways, i.e., in the lateral geniculate nucleus and the geniculorecipient layers of cortical area V1. This kind of shifter circuit would not only stabilize the cortical representation of moving objects (at least for short periods of time), but would also allow a fine alignment of the images of both eyes relative to each other as is required for stereoscopic depth perception. As a third possible virtue, shifter circuits could easily explain the short-range process of apparent motion (Braddick, 1980) as well as spatio-temporal interpolation (Morgan, 1980; Fahle & Poggio, 1981). By compensating the spatial displacement in the cortical representation of an (apparently) moving stimulus, shifter circuits would transform a discontinuous presentation of this stimulus, as in apparent motion, to a mere flickering in its cortical representation. Similarly, they would interpret a temporal delay at each station of the apparent motion as a spatial offset in the cortical representation.

Evidence for or against this hypothesis is difficult to obtain with electrophysiological recordings. Here, I present the results of psycho-physical experiments that cannot be explained by shifter circuits in their proposed form. The neurones that are believed to shift are not direction selective; they would shift the complete representation of a region of the visual field into one direction. If two stimuli move in opposite directions in the same region, only one can be stabilized, while the other one should appear blurred. This is not what one perceives.

Material and Method

Stimuli were produced on a 32bit personal computer and displayed on a high resolution x/y monitor (Tektronix 608, P31) via fast 16bit D/A converters. The smallest displayable displacement was below 1" (arcsec) at the observation distance of 2.5 m. Stimuli were displayed as vertical bright bars on a dark surround. The vernier targets were 21' long and 1' wide, with a 1' vertical gap between the two elements. Their luminance was 100 cd/m^2 on a homogeneous background of 1.3 cd/m^2, supplied by indirect incandescent lighting.

In the experiments measuring spatial vernier thresholds (Fig. 1), two vernier targets moved in a pseudo-continuous fashion (stepsize between the stations along the motion path, dx= 0.5') in opposite directions over the same area of the monitor. One vernier started at the left of the fixation point, moving rightward by twice its distance from the fixation point so that it stopped (and disappeared) as far to the right of the fixation point as it had started to the left. The second vernier started simultaneously with the first, but at the endpoint of the first vernier's trajectory. It moved leftward at the same speed as the first vernier, crossed the first vernier at the fixation point, and stopped at the starting point of the first vernier. The velocity of both verniers varied between 0.5 and 8°/sec but was constant within each presentation. Presentation time was 75 msec (Fig. 1d) or 150 msec (Fig. 1a-c) — too short for voluntary eye movements (Westheimer, 1954). The length of the trajectory of the stimuli, and the number of stations displayed, necessarily increased with velocity at any constant presentation time. In control experiments, the one, two, or three last stations of an offset vernier lacked offset ('masked edge condition'), in order to prevent observers from recovering the structure of the stimulus from the after-image of the last station(s) (Fig. 1c,d). In another control experiment, only one of the targets moved while the second target, without an offset, was displayed stationary at the fixation point (Fig. 1b). Only one of the verniers was offset, the other one was straight. Observers had to indicate the direction of offset by pushing a button.

In the second experiment, on spatio-temporal interpolation, the distance dx between adjacent stations of the pseudo-continuous motion increased to 1.5'. Here, the two elements of each vernier stimulus were perfectly aligned one above the other, but one element of each of the verniers was delayed by a preset amount at each station of the (apparent) motion. Under appropriate conditions, the

temporal delay was then perceived as a spatial offset between the two elements of each vernier (Burr, 1979; Morgan, 1980; Fahle & Poggio, 1981). Using the velocity of the (apparent) motion (v), the (apparent) spatial offset (dx) was calculated from the temporal delay (dt) according to: $dx = v\ dt$. In half of the presentations, only one of the two moving stimuli had a (spatial or temporal) vernier offset. In the other half of presentations, both stimuli were perfectly aligned. In a two alternative forced choice task, the observers had to decide whether or not they perceived an offset. In the second part of the experiments, again only one of the stimuli had an offset at each presentation and the observer had to indicate the direction of offset (right versus left). No clear differences were found between the results of these two response schemes. Each run contained 120 presentations, with usually three different sizes of offset in both directions. Thresholds were calculated using probit analysis, with the standard criterion of 75% correct responses (Finney, 1971).

