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Motion Contrast and Motion Integration

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When a moving aperture contains a drifting grating, the perception of aperture movement is strongly affected by the grating movement. We have studied this interaction, using a moving circular patch of sinusoidal grating matched to the background in mean luminance. The circular window, or aperture, could be defined either by an abrupt transition from a full-contrast grating to the background (hard aperture) or by a two-dimensional Gaussian fall-off in contrast (soft aperture). The grating movement could be controlled independently of the aperture motion. Subjects judged the direction of the aperture movement (i.e. the movement of the patch as a whole). We find that an illusory motion of a stationary aperture can be induced depending on the direction of the grating drift. A hard aperture presented in the fovea appears to move in the direction opposite the grating movement, demonstrating simultaneous motion contrast. However, a soft aperture presented in the periphery appears to move in the same direction as the drifting grating, demonstrating motion integration (assimilation). These results are discussed in the context of interactions between short-range and long-range motion mechanisms and with respect to the significance of boundaries in determining the figure–ground relationship of motion signals.

Aperture Grating Motion contrast Motion integration

1. INTRODUCTION

The visual perception of motion in the fronto-parallel plane can be produced by two distinctive mechanisms (see Braddick, 1980). The first motion mechanism, sometimes called the short-range or Fourier mechanism, is based on the spatial-temporal correlation of image luminance intensity distributions (Braddick, 1974; Morgan & Ward, 1980; van Doorn & Koenderink, 1982a, b), or equivalently, the extraction of information about the Fourier power spectrum of the luminance distribution in any moving pattern (van Santen & Sperling, 1985; Adelson & Bergen, 1985; Watson & Ahumada, 1985). Smoothly drifting sinusoidal luminance gratings are powerful stimuli for this motion mechanism. A probable neurophysiological substrate of this mechanism would be the direction-selective cells of the primary visual cortex within any hypercolumn (Baker & Cynader, 1986; Reid, Soodak & Shapley, 1987, 1991; Hamilton, Albrecht & Geisler, 1989).

The second motion mechanism, sometimes called the long-range or non-Fourier (Chubb & Sperling, 1988) mechanism, appears to be based on the temporal correspondence or successive "matching" of one or several cues in a moving object. Any salient feature extracted through early vision (such as a distinctive texture, color, contour, flicker, brightness contrast, etc.) can serve as a potential cue for this correspondence process. A change in the retinotopic position of a well-localized visual stimulus (object) as it translates across space will produce successive activation of multiple cortical regions that represent these positions. The change of object position is a sufficiently strong cue to this mechanism to produce a compelling sense of motion, even when the object is simply flashed sequentially at separate locations in the visual field (Wertheimer, 1912). A possible neurophysiological substrate of this long-range mechanism would be a certain population of MT cells with large receptive fields extending across dozens of V1 hypercolumns (Mikami, Newsome & Wurtz, 1986a, b; Newsome, Mikami & Wurtz, 1986), and it is likely to involve cortical area V2 as well (Wilson, Ferrera & Yo, 1992). Indeed, these MT cells seem to have invariant tuning functions for moving stimuli defined by various cues such as luminance, flickering or contrast modulation (Albright, 1992).

The two motion mechanisms show a number of important differences with respect to the maximal or optimal size of spatial displacement and/or exposure duration (Korte, 1915; Braddick, 1974; Morgan & Ward, 1980; Chang & Julesz, 1983; Baker & Braddick, 1985; Cleary & Braddick, 1990a, b), effectiveness of dichoptic presentation (Braddick, 1974), and effectiveness of masking during the inter-stimulus interval (Braddick, 1973), etc. In terms of perceptual experience, stimulation of the first (short-range) mechanism yields a compelling sense of smooth movement, yet the object that appears to move does not necessarily end up in a new position, whereas stimulation of the second

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(long-range) mechanism is always accompanied by or may even be deduced from a change of the object's spatial location. An example of the perceptual dissociation between motion sensation and consistent and constant positional change is the motion aftereffect (Wohlgemuth, 1911), in which adaptation to a pattern moving in one direction makes a subsequently viewed stationary pattern appear to move in the opposite direction, although its apparent (and real) location does not deviate from its original position. This may result from adaptation to the former (short-range) but not the latter (long-range) mechanism.

Of course, the translatory motion of a real-world object always results in a change of its position in space, thereby activating both motion systems, unless the object is being tracked by eye movements. If the long-range mechanism is activated without an appropriate co-activation of the short-range mechanism, however, perceived motion may not be smooth. MacKay (1976) showed that when a static noise field (composed of random dots) was viewed as though through a moving rectangular window "cut" out of another dynamic noise pattern (i.e. the successive portions of the static noise field were revealed by the moving window), the movement of the rectangle did not appear smooth. Rather, it appeared to jump in large, discrete steps from one loction to another, even though its real movement was smooth. It had been suggested (MacKay, 1973) that normal perception of object-motion depends on a subtle integration between image drift and location-change (with possible indications from tracking eye-movements). On the other hand, perceived location may not be veridical if only the short-range mechanism is activated without other positional cues. Ramachandran and Anstis (1990) showed that when a rigid, coherently drifting random-dot pattern was viewed as though through a stationary window cut out of another static (or twinkling) noise field (i.e. the successive portions of the drifting random-dot pattern revealed itself as the dots passed "behind" the stationary window), the window, which was formed by the boundaries of coherent motion, appeared displaced in its spatial position. The direction of this positional displacement was parallel to the direction of dot motion. The illusion did not occur if the dots in the window were made to differ in mean luminance from the background dots. Anstis (1989) suggested that motion-defined edges were inferred or interpolated by integration of velocity signals in the absence of luminance cues, in a way analogous to the interpolation of momentary spatial position in sampled motion (Morgan, 1980; Morgan & Ward, 1982).

In a recent paper (De Valois & De Valois, 1991), the influence of the movement signal from the short-range mechanism on the perception of an object's static position was studied quantitatively by using a stationary moving Gabor stimulus, in which a moving sinusoidal luminance grating was windowed (and therefore delimited in its extent) by a stationary, two-dimensional Gaussian envelope. The sinusoid could drift in either direction, while the Gaussian envelope (patch) remained stationary at all times. The drift of the grating produced a pronounced (but static) shift in the perceived location of the patch. The amount of the static positional shift depended on spatio-temporal variables, as well as on retinal eccentricity.

We have now studied the influence of the motion signal from the short-range mechanism on the perception of the object's positional change over time (i.e. motion from the long-range mechanism) by using a *moving* circular aperture that enclosed a patch of sinusoidal grating. The grating inside the aperture and the patch as a whole could be drifted independently of each other. For instance, the grating, which was vertically oriented, could be drifted to the left while the entire patch (aperture) moved to the right. The rationale for choosing such a stimulus is as follows. First, a drifting grating enclosed in or confined by a stationary aperture will primarily activate those directionally-selective cells within certain hypercolumns corresponding to restricted retinotopic locations. We believe this to be a powerful stimulus to the short-range mechanism. There is a local motion signal, with a movement direction corresponding to the grating drift. When the aperture is also in motion, i.e. when the entire stimulus patch moves, cells in different hypercolumns at adjacent retinotopic locations are stimulated successively. We suggest that this provides a powerful stimulus to MT cells which may be driven by successive activation of different V1 hypercolumns, or the long-range mechanism. One obtains, therefore, a global motion signal from the displacement of the pattern position. Thus, the moving aperture pattern is designed to stimulate the two motion mechanisms with controllable and largely separable amplitudes, thereby allowing us to address the roles of each system in motion perception and examine their interaction. We realize that the separation of the two motion systems using this stimulus is in no sense complete. In particular, the drifting grating will also stimulate the long-range system because of the conspicuous features of bright and dark stripes that are inherently present in any such grating. Conversely, moving the entire patch will change the Fourier spectrum of the stimulus and thereby have an effect on the short-range system. To minimize the effects of this complication, we always let the gratings drift at a (usually much) higher speed than the aperture. The aperture moved slowly enough that its motion should not seriously alter the motion energy of a simple drifting grating, and the grating moved fast enough and over a sufficient number of cycles to discourage the possible tracking of its light and dark stripes.

