



# Modulation of Motion Aftereffect by Surround Motion and its Dependence on Stimulus Size and Eccentricity

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**As a mechanism to detect differential motion, we have proposed a model of ‘a motion contrast detector’ and have shown that it can explain the perceptual change from motion capture to induced motion with increasing stimulus size and decreasing eccentricity. To further test the feasibility of the model, we examined the effect of surround motion on the motion aftereffect (MAE) elicited in the center. Using a drifting grating surrounded by another drifting grating, the duration of MAE in the center after adaptation was measured for various surround velocities (Expt 1). MAE was stronger when the surround moved oppositely to, than together with, the center. This finding was consistent with some previous reports. Using similar stimuli, MAE was measured at various stimulus sizes and eccentricities by the cancellation technique (Expt 2). The effect of surround modulation turned out to vary with both size and eccentricity. We examined if the apparent dependence on eccentricity could reflect a simpler effect of cortical size when the data were rescaled according to a linear scaling factor. We interpret our results in terms of motion contrast detectors, possibly located in the area MT.**

Motion aftereffect   Motion contrast   Scaling factor   Center-surround antagonism   Area MT

## INTRODUCTION

Motion in the retinal image is used for various visual functions (Nakayama, 1985). These include to segregate moving objects from their background, to extract the contour of objects, to recover the depth and 3-D structure. Evidently, information processing to achieve these functions require mechanisms sensitive to relative motion between adjacent points in the image. In the present study, we aim to show psychophysical evidence for a mechanism to detect motion whose direction is opposite to that of its surround.

A psychophysically feasible way to explore the possibility for such a mechanism is to examine whether motion perception within one region in the image is influenced by motion surrounding that region. Induced motion, an illusory motion of a stationary stimulus in the opposite direction to its moving surround, has been studied extensively in this context by a number of researchers (see Reinhardt-Rutland, 1988 for review). Some of them have proposed as its underlying mechanism a directionally antagonistic unit that is inhibited by moving stimuli in the surround (Anstis & Reinhardt-

Rutland, 1976; Loomis & Nakayama, 1973; Nakayama & Tyler, 1978; Nawrot & Sekuler, 1990; Reinhardt-Rutland, 1981, 1983; Strelow & Day, 1975; Tynan & Sekuler, 1975; Walker & Powell, 1974). We will tentatively call such a motion processing unit ‘a motion contrast detector’. What we mean by ‘motion contrast’ is the difference in physical velocity between adjacent regions in the visual field [as originally defined by Regan and Beverley (1984)].

Ramachandran (1987) reported a phenomenon called motion capture, an illusory motion of a stationary equiluminant stimulus in the same direction as its moving surround. Murakami and Shimojo (1993b) have recently found that, when the overall size of the stimulus was decreased, induced motion could change to motion capture, even if the stationary stimulus is not equiluminant. Furthermore, the critical size at which induced motion changes to motion capture differed across eccentricities. To interpret these results, Murakami and Shimojo (1993b) suggested that a population of the hypothetical mechanism is distributed around a certain stimulus size at each eccentricity—a stimulus of the optimal size results in a percept due to relative motion processing (induced motion). A smaller stimulus, where both the inducer and the target are within the center field, results in another percept due to non-selective pooling of motion information below resolution limit (motion capture).

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Since induced motion has often been *explained* by such a hypothetical mechanism having center-surround antagonism, the next step is to *test* the hypothesis that such a mechanism does exist in the human visual system. For this purpose, adaptation paradigm would be promising. After prolonged exposure to an adapting stimulus moving in one direction, a stationary stimulus appears to move in the direction opposite to that of the adapting stimulus (Wohlgemuth, 1911). This effect called 'motion aftereffect (MAE)' has been taken as strong evidence for a mechanism specialized for motion processing. What kind of aftereffect will occur when the visual system is adapted to relative motion, rather than ordinary unidirectional motion? If the aftereffect is significantly enhanced, then that would indicate existence of the mechanism for relative motion.