Three of the four observers had normal vision; the fourth obtained full visual acuity with suitable contact lenses (RR). Three observers were extensively trained in hyperacuity tasks, the fourth (RR) was less experienced, slightly myopic, and had a history of strabismus, but attained normal visual acuity in both eyes.

Results

When the two vernier stimuli moved in opposite directions, they were clearly discernable, sharp and without motion blur at velocities of up to 2° to 4°/sec for all observers. Thresholds for the detection of real vernier offsets increased with the velocity of motion, especially for velocities above 4°/sec, the slope of increase differing markedly between observers (Fig. 1a). Thresholds even at low velocities were higher by a factor of 2 to 3 than the thresholds typical for single moving verniers. The increase of thresholds can be attributed to the two vernier targets being in close spatial proximity, moving in opposite directions (cf. Snowden, 1989). They supposedly interfered with each other, as flanking lines do with a vernier target, thus increasing thresholds (cf. Westheimer & Hauske, 1975). To test this assumption, one of the targets was displayed stationary at the fixation point while the other one moved. The results were very similar, at least at low velocities, except in one observer (MF; Fig. 1b), and still above typical vernier thresholds. With offsets created by spatio-temporal interpolation, the increase in thresholds caused by the stationary bar was much more pronounced than in the real vernier targets