We find that the judgment of the aperture motion (i.e. motion of the patch as a whole) is strongly affected by the grating movement. *Motion contrast* is said to occur if the perceived speed of the patch is slower when the grating and the aperture move in the same direction, and faster otherwise. *Motion integration* (*assimilation*) is said to occur if the perceived speed of the patch is faster when the two move in the same direction, and slower otherwise. With respect to a physically stationary patch, motion contrast refers to an apparent (illusory) motion

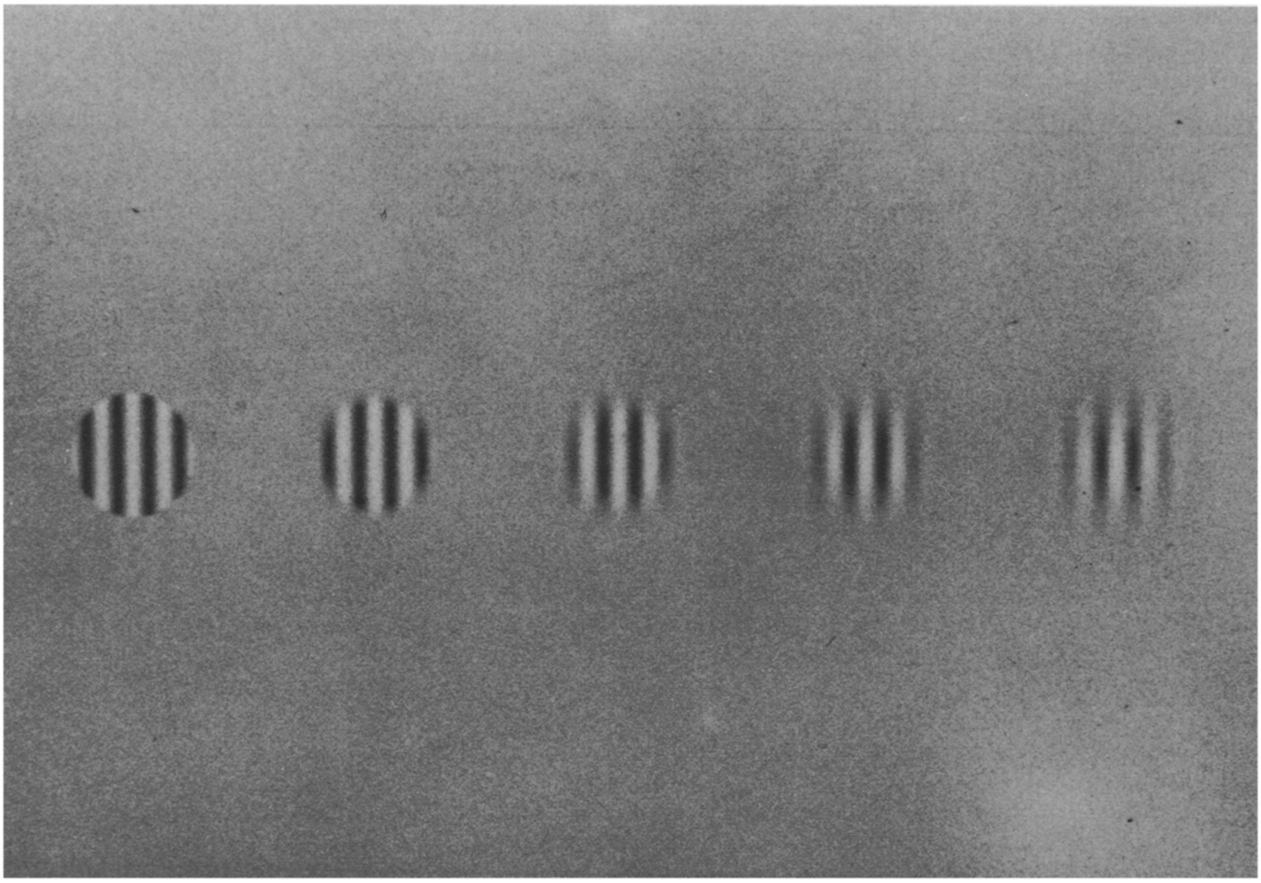

FIGURE 1. Patches of gratings enclosed in apertures of different boundary "softness". The transition is between the full-contrast (hard aperture) and gradual ("soft" aperture). The "softness" of the aperture (i.e. the spatial extent over which the contrast of the grating falls from maximum to zero) increases from left to right. The hardest aperture (on the left) and the softest aperture (on the right) were used in most of the manipulations. The mean luminance of the grating and the background luminance were matched. The grating and the aperture (patch as a whole) were moved independently.

of the patch in a direction opposite that of the grating drift, while motion integration refers to the apparent motion in the same direction as the grating drift. Collectively, we refer to these as motion induction.* We demonstrate both motion contrast and motion integration for the stationary patch within a single paradigm, depending on the distinctiveness of the aperture boundary (border) and retinal eccentricity.

2. METHODS

Apparatus and stimuli

Visual stimuli were presented on a 16 in. Sony RGB monitor under control of a SUN 3/160 computer with a TAAC graphics accelerator having four independent, overlaid graphic channels. The monitor was calibrated (Minolta photometer) and its output was linearized under software control. The frame rate of the monitor was 66 Hz, with a spatial resolution of 1152 × 900 pixels and a gray-level resolution of 8 bits.

*Note that in the classic experiment of Duncker (1929), the term motion induction only refers to what we call motion contrast here. Motion integration in the case of a stationary target is also called motion capture (Ramachandran, 1981). Recently, Nawrot and Sekuler (1990) used the terms "heterokinesis" and "homokinesis" to refer to motion contrast and motion integration, respectively.

The stimulus pattern was a circular patch of a sinusoidal luminance grating, i.e. a grating with spatially delimited extent (Fig. 1). The contrast profile can be described as a central constant region (plateau) with radius r_0 surrounded by a region in which contrast falls in a Gaussian fashion with predetermined σ to reach a zero contrast level (mean background luminance). Mathematically, the contrast modulation is

$$C(r) = \begin{cases} C_0, & r \leqslant r_0, \\ C_0 \exp(-(r - r_0)^2/2\sigma^2), & r > r_0, \end{cases} \quad (1)$$

with $r = \sqrt{x^2 + y^2}$, and the pattern luminance distribution is

$$L(x, y) = L_0(1 + C(r)\cos 2\pi f x). \quad (2)$$

The "softness" of the aperture refers to the steepness of the Gaussian tapering and is controlled by the σ parameter. When σ is large, the tapering is smooth and gradual, or "soft". When σ is small, the tapering is sharp and steep, or "hard". The spatial extent of the pattern, however, is determined by both the size of the plateau region (r_0) and the steepness of the Gaussian taper (σ). The size of the hard aperture ($\sigma = 0$) is simply given by r_0. Since the size of the soft aperture is ambiguous, its apparent size was determined individually by a matching procedure as follows. In the beginning of all experiments, each subject matched the apparent size of a stationary soft aperture (with zero plateau region, or $r_0 = 0$) to that of a stationary hard aperture with size r_0 by adjusting σ of the soft aperture. Once the "matching" value σ_0 was determined, we could create a series of apertures with different softness by decreasing σ while increasing r_0 accordingly. For instance, we obtained five apertures, from hardest to softest in a series, by using the following sequence of paired values $(r_0, 0)$, $(0.75r_0, 0.25\sigma_0)$, $(0.5r_0, 0.5\sigma_0)$, $(0.25r_0, 0.75\sigma_0)$, and $(0, \sigma_0)$. Note that for the last entry (softest aperture), the stimulus pattern is simply a Gabor function (a sine wave enveloped by a Gaussian).