The influence of surrounding stimuli on MAE was demonstrated clearly by Day and Strelow (1971) and Strelow and Day (1971). They showed that MAE was stronger when there was some patterned background than when the background was dark. Bell, Lehmkuhle and Westendorf (1976) showed a similar result. Also, Richards (1971) observed that there was some optimal stimulus size for the MAE of spiral motion, suggesting surround inhibition. Recently, Shioiri, Ono and Sato (1991) found that the detection threshold for shearing motion was elevated selectively after prolonged observation of shearing motion and argued for the possibility of relative motion detectors. Besides, some studies have showed that after the prolonged observation of a stationary region surrounded by motion, MAE could occur in the center, as though induced motion during the adaptation period behaved as an adapting 'stimulus' (Anstis & Reinhardt-Rutland, 1976; Reinhardt-Rutland, 1981, 1983; Swanston & Wade, 1992). In short, there are numerous studies suggesting certain spatial interactions between processings of one region and its surround. Yet, there has been no study so far, testing MAE in the center-surround stimulus configuration and systematically examining its dependence on size.

In the present study, we examined the effect on MAE of the velocity of the surrounding motion, in order to confirm the relevance of relative motion processing units.

### EXPERIMENT 1

In this experiment, we examined effects of the velocity of a surround on the duration of MAE elicited in a center region, where a moving stimulus like a normal condition of MAE was presented during adaptation. Effects of size and eccentricity, which are to be examined more systematically in Expt 2, were also sought tentatively.

#### Methods

Three males (aged 23–29 yr; two were naive volunteers) participated. All had normal or corrected-to-normal visual acuity.

The experiment was done in a dark room. Each session was preceded by dark adaptation for at least 5 min. The

stimulus was presented on a CRT monitor (Apple 13" CRT; 640 × 480 pixels; vertical scanning frequency 66.7 Hz, non-interlaced) controlled by a personal computer (Apple Macintosh). Intensity parameter had an 8-bit resolution. The subject used only his right eye with a natural pupil, with the left eye occluded by an eye-patch. The subject's head was stabilized with a chin rest. The viewing distance was 57 cm.

A schematic view of the stimulus configuration is shown in Fig. 1. A bull's eye (10 min in diameter) was presented as a fixation point. Two sinusoidal gratings were presented. Both of them were achromatic (CIE: 0.33, 0.33), were oriented horizontally, and had the spatial frequency of 1 c/deg. Their maximal and minimal luminances were 118 and 0.3 cd/m<sup>2</sup>, respectively. One of the gratings (referred to as *center grating*) was presented within a circular region in the nasal visual field and was drifted vertically at 2.2 deg/sec. The diameter of the circle was varied in four steps (1°20', 2°40', 4° and 5°20') and the eccentricity (the distance between the center and the fixation point) was varied in four steps (3°, 5.5°, 8° and 10.5°). In a rectangular region (23.5 × 17.6°) outside the center grating, the other grating (*surround grating*) was drifted at one of the following velocities: -4.4, -2.2, 0, 2.2, 4.4 deg/sec, where positives indicate the same direction as the center grating's, and negatives indicate the opposite direction. When both gratings drifted at the same velocity, the phases of the two waves were shifted relative to each other by  $\frac{1}{2}\pi$  radians so that the contour of the circular region should be visible, just as was seen clearly in other conditions.

One trial consisted of three stages: the adaptation, the test, and the recovery.

At first, only the fixation point was presented in a dark background. Three sec later, both gratings appeared simultaneously and served as adapting stimuli. The center