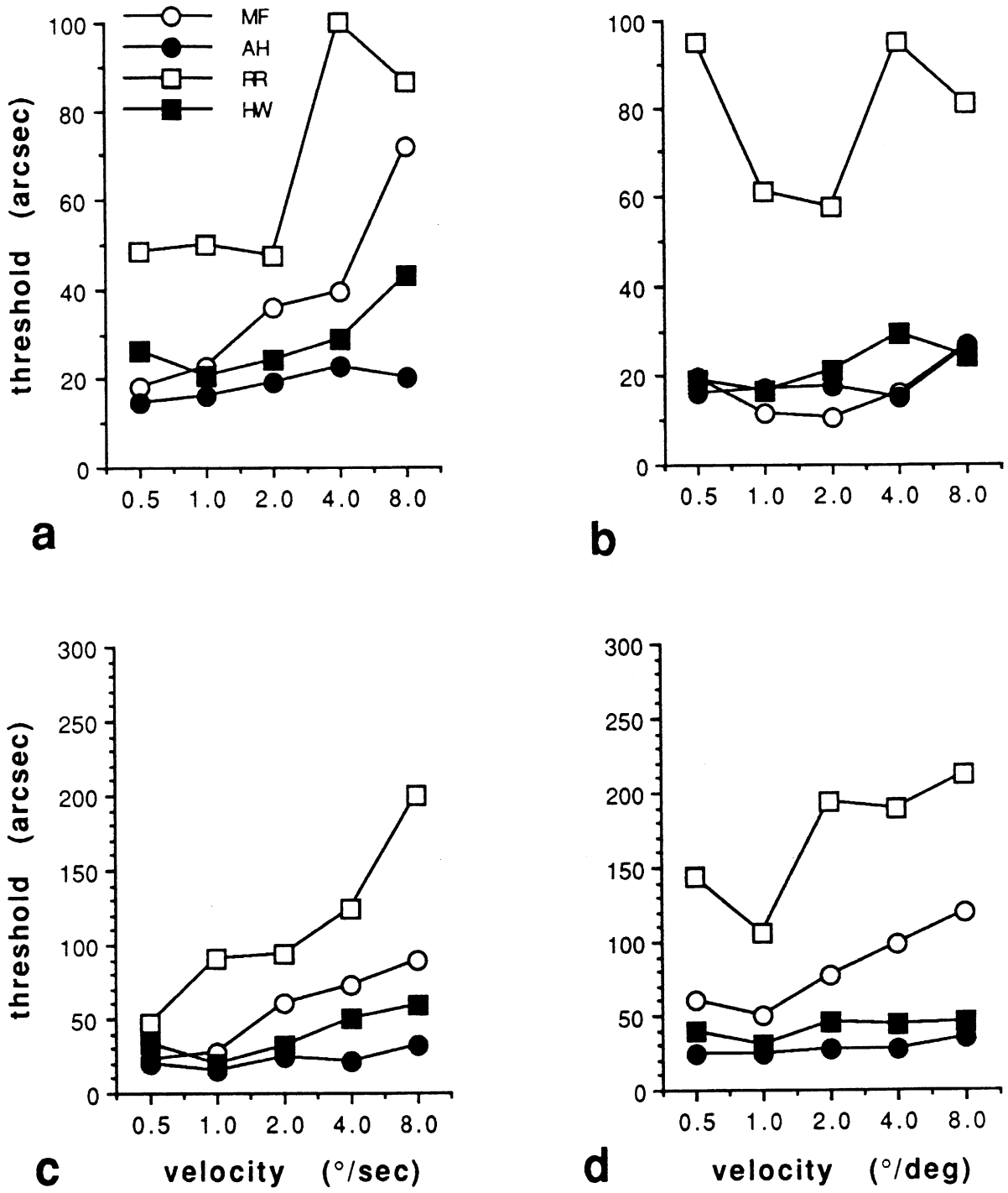

Fig.1 Thresholds for two simultaneously presented targets, moving in opposite directions, as a function of target velocity. Results of four observers. See text for details. (Note the change in scale of the ordinate.)

It should be noted that thresholds for medium velocities, such as 0.5 and 1.0°/sec were below a photoreceptor diameter — in spite of the stimuli moving across approximately 10 and 20 photoreceptors, respectively, during the 150 msec presentation time! Even at a velocity of 8°/sec, the best thresholds corresponded to the size of a photoreceptor, while the stimuli moved over approximately 80 photoreceptors.

In Fig. 1c, the last one or two stations were aligned (masked edge condition), in order to prevent observers from recovering the direction of offset, e.g., from the after image of the last station of the motion sequence. If the vernier thresholds were larger than the distance between adjacent stations, not only the very last station but the two or three last stations were displayed without an offset. Thresholds were higher under these conditions, but still around one photoreceptor diameter for some observers, while others were barely able to solve the task at velocities of 4°/sec and above (Fig. 1c). Curtailing the duration of motion to 75 msec slightly elevated thresholds for the masked edge condition (Fig. 1d). Preliminary experiments showed that moving the stimuli from further outwards towards the fixation point and stopping there, or starting the stimuli at the fixation point and moving them peripherally in opposite directions yielded similar results (not shown). The same is true for vertical separation of the trajectories, i.e., when the vernier targets moved horizontally in opposite directions, one above and the other below the fixation point.

In the second experiment, the vernier targets were perfectly aligned, but one segment of one of the verniers was delayed at each of the stations of the (apparent) motion. Most noteworthy, spatio-temporal interpolation reconstructed the underlying trajectories even under these conditions. With sufficiently long delays (of several milliseconds, corresponding to distinct offsets), a clear subjective impression of a spatial offset was construed in the visual system (Fig. 2a). Results for a distance of 0.5' (instead of 1.5') between stations yielded even lower thresholds (not shown). Usually, observers were not able to indicate whether the offset they perceived was due to a spatial offset or to a temporal delay! Thresholds for spatio-temporal interpolation closely resembled those for the masked edge condition in spatial offsets, except for a higher susceptibility for faster velocities. Curtailing the duration of the (apparent) motion to 75 msec clearly increased thresholds (Fig. 2b). The distance between stations was 1.5', the response scheme right versus left.

Additional experiments with the alternative response scheme of offset versus no offset yielded similar results. The same is true for a distance between stations of 0.5' (not shown).