The mean luminance of the grating was always equal to the background luminance of the monitor (unless explicitly stated to be otherwise), which was maintained at a white (CIE coordinates $x = 0.253$, $y = 0.289$) of 40 cd/m^2. Incandescent lamps were used to provide a soft, ambient illumination of the experimental chamber. In all experiments, the spatial frequency of the grating was 4 c/deg and the peak (plateau) contrast was 40% [Michelson contrast $(L_{max} - L_{min})/2L_{mean}$]. At the 115 cm viewing distance used, the radius of the hardest patch (r_0) subtended 0.5 deg (the pixel size of the monitor is 1/77 deg at this viewing distance). The grating was vertically oriented and could be drifted either to the left or to the right, while the patch could also be made to move leftward or rightward independently of the direction of the internal grating drift. Technically, the movement of the patch was realized by software panning (scrolling) the display region of an image buffer, while the movement of the grating was produced by spatiotemporal quadrature modulation in two independent graphic channels of two superimposed sinusoidal gratings [the details are described in De Valois and De Valois (1991)]. When drifting, the 4 c/deg grating always moves with a temporal frequency of 6 Hz, or at a speed of 1.5 deg/sec relative to the external world (but not to the aperture).

Experimental procedures

A two-alternative, forced-choice paradigm was employed in conjunction with the method of constant stimuli. On each trial, a pattern was presented in which the internal grating could either drift to the left, remain stationary, or drift to the right (three possibilities). The aperture could, independently, move either leftward or rightward, each at three possible speeds, or remain stationary (seven possibilities). This gives a total of $3 \times 7 = 21$ combinations of aperture-grating movement. A session comprised five presentations of each combination, or $5 \times 21 = 105$ trials, in randomized sequence. The presentation time was either 200 or 400 msec (for different subjects). The subject's task was to indicate whether the aperture (the patch as a whole) moved towards the left or towards the right. The button press initiated the next presentation (trial) after an interval of 1 sec. A session typically lasted about 4 min. No feedback was given. The subject's head was stabilized by chin and forehead rests. Binocular viewing was used, with natural pupils. The subject fixated a small paper dot for the peripheral viewing conditions; the center of the screen was fixated freely in foveal cases. Four subjects were tested, two of the authors (SY and JZ) and two naive, paid observers (MF and KM), all with normal or corrected-to-normal vision. (Subjects with significant refractive errors used appropriate spectacle correction.) The pattern presentation time was 200 msec for subjects SY and MF, and 400 msec for subjects KM and JZ (for those two subjects, 200 msec presentation is too brief to achieve robust performance).*

Psychometric functions relating the true aperture movement to percent judged "left" were plotted for each subject for all conditions of grating drift. Each point on the curve, i.e. percentage judged left for each combination of aperture/grating movement, was based on the results of 10 sessions (or 50 responses), unless otherwise noted. From the psychometric function, the point at which 50% of the direction judgments are "left" can be estimated by probit analysis (Finney, 1971), and is taken as the measure of the strength of motion induction in each situation. The best-fitting curves from the probit analysis are shown along with the data.

3. RESULTS

The first two experiments were designed to demonstrate both motion contrast and motion integration effects under different stimulus and viewing conditions. Impressions from initial observations indicated that the apparent speed of a hard aperture viewed foveally is decreased when the grating drifts in the same direction as the aperture, but increased otherwise, suggesting simultaneous motion contrast. However, the apparent speed of a soft aperture viewed peripherally appears to increase when the grating drifts in the same direction, and decrease otherwise, suggesting motion integration (assimilation). To quantify these informal observations, a directional discrimination task was employed. We show the results by plotting the psychometric functions of all four subjects for judgments of aperture motion direction for both the hard aperture, foveal case (Fig. 2) and the soft aperture, peripheral case (Fig. 3). Seven different aperture velocities, from leftward directions (negative) to rightward directions (positive) in equal incremental steps, were coupled with different modes of grating motion, either drifting to the left (dotted line, solid squares) or drifting to the right (dashed line, solid diamonds). The aperture velocity step was 0.2 deg/sec, and the 4 c/deg grating drifted at 6 Hz (or 1.5 deg/sec). The viewing time was 200 msec for subjects MF and SY and 400 msec for KM and JZ. As can be seen, the faster the aperture moves leftward (the more negative the

*It was pointed out by an anonymous reviewer that at shorter presentation durations, direction discrimination of the grating is possible, but motion contrast or integration may not occur as they require higher level visual processings. von der Heydt and Peterhans (1989) reported that there is a 77 msec delay in the processing of non-Fourier motion information in V2.

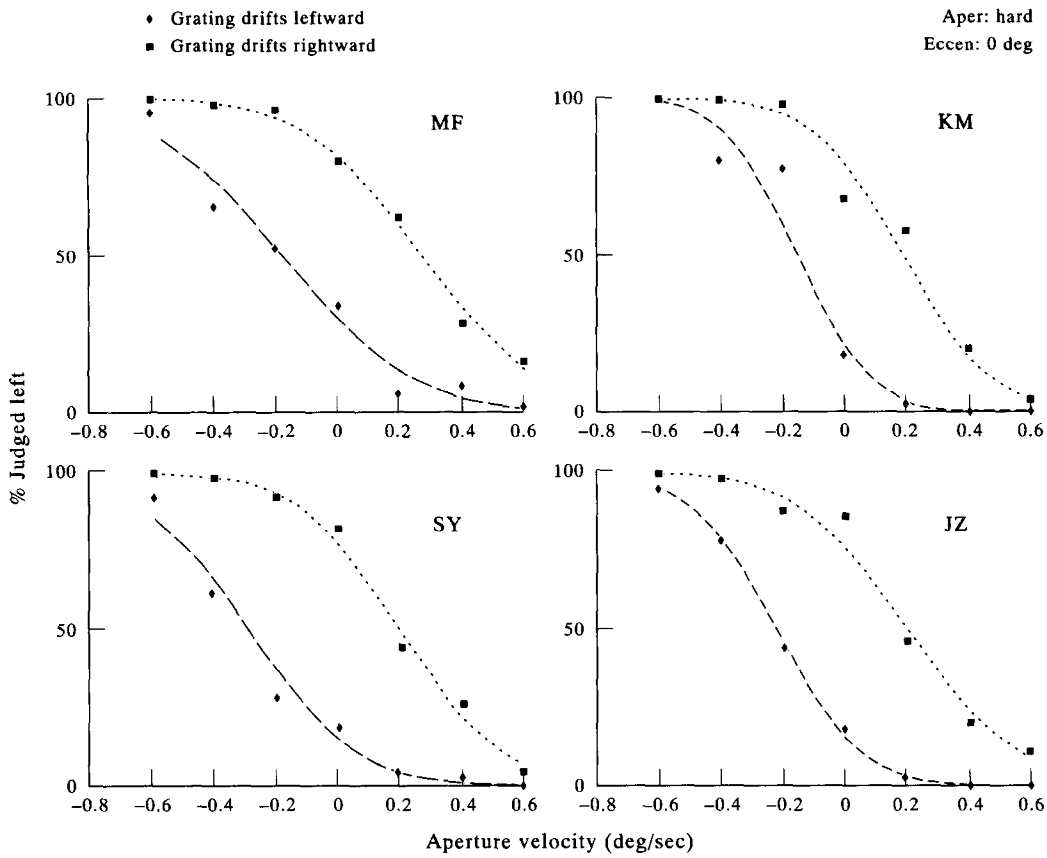

FIGURE 2. Psychometric functions for four subjects reflecting motion judgment of a hard aperture viewed foveally in the presence of a drifting grating. The percentage judged leftward is plotted against the velocity of the moving aperture (positive is rightward), when the 4 c/deg grating is drifting at 6 Hz either toward the left (solid diamonds) or towards the right (solid squares). Also shown along with the data points are best-fitting curves based upon probit analysis. The stimulus duration is 200 msec for subjects MF and SY and 400 msec for subjects KM and JZ.