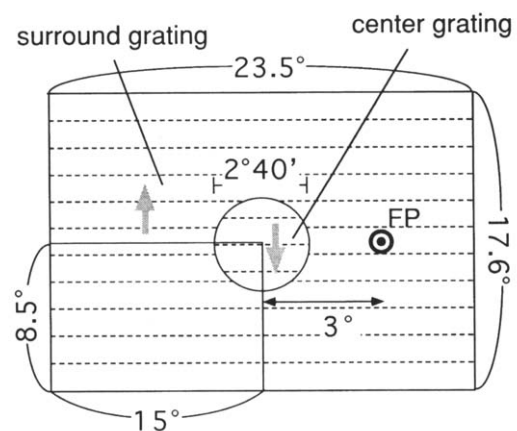


FIGURE 1. A schematic view of the stimulus configuration of Expt 1. The size and the eccentricity were not fixed to the values indicated in the figure (see text). The stripe with broken lines depicts a sinusoidal grating. 'FP' refers to the fixation point. The center grating was presented within a circular window in the middle of the display, and drifted vertically in the adaptation period. The surround grating covered the whole display outside the center grating, and drifted at a velocity between -4.4 and 4.4 deg/sec in the adaptation period. In the test period, the surround grating was extinguished and there remained only the center grating (which was physically stationary) in a dark background.

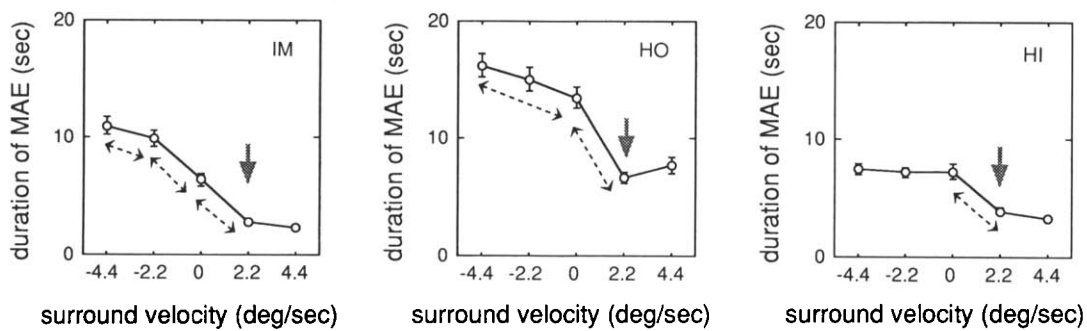


FIGURE 2. Results of Expt 1 for three subjects. The duration of MAE is plotted against the velocity of the surround grating in the adaptation period. Positive and negative velocities indicate the same direction as, and the opposite direction to, respectively, the velocity of the center grating in the adaptation period (indicated by the downward arrows). Each point is based on 64 repeated measurements (data for various sizes and eccentricities are combined to see the main effect of the velocity). The bars indicate SEs. Arrows with broken lines depict major significant differences between data points.

grating drifted upward (or downward, in a half of sessions), while the surround grating drifted at one of the five velocities. Making sure to keep foveating the fixation point, the subject observed the drifting gratings for 40 sec. This was long enough to produce a strong MAE.

After the adaptation period, the surround grating disappeared, only the fixation point and the center grating remained in a dark background.\* The center grating was set to be physically stationary while other parameters were unchanged. The subject perceived MAE in the region of the center grating. The subject's task was to observe the stimuli with no eye movement and to push a button at the cessation of MAE. The subject's response was monitored at 60 Hz sampling rate. The duration of MAE was defined as the interval between the beginning of the test period and the subject's response.

The subject's response immediately triggered a change of the display to a dynamic Mondrian-like noise pattern. The subject observed it for 40 sec in order to extinguish any residual MAE carried over.

In each session, the velocity of the surround grating, and the size and eccentricity of the center grating, were varied randomly. Each subject took four sessions, one session one day (two for upward motion and two for downward motion in the center; the data obtained for these two conditions showed no systematic difference and were combined in the analysis).

## Results

The main result is shown in Fig. 2. Here the duration of MAE elicited in the center grating is plotted against the velocity of the surround grating. The data for various sizes and eccentricities are combined in order to see

the main effect of the velocity, which was significant ( $F_{4, 240} = 124.7$  for IM, 25.2 for HO and 32.1 for HI;  $P < 0.0001$  for all). Arrows with broken lines depict major significant differences between data points (Fisher's protected least significant difference;  $P < 0.05$ ). As obvious, the duration of MAE