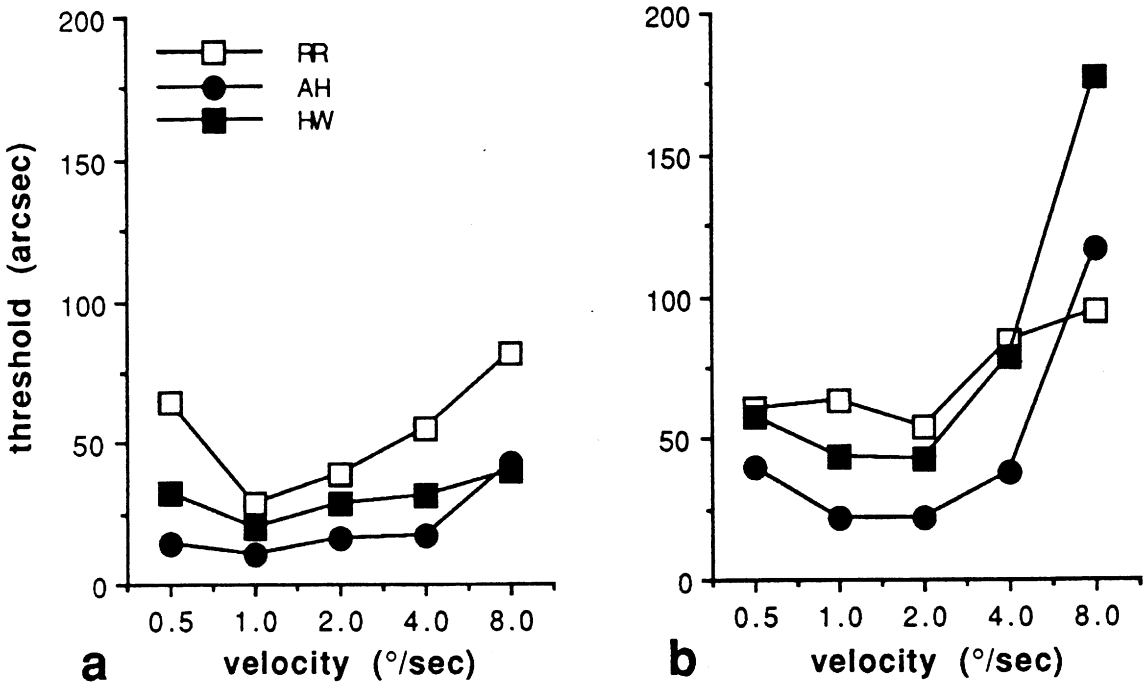

Fig.2 Thresholds as in Fig. 1 but instead of spatial offsets, temporal delays were used. Thresholds have been converted into the spatial offset corresponding to the delays actually used: the distance that a stimulus would have moved during the delay, at the given velocity. Results of four observers. Presentation time, i.e., duration of the motion sequence, was 150 msec in (a), and 75 msec in (b).

Because the differences between the two presentation times were more pronounced for temporal offsets (Fig. 2) than for spatial ones (Fig. 1c,d), temporal offsets were used in the third experiment. But here the two presentation times of 150 and 75 msec were randomly interdigitated — the observers never knew how long the next presentation time would be. Hence, even if it would be possible to switch the direction of shift in the shifter circuits within less than 100 msec (a quite improbable feat), the visual system had no prior information about the duration of the stimulus, and thus could not know whether to switch directions after 37 msec or 75 msec. The results for the interdigitated presentations were virtually identical

to the ones for separated durations, with clearly lower thresholds at the longer presentation duration (Fig. 3; the only exception were thresholds for low velocities for observer RR in 3b. These results had large standard errors). The same holds true if spatial offsets instead of temporal delays were used, but there the threshold differences between the two presentation times were relatively small anyhow.