aperture velocity), the more likely it is to be judged as moving towards the left. When the aperture is hard (abrupt change in luminance contrast) and presented at 0 deg eccentricity (Fig. 2), the aperture is always more likely to be judged as moving leftward when the grating drifts to the right than when the grating drifts to the left (the dotted line is shifted to the right of the dashed line). The opposite trend was found, however, when the aperture was soft (Gaussian fall-off in luminance contrast) and viewed at 2 deg eccentricity (Fig. 3). Here the velocity increments were 0.3 deg/sec with all other conditions identical to the previous case. The aperture was more likely to be judged as moving leftward when the grating drifted to the left than when the grating drifted to the right (the dotted line is shifted to the left of the dashed line). In particular, a stationary aperture was judged to move leftward less than half the time if the grating drifted to the right, and more than half the time if the grating drifted to the left. This is the opposite of the previous case with a hard aperture and foveal viewing.

In both cases, the actual aperture velocity at which the aperture is judged to move left on 50% of the trials represents the physical motion of the aperture required to null out its perceived illusory motion induced by the grating drift. This motion nulling point is a measure of the strength of these motion contrast and assimilation effects. To avoid subjects' possible intrinsic bias, the difference between the motion nulling points from the two directions of grating drift was taken to yield a number characterizing the amount of motion induction under each experimental condition. Operationally,

$$\text{amount of motion induction} = \tfrac{1}{2}(\text{motion nulling point for grating rightward} - \text{motion nulling point for grating leftward}). \quad (3)$$

A positive value indicates motion contrast, while a negative value indicates motion integration. This measure is used in all subsequent manipulations. If this number increases under a certain manipulation, this would imply either an increase in motion contrast or a decrease in motion integration. We can then say that such a manipulation favors a motion contrast mechanism or disfavors a motion integration mechanism.

While the judgment bias in (or accuracy at) discriminating motion directions is reflected in the locus of the 50% point in the psychometric function, the sensitivity (or reliability) of the judgment is reflected in the slope of the psychometric function at the 50% point (alternatively, as half the distance between the 25 and 75% points). The steeper the slope, the greater the sensitivity of directional discrimination. In Fig. 4, the results for two standard conditions are plotted. The experimental conditions are identical to those of Fig. 2 (for hard aperture at 0 deg eccentricity) and Fig. 3 (for soft aperture at 2 deg eccentricity), except that the grating was stationary instead of drifting to the left or right. This is essentially a measure of the accuracy and reliability of direction judgments in the fovea and at 2 deg eccentricity without the added complexity of an inducing stimulus. Not surprisingly, the slopes were quite different in the two conditions: all subjects are much more sensitive at discriminating the motion of a hard aperture in the fovea than that of a soft aperture in the periphery (Fig. 4). The results of Figs 2–4 are summarized as Table 1.

Manipulation of aperture softness

In order to study the determinants of this motion induction systematically, we first varied the softness of the patch, or the steepness of the fall-off in luminance contrast of the grating at the boundary (see Fig. 1). All patches had the same apparent size, predetermined individually for each subject before this manipulation (see Methods). Psychometric functions were obtained separately for each, based on 100 responses per data point. Plotted in Fig. 5 is the amount of motion induction calculated by equation (3) for two subjects as a function of aperture softness. Here values on the abscissa have been scaled by the σ value for the softest case, therefore representing a relative measure of softness (i.e. 0 for the hardest case and 1 for the softest case). All other parameters (except the softness of the patch) were the same as previously described, and the viewing condition was foveal with free fixation. As can be seen, this measure of motion induction decreased with aperture softness for both subjects. Remember that a positive value of this measure indicates motion contrast, while a negative value implies motion integration. In other words, the data of Fig. 5 suggest that increasing aperture softness favors a motion integration mechanism, while decreasing softness favors a motion contrast mechanism. Interestingly, for these two subjects, the positive number for the hardest aperture changes to a negative number for the softest aperture. A complete reversal of the direction of motion induction effects (from motion contrast to motion integration) was observed. (Two-tailed t-test revealed that for JZ, the amount of motion induction for softest and hardest apertures differ significantly, $P < 0.0001$.) We have not observed this complete reversal in all other subjects, though the decrease in this measure of motion induction with increasing aperture softness is robustly found.

Manipulation of eccentricity

Another way of manipulating the apparent boundary distinctiveness is to change the viewing eccentricity, since contrast sensitivity to high spatial frequencies (abrupt luminance changes) decreases with increasing eccentricity. Based on the previous observations, we would expect

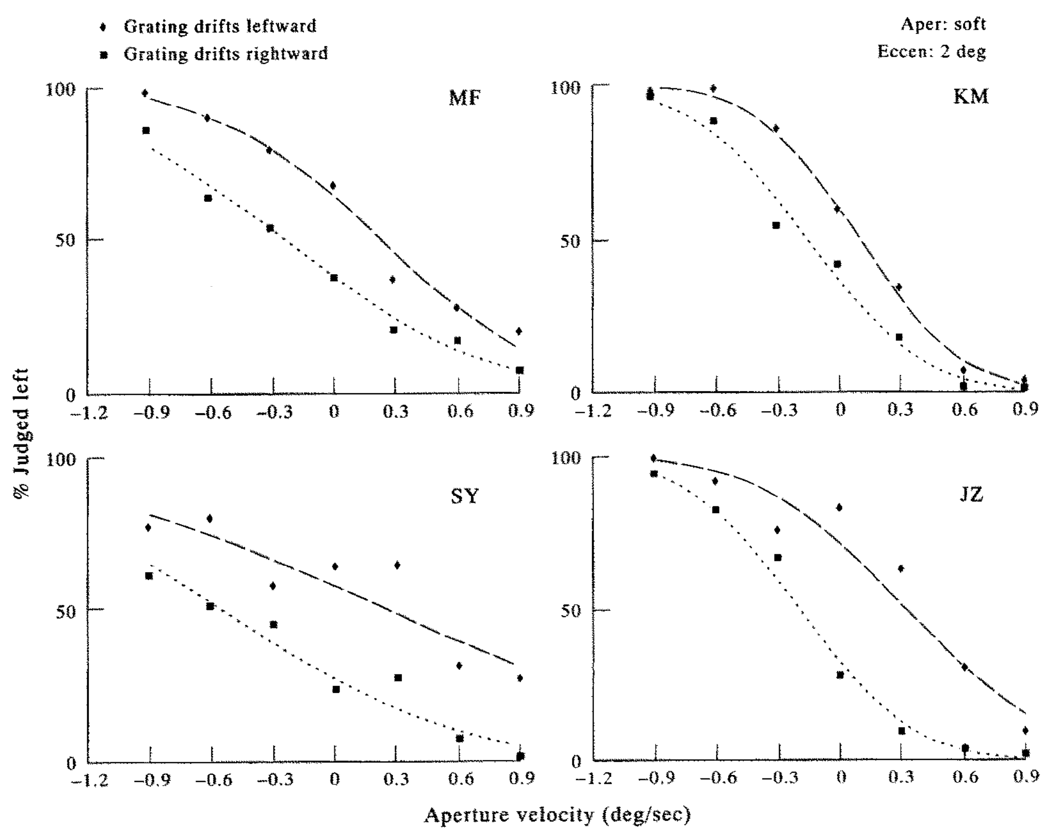

FIGURE 3. Psychometric functions for four subjects reflecting motion judgment of a soft aperture viewed at 2 deg eccentricity in the presence of a drifting grating. The percentage judged leftward is plotted against the velocity of the moving aperture (positive is rightward), when the 4 c/deg grating is drifting at 6 Hz either toward the left (solid diamonds) or toward the right (solid squares). Also shown along with the data points are best-fitting curves based upon probit analysis. The stimulus duration is 200 msec for subjects MF and SY and 400 msec for subjects KM and JZ.

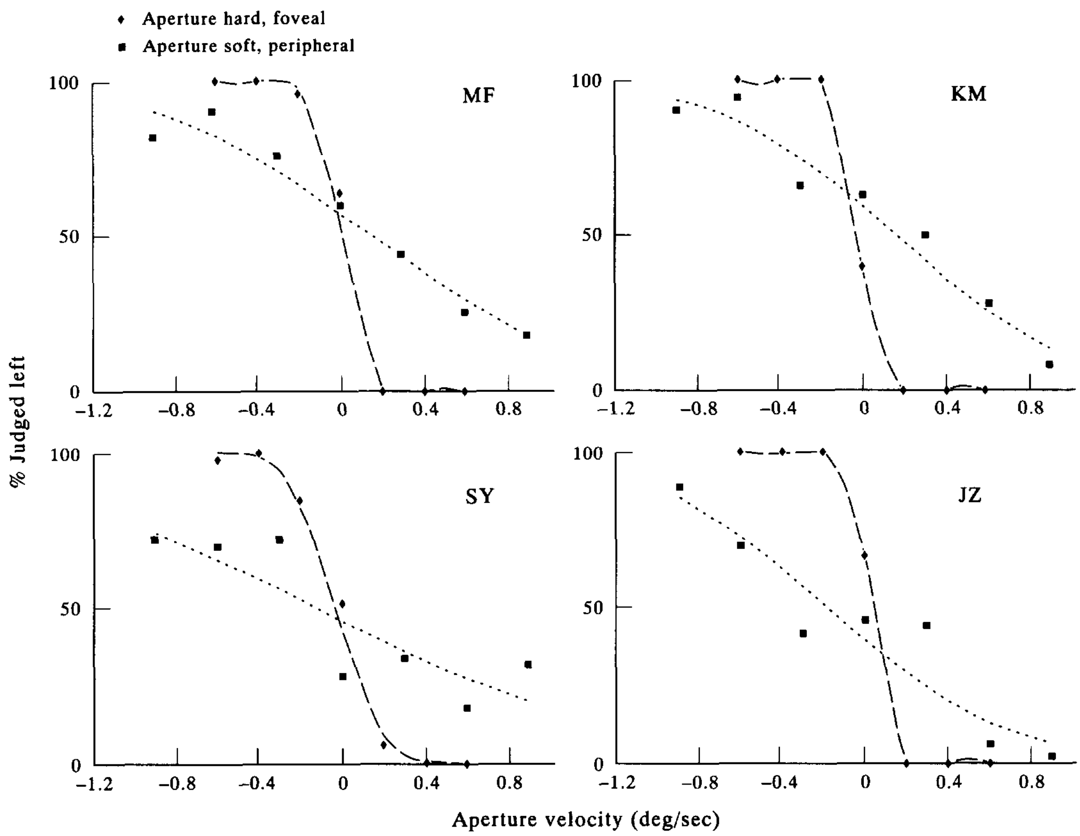

FIGURE 4. Psychometric functions for four subjects reflecting judgment of aperture movement in the presence of a stationary grating. The percentage judged leftward is plotted against the velocity of the moving aperture (positive is rightward), which is either hard and presented in the fovea (solid diamonds), or soft and presented at 2 deg eccentricity (solid squares). Also shown along with the data points are best-fitting curves based on probit analysis. The presentation time was 200 msec for subjects MF and SY and 400 msec for subjects KM and JZ.

that motion integration would be favored with increasing eccentricity, just as it was with increasing aperture softness. Indeed, for the two subjects tested, the amount of motion induction decreased (i.e. motion integration is favored) when the pattern was presented more and more peripherally (Fig. 6). This was true for both hard apertures (solid line) and soft apertures (dashed line). Note that at each eccentricity, this measure is always larger (more positive) for the hard aperture than for the soft aperture, consistent with the results of the previous manipulation. Again, sign reversal is present in some conditions.

Manipulation of background luminance

We also manipulated the background luminance with respect to the mean luminance of the grating for the hard aperture condition (Fig. 7). Here the numbers on the abscissa are the values of the background luminance scaled by the grating (or patch) mean luminance, which was always at 40 cd/m^2. As can be seen, the amount of motion induction (motion contrast in this case) peaked at the point at which the grating mean luminance and background luminance are matched, i.e. when the luminance ratio is 1.0 as shown on the abscissa. (Two-tailed t-test revealed that for MF, the amount of motion induction for luminance ratio 0.0 compared with 1.0, and for luminance ratio 1.0 compared with 2.0, differ significantly, $P < 0.0005$ and $P < 0.05$, respectively.) Note that when the grating was either brighter (abscissa value < 1.0) or darker (abscissa value > 1.0) than the background, the judgment of motion direction of the aperture was closer to being veridical (the amount of motion induction was closer to zero). The implication of this observation will be discussed later.

Manipulation of temporal frequency

Lastly, we examined the influence of temporal frequency (or velocity) of the grating on motion induction. Three temporal frequencies were used, 3, 6, and 12 Hz. The spatial frequency of the grating was always 4 c/deg. The aperture was hard and was viewed foveally. For the two subjects tested on this condition, the amount of motion induction (motion contrast in this case) increased with increasing temporal frequency (Fig. 8).*

*For a constant spatial frequency, a higher temporal frequency means a faster speed of grating drift. In a study of classical motion induction using a single dot enclosed by a "frame of reference" (Wallach & Becklen, 1983), motion contrast was shown to decrease with increasing inducing velocity. However, Tynan and Sekuler (1975) found that motion contrast increased with increasing inducing velocity, which is consistent with our present results. This is also consistent with our suggestion that the inducing stimulus in our moving aperture paradigm (i.e. the grating), as well as that of Tynan and Sekuler (random-dot pattern), stimulates a low level mechanism, while the classic demonstration of motion induction by a "frame of reference" may be due to a higher level interpretation of moving signals.

TABLE 1. Point of subjective equivalence (PSE), its standard error (SE), and the threshold of psychometric functions for each subject when the grating drifts leftward, rightward, or is stationary, under hard aperture (at foveal presentation) and soft aperture (presented at 2 deg eccentricity) conditions

		MF	KM	SY	JZ
Hard ecc = 0					
Leftward	PSE	−0.18	−0.15	−0.29	−0.23
	SE	0.02	0.02	0.03	0.02
	Threshold	0.19	0.13	0.19	0.15
Stationary	PSE	0	−0.01	−0.03	0.02
	SE	0.01	0.01	0.02	0.01
	Threshold	0.06	0.06	0.12	0.06
Rightward	PSE	0.37	0.19	0.19	0.2
	SE	0.02	0.02	0.03	0.03
	Threshold	0.19	0.16	0.18	0.19
Soft ecc = 2					
Leftward	PSE	0.25	0.11	0.28	0.32
	SE	0.05	0.04	0.1	0.05
	Threshold	0.44	0.28	0.88	0.39
Stationary	PSE	0.17	0.16	−0.11	−0.18
	SE	0.06	0.05	0.09	0.05
	Threshold	0.56	0.46	0.82	0.47
Rightward	PSE	−0.22	−0.14	−0.53	−0.19
	SE	0.06	0.04	0.08	0.04
	Threshold	0.53	0.31	0.61	0.3

This table summarizes the curve-fitting values for psychometric functions presented in Figs 2–4. PSE indicates the point at 50% judged left, measuring the bias of direction judgment. Threshold indicates the difference between the points corresponding to 75 and 50% judged left, measuring the sensitivity of the psychometric function.