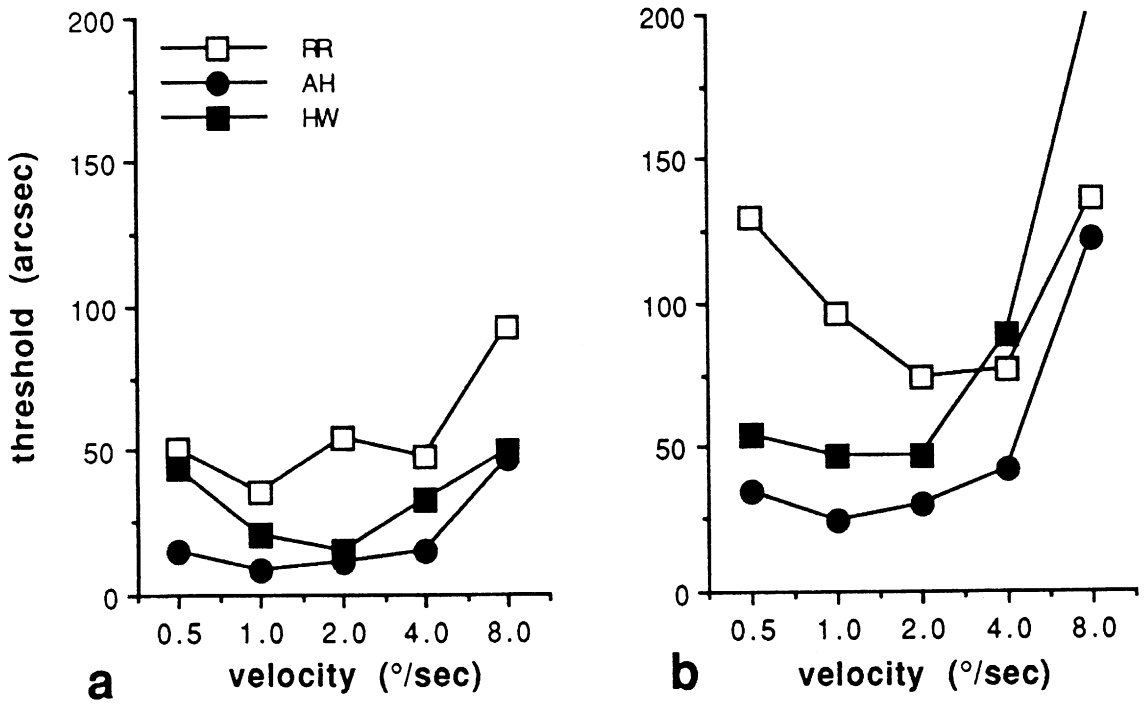

Fig.3 Thresholds for two simultaneously presented moving verniers, with one of them delayed, creating an interpolative displacement. Presentation times of 150 msec (as in Fig. 2a) and of 75 msec (as in Fig. 2b) were randomly interdigitated but thresholds were calculated and displayed separately. Three observers. Most standard errors were around 15% of the results.

Discussion

Morgan and Benton (1989) found that thresholds for spatial interval comparison increased even at velocities below 2°/sec, which indicates that the visual system cannot compensate for the effects of motion in all kinds of stimuli, a finding that casts some doubt on the notion of shifter circuits' capability to eliminate all the effects of motion blur. Still, one could argue that in the case of moving double lines, as in Morgan and Benton's experiment, masking occurs on the

photoreceptor level, since photoreceptors are stimulated twice in short temporal sequence by the two lines. Our finding, that two verniers moving in opposite directions are not blurred and can yield thresholds below a photoreceptor diameter, poses even more severe difficulties for an explanation in terms of shifter circuits. A shifter circuit operating on the level of the lateral geniculate nucleus or the geniculorecipient parts of the visual cortex should shift *all* the receptive fields at least in a circumscribed area of the visual field. It is noteworthy in this context that the verniers moved with an amplitude as small as 4′ within the 150 msec presentation time at the lowest velocity, and over around 1° at the highest velocity — hence over distances that correspond roughly to the receptive field centers of cortical neurones.

Receptive fields in the lateral geniculate body have a circularly symmetric, antagonistic center-surround structure and are *not* direction selective (Hubel & Wiesel, 1961). They are unable to discriminate between two stimuli moving in opposite directions on the basis of their direction of movement, and thus a shifter circuit could remove motion blur from only one of the stimuli. We never observed a difference between the two stimuli in the sense that one was blurred whereas the other was sharply focused. In order to solve the task of discriminating between offset or non-offset stimulus presentations, both verniers had to be analyzed. (Though the thresholds are based on the standard criterion of 75% correct responses, I verified that more than 80% correct responses were obtained with slightly larger offsets - which requires the identification of both vernier targets). The increase of thresholds for two simultaneously moving targets can be explained by the presence of inhibitory interactions between the two targets that are, to a first approximation, independent of the motion: similar interactions can also be exerted by a stationary target (Fig. 1b).