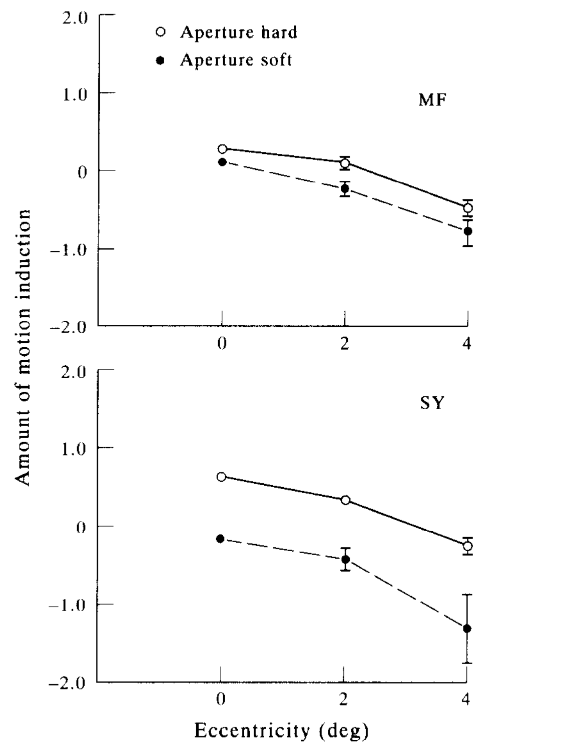

FIGURE 6. Amount of motion induction (in deg/sec) plotted against viewing eccentricity for two subjects for both hard (solid line, open circles) and soft (dashed line, solid circles) apertures. Error bars reflect 95% confidence level in the t distribution. Each data point is based on two psychometric functions (similar to the ones reported in Figs 2 and 3, with aperture speed at 0.3 deg/sec steps), each of which is on 50 trials per point. A positive amount of motion induction indicates motion contrast, while a negative amount implies motion integration. The presentation time for both subjects was 200 msec.

4. SUMMARY

In this moving aperture paradigm, the judgment of aperture motion (motion of the patch as a whole) was strongly influenced by the drifting of an internal grating that the patch enclosed. A stationary aperture appeared to move either in the same direction (motion integration) or in the opposite direction (motion contrast) of the grating drift, depending on stimulus conditions and viewing eccentricity.

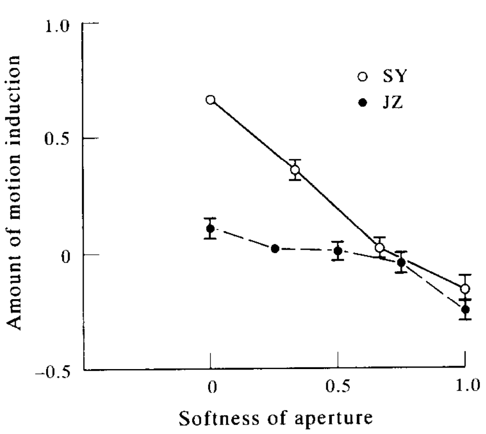

FIGURE 5. Amount of motion induction (in deg/sec) plotted against softness of aperture for two subjects. Here 0 represents the hardest case and 1 represents the softest. Error bars reflect the 95% confidence level in the t distribution. Each data point is based on two psychometric functions (similar to the ones reported in Figs 2 and 3, with aperture speed at 0.3 deg/sec steps), each of which is based on 100 trials per point. A positive amount of motion induction indicates motion contrast, while a negative amount implies motion integration. The stimulus was foveally presented. The presentation time was 200 msec for SY and 400 msec for JZ.

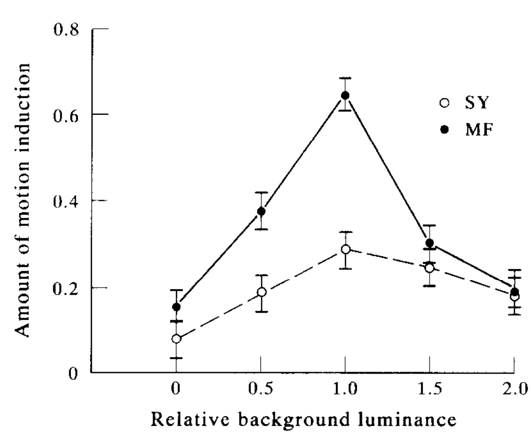

FIGURE 7. Amount of motion induction (in deg/sec) plotted against relative background luminance for two subjects. The numbers on the abscissa are the background luminance values scaled by the grating (patch) mean luminance, which is always set at 40 cd/m^2. Error bars reflect the 95% confidence level in the t distribution. Each data point is based on two psychometric functions (similar to the ones reported in Fig. 2, with aperture speed at 0.3 deg/sec steps), each of which is based on 50 trials per point. The pattern was with hard aperture and viewed foveally. The presentation time was 200 msec for both subjects.

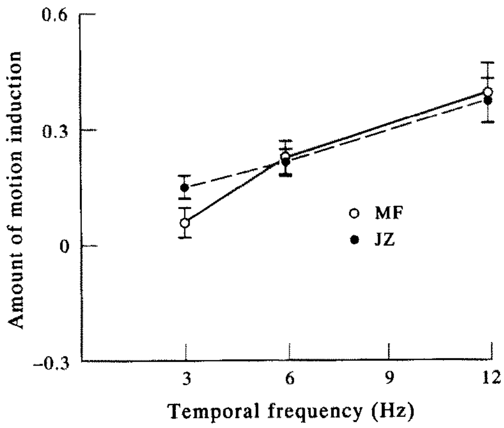

FIGURE 8. Amount of motion induction (in deg/sec) plotted against temporal frequency of the grating for two subjects. Three temporal frequencies were used, 3, 6, and 12 Hz. Error bars reflect the 95% confidence level in the t distribution. Each data point is based on two psychometric functions (similar to the ones reported in Fig. 2, with aperture speed at 0.2 deg/sec steps), each of which was based on 50 trials per point. The pattern was with hard aperture and viewed foveally. The presentation time was 200 msec for MF and 400 msec for JZ.

(1) When the boundary of the aperture was sharp (abrupt decrease in luminance contrast, or "hard" aperture) and the pattern was viewed at 0 deg eccentricity, the direction of illusory movement of the stationary patch was opposite to the drifting direction of the inducing grating, demonstrating motion contrast.

(2) When the boundary of the aperture was fuzzy (gradual decrease in luminance contrast, or "soft") and the pattern was viewed at 2 deg eccentricity, the direction of illusory movement of the stationary patch was the same as the drifting direction of the inducing grating, demonstrating motion integration.

(3) In addition to the judgment bias (or accuracy), the sensitivity (or reliability) of the aperture motion judgment also differed in the two cases, being greater for the motion of a hard aperture under foveal viewing than for that of a soft aperture under peripheral viewing.

(4) Increasing viewing eccentricity appears to favor motion integration for both hard and soft apertures.

(5) Decreasing aperture softness appears to favor motion contrast under foveal viewing.

(6) For a hard aperture viewed foveally, the amount of motion contrast appears to: (i) increase with temporal frequency of the grating, and (ii) become maximal when the grating mean luminance is matched to the background luminance.

5. DISCUSSION

The illusory motion of a stationary object produced by motion of its surround was first studied by Duncker (1929), who used a rectangular frame rocking back and forth, enclosing a stationary dot within. The induced motion of the dot was in the direction opposite to the movement of the frame, and has been explained by Gestalt theories in terms of a subjective "frame of reference". However, motion induction can be shown to occur even when no explicit reference frame is present. As Loomis and Nakayama (1973) and Tynan and Sekuler (1975) demonstrated, the perceived velocity of a moving object is influenced by the motion of its immediate surround. This simultaneous motion contrast, like other contrast effects in vision, may reflect a center-surround organization of underlying velocity-tuned units, perhaps in cortical area MT (Allman, Miezin & McGuinness, 1985). In distinction to motion contrast, a stationary object may also appear to move in the same direction as another moving (inducing) object under certain circumstances. This is known as motion capture or motion integration. An example is the illusory motion of a yellow square on a white background which is induced by the motion of a cluster of superimposed black dots (Ramachandran, 1981). This illusion is strongest when the background and the square are isoluminant and viewed peripherally, suggesting that positional uncertainty may contribute to such an effect.

In order to study the parametric conditions for motion contrast and motion integration (motion capture), it is desirable to demonstrate both these effects within a single experimental paradigm but under different experimental controls. In our experiments, a delimited patch enclosing a grating was made to move against a uniform background while the grating inside was drifted independently. Motion contrast and motion integration effects were both revealed in the judgment of the direction of patch movement under different conditions. Specifically, if the edge of the patch is sharp ("hard" aperture) and the pattern is presented in the fovea, motion contrast is seen. On the other hand, if the edge is fuzzy ("soft" aperture) and the pattern is presented in the periphery, motion integration is observed. This difference can be understood in terms of the importance of a boundary in determining the figure–ground relationships of motion signals. A hard aperture viewed foveally has a clear boundary within which the grating is enclosed. The sharp transition between a full-contrast drifting grating and the background results in a discontinuity in local motion signals near the boundary of the aperture. The grating and the aperture are seen as distinctively different objects undergoing separate motions—the boundary of the circular aperture appears to move against a background of a moving grating, which is seen as though through a window. A contrast mechanism such as that reflected here is useful for enhancing the motion signal of a figure in the presence of a moving surround.

In the case of a soft aperture under peripheral viewing, the boundary of the grating is not well-defined at all. There is no abrupt transition or discontinuity in the local motion signals or the edges of the figure. The whole patch can be seen as a single figure moving against a uniform background. The fall-off of luminance contrast is gradual, resulting in smooth change of local motion signals. The motions of the grating and the aperture are integrated so as to increase the signal strength of the figure, i.e. a patch of grating. In either case, the design principle underlying motion contrast and motion integration effects can be viewed as one that increases the signal strength of the figure and suppresses the signal strength of the ground, the only difference being in what constitutes the "figure" and "ground" in each situation. Indeed, our results with aperture softness and eccentricity can also be taken to imply that the assignment of figure and ground can depend upon, among other things, the size and density of underlying cortical receptive fields.

Further speculations may be made under the general framework of the short- and long-range motion systems. We noted in the Introduction that the moving aperture probably stimulates the two motion systems quasi-independently. This is to say that the movement of the grating provides a strong input to the short-range system based on its Fourier motion energy, while the movement of the patch as a whole activates primarily the long-range system based on the displacement of the patch locus. By manipulating border distinctiveness, the aperture of the patch may become associated or dissociated with the enclosed grating. Our experimental results suggest that when the aperture and grating are regarded as representing separate entities (hard aperture), the local motion signal (short-range mechanism) and the global motion signal (long-range mechanism) become dissociated, and there is motion contrast between the two signals which seem to represent two different moving objects. When the aperture and the grating are perceived as a single entity (soft aperture), the short-range mechanism and long-range mechanism became associated in that the local motion (measured by its Fourier motion energy) now serves as a cause of the global motion (measured by its overall spatial displacement over time). There is integration between the local motion signal (Fourier motion energy) and the global motion signal (positional displacement).

In the manipulation of background luminance with respect to the mean luminance of the grating, the amount of motion contrast is largest when the luminances are matched and decreases when the patch is either brighter or darker than its surround. This can be understood as follows. The subject's task of judging the global motion of an aperture could be mediated through the long-range motion system, which appears to be based on the computation of positional displacement of a distinct feature. The more salient the feature, the stronger is its input to this long-range system, and the less powerful should be the influence of the short-range system. In other words, by increasing or decreasing the mean luminance of the patch with respect to background luminance, the circular patch becomes more distinct from its surround so that the proportion of activation of short-range and long-range motion systems changes in favor of the long-range system. Therefore, more veridical judgment of aperture motion is possible, with accordingly less effect of the inducing grating movement.

Directly related to our study is a preliminary report by Murakami and Shimojo (1991). The paradigm they employed is similar to the one used by Ramachandran (1981), i.e. a static green disk on a large red background with a cluster of moving black dots superimposed upon and covering the extent of the target disk. In addition to motion capture by the moving dots when the green disk and the background are isoluminant and under peripheral viewing, as Ramachandran previously reported, these authors also reported a motion contrast effect when the pattern was away from the isoluminant condition and viewed foveally. In other words, within a range near the isoluminant point (between the disk and the background), the static disk appeared to move in the same direction as the moving black dots (motion capture). Outside this range, the disk and the dots appeared to move in opposite directions (motion contrast). Increasing eccentricity increased the luminance range within which motion capture occurred. These results are in agreement with our observations and with the suggestion that clear-cut boundaries (a luminance edge in their case and a sharp aperture in our case) under foveal viewing favors motion contrast, while uncertain boundaries (an isoluminant chromatic edge in their case and a fuzzy aperture in our case) under peripheral viewing favor motion integration.

Nawrot and Sekuler (1990) studied the spatial conditions of motion contrast and motion integration (assimilation) using cinematograms comprising alternating strips of dot patterns within which dots either move in one direction or in random directions. They found that depending on the strip size, the strip of dots which are actually moving in random directions appears to move collectively in the same (motion assimilation) or opposite (motion contrast) direction as the adjoining strips of dots which are in correlated motion. Narrower strips favor assimilation (motion capture) while wider strips favor contrast. They also reported hysteresis in these effects, suggesting a cooperative interaction between local motion signals across distances. Their study and ours, as well as the preliminary study of Murakami and Shimojo, all used a single paradigm to demonstrate both motion contrast and motion integration effects under different conditions. Taken together, these results suggest that motion contrast is strongest with clear figure boundaries, wide spatial separations and foveal viewing, while motion integration is favored by narrow spatial separation, uncertain (fuzzy or isoluminant chromatic) figure boundaries and peripheral viewing conditions.

With respect to possible neurophysiological substrates, many neurons in area MT are known to be selective for the velocity (direction and speed) of a stimulus (Maunsell & Van Essen, 1983; Albright, 1984; Mikami *et al.*, 1986a, b). Their responses are frequently influenced by stimuli presented outside the classical receptive field (Allman *et al.*, 1985). Most recently, Born and Tootell (1992) reported that there are two anatomically segregated sub-populations of MT cells, one with antagonistic surrounds (their responses become suppressed by motion in the surround in the same direction as the optimal direction of motion for the center), and the other with synergestic surrounds (these show summation of motion cues over large areas of the visual field). These interactions are similar to the psychophysical observations of motion contrast and motion integration reported and discussed earlier. The presence or absence of surround inhibition reportedly occurs in clusters within tangential penetrations and is constant within a particular perpendicular penetration (a vertical column). The only exceptions were in the input layers (upper layer 4 and 6) where antagonistic surrounds appear to be absent, suggesting that motion contrast and motion integration occurred as a result of processing within MT rather than earlier in the stream (say in V1). This is consistent with the suggestion that the functional role of area MT is to extract the velocity of identified visual objects and that its velocity extraction is influenced by the way objects are segmented or identified in the first place.