The presentation time of 150 msec was just sufficient for the mechanisms responsible for the elimination of motion blur to become fully effective (Fig. 1a); these mechanisms require around 100 msec (Burr, 1979; Anderson & vanEssen, 1987). As to be expected, thresholds increased with the 75 msec presentation time, especially for the temporal or 'interpolative' verniers (Figs. 1d, 2b). The thresholds for spatial offsets were clearly higher in the masked edge condition (Fig. 1c,d) than without the mask (Fig. 1a). This implies that the visual system can extract crucial information from the last one or two stations of even very long motion sequences with more than 100

stations — possibly from the quasi-stationary afterimages of the last station(s). Thresholds for spatio-temporal interpolation were even higher than those for the masked edge condition in spatial offsets.

A logically sound (but rather ad-hoc) way to explain the results with two simultaneously moving stimuli by means of shifter circuits would be to postulate that the direction of shifting can be inverted within less than 100 msec, so that the shifter circuit would first stabilize one of the stimuli for roughly half of the presentation time and subsequently the stimulus moving in the opposite direction for the second half of the presentation time. To rule out this possibility, presentations of 75 and 150 msec were randomly interdigitated for 'interpolative' verniers. Because the duration of the subsequent presentation was unknown, the switch between the directions of shift would be due after 37 msec. Otherwise, only one stimulus could be analyzed in the 75 msec presentations, allowing best results of around 75% correct responses. Switching directions after 37 msec would leave thresholds unchanged for the 75 msec presentations as compared to Fig. 2b, but should increase thresholds for the 150 msec durations significantly, almost to the level of the 75 msec presentations. This is not what we found. Thresholds for the mixed durations (Fig. 3) were very similar to those in the separated durations.

Another modification of the shifter hypothesis could rely on several shifter circuits for each visual field position. Given the large number of neurones necessary for the shifter circuits, this extension does not appear reasonable. In the light of the new experiments, it seems far more plausible that the mechanisms responsible for the elimination of motion blur are direction selective. One possible model consists of direction selective, spatial frequency tuned filters, as proposed, e.g., by Burr (1981b) for motion detection and by Fahle and Poggio (1981) for the spatio-temporal interpolation in discontinuously presented moving targets. These filters can retrieve the original frequency spectrum of a moving stimulus from a sufficient number of discrete sampling points. The original frequency spectrum in the domain of spatial and temporal frequencies of a stimulus can be represented as a line support in the (Fourier) frequency-domain. It relates, unambiguously, the spatial and temporal components of the stimulus to each other. For short presentation times, the line supports in the frequency domain are somewhat spread out such that the unambiguous relation does not hold, and motion blur might be the subjective perceptual correlate to this description of the stimulus in the

language of physics. Longer presentations times decrease the spread of the line supports, and observers experience less motion blur. If the filters are direction selective, they can extract the frequency spectra of two stimuli moving in opposite directions in the same part of the visual field.

Thresholds increase in a more pronounced way with velocity of the stimuli for interpolative verniers than for real ones. This finding might tentatively be attributed to the fact that sidelobes in the Fourier domain exist in the case of discontinuous presentation of the stimuli. Curtailing the duration of presentation expands the widths of these sidelobes and eventually leads to the spilling of side-lobe information into the interpolation channel. This spilling of the side lobes impends especially at higher velocities and deteriorates results especially for 'temporal' verniers (Fahle & Poggio, 1981). It might be the reason for the perceptual deterioration and increased thresholds under these conditions.

The model of direction selective filters, then, is compatible with the experimental results and avoids motion blur with a much simpler neuronal mechanism than the shifter-circuits — without the need of positional shifts. (Though positional shifts in the fine tuning of stereoscopically activated cortical neurones may occur; cf. Poggio & Poggio, 1984.) There are no indications that the plasticity and variability of receptive fields of cortical single neurones as revealed recently by single cell recording (e.g. Eckhorn et al., 1988) adding to the need of redefining (von der Heydt, Peterhans & Baumgartner, 1984) the classical concept of receptive fields, are indeed related to the compensation of motion blur.

In summary, the results demonstrate that the visual system can prevent the effects of motion blur and the increase of perceptual thresholds even when stimuli in a given area of the visual field move in opposite directions. This finding is in contradiction to the hypothesis of shifter-circuits (at least in its present form). Even spatio-temporal interpolation between the stations of the discontinuously presented targets is achieved for stimuli moving in opposite directions within the same portion of the visual field.

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