REFERENCES

Adelson, E. H. & Bergen, J. R. (1985). Spatio-temporal energy models for the perception of motion. *Journal of the Optical Society of America A, 2*, 284–299.

Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology, 52*, 1106–1130.

Albright, T. D. (1992). Form-cue invariant motion processing in primate visual cortex. *Science, 255*, 1141–1143.

Allman, J. M., Miezin, F. & McGuinness, E. (1985). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception, 14*, 105–126.

Anstis, S. (1989). Kinetic edges become displaced, segregated, and invisible. In Lam, D. M.-K. & Gilbert, C. D. (Eds), *Proceedings of the retina research foundation symposia, Vol. 2, neural mechanisms of visual perception*. Woodlands, Tex.: Portfolio.

Baker, C. L. Jr & Braddick, O. J. (1985). Temporal properties of the short-range process in apparent motion. *Perception, 14*, 181–192.

Baker, C. L. Jr & Cynader, M. S. (1986). Spatial receptive field properties of direction selective neurons in cat striate cortex. *Journal of Neurophysiology, 55*, 1136–1152.

Born, R. T. & Tootell, R. B. H. (1992). Segregation of global and local motion processing in primate middle temporal visual area. *Nature (London), 357*, 497–499.

Braddick, O. J. (1973). The masking of apparent motion in random-dot patterns. *Vision Research, 13*, 355–369.

Braddick, O. J. (1974). A short-range process in apparent motion. *Vision Research, 14*, 519–527.

Braddick, O. J. (1980). Low-level and high-level processes in apparent motion. *Philosophical Transactions of the Royal Society of London B, 290*, 137–151.

Chang, J. J. & Julesz, B. (1983). Displacement limits for spatial frequency filtered random-dot cinematograms in apparent motion. *Vision Research, 23*, 1379–1385.

Chubb, C. & Sperling, G. (1988). Drift-balanced random stimuli: A general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A, 5*, 1986–2007.

Cleary, R. & Braddick, O. J. (1990a). Direction discrimination for band-pass filtered random dot kinematograms. *Vision Research, 30*, 303–316.

Cleary, R. & Braddick, O. J. (1990b). Masking of low frequency information in short-range apparent motion. *Vision Research, 30*, 317–327.

De Valois, R. L. & De Valois, K. K. (1991). Vernier acuity with stationary moving gabors. *Vision Research, 31*, 1619–1626.

van Doorn, A. J. & Koenderink, J. J. (1982a). Temporal properties of the visual detectability of moving spatial white noise. *Experimental Brain Research, 45*, 179–188.

van Doorn, A. J. & Koenderink, J. J. (1982b). Spatial properties of the visual detectability of moving spatial white noise. *Experimental Brain Research, 45*, 189–195.

Duncker, K. (1929). Ueber induzierte Bewegung (ein Beitrag zur Theorie optisch Wahrgenommenor). *Psychologische Forschung, 12*, 180–259. Excerpts translated and reprinted in (1938) Ellis, W. D. (Ed.), *A source book of Gestalt psychology*. London: Routledge (& Kegan Paul).

Finney, D. J. (1971). *Probit analysis*. Cambridge: Cambridge University Press.

Hamilton, D. B., Albrecht, D. G. & Geisler, W. S. (1989). Visual cortical receptive fields in monkey and cat: Spatial and temporal phase transfer function. *Vision Research, 29*, 1285–1308.

von der Heydt, R. & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex—I. Lines of pattern discontinuity. *Journal of Neuroscience, 9*, 1731–1748.

Korte, A. (1915). Kinematoskopische Untersuchungen. *Zeitschrift für Psychologie, 72*, 193–296.

Loomis, J. M. & Nakayama, K. (1973). A velocity analogue of brightness contrast. *Perception, 2*, 425–428.

MacKay, D. M. (1973). Visual stability and voluntary eye movement. In Jung, R. (Ed.), *Handbook of sensory physiology* (VII/3A, pp. 307–332). Heidelberg: Springer.

MacKay, D. M. (1976). Perceptual conflict between visual motion and change of location. *Vision Research, 16*, 557–558.

Maunsell, J. H. R. & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey—I. Selectivity for stimulus direction, speed and orientation. *Journal of Neurophysiology, 49*, 1127–1147.

Mikami, A., Newsome, W. T. & Wurtz, R. H. (1986a). Motion selectivity in macaque visual cortex—I. Mechanisms of direction and speed selectivity in extrastriate area MT. *Journal of Neurophysiology, 55*, 1308–1327.

Mikami, A., Newsome, W. T. & Wurtz, R. H. (1986b). Motion selectivity in macaque visual cortex—II. Spatiotemporal range of directional interactions in MT and V1. *Journal of Neurophysiology, 55*, 1328–1339.

Morgan, M. J. (1980). Spatiotemporal filtering and the interpolation effect in apparent motion. *Perception, 9*, 161–174.

Morgan, M. J. & Ward, R. (1980). Conditions for motion flow in dynamic visual noise. *Vision Research, 20*, 431–435.

Morgan, M. J. & Ward, R. J. (1982). Mechanisms of interpolation of human spatial vision. *Nature (London), 299*, 553–555.

Murakami, I. & Shimojo, S. (1991). Motion capture changes to induced motion at higher contrasts and smaller eccentricities. *Investigative Ophthalmology and Visual Science (Suppl.), 32*, 830.

Nawrot, M. & Sekular, R. (1990). Assimilation and contrast in motion perception: Explorations in cooperativity. *Vision Research, 30*, 1434–1451.

Newsome, W. T., Mikami, A. & Wurtz, R. H. (1986). Motion selectivity in macaque visual cortex—III. Psychophysics and physiology of apparent motion. *Journal of Neurophysiology, 55*, 1340–1351.

Ramachandran, V. S. (1981). Perception of apparent motion. In *Studies in the cognitive sciences* (Vol. 11). Bulletin issued by School of Social Sciences, University of California at Irvine, Calif.

Ramachandran, V. S. & Anstis, S. M. (1990). Illusory displacement of equiluminous kinetic edges. *Perception, 19*, 611–616.

Reid, R. C., Soodak, R. E. & Shapley, R. M. (1987). Linear mechanisms of directional selectivity in simple cells of cat striate cortex. *Proceedings of the National Academy of Science, U.S.A., 84*, 8740–8744.

Reid, R. C., Soodak, R. E. & Shapley, R. M. (1991). Directional selectivity and spatiotemporal structure of receptive fields of simple cells in cat striate cortex. *Journal of Neurophysiology, 66*, 505–529.

van Santen, J. P. H. & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America A, 2*, 300–321.

Tynan, P. & Sekular, R. (1975). Simultaneous motion contrast: Velocity sensitivity and depth responses. *Vision Research, 15*, 1231–1238.

Wallach, H. & Becklen, B. (1983). An effect of speed on induced motion. *Perception & Psychophysics*, *34*, 237–242.

Watson, A. B. & Ahumada, A. (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America A*, *2*, 322–341.

Wertheimer, G. (1912). Experimentelle Studien uber das Sehen von Bewegungen. *Zeitschrift Psychologische*, *61*, 161–265. Partly in Shipley, T. (Trans.), *Classics in psychology*. New York: Philosophical Library.

Wilson, H. R., Ferrera, V. P. & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience*, *9*, 79–97.

Wohlgemuth, A. (1911). On the aftereffect of seen movement. *British Journal of Psychology Monographs (Suppl.)*, *1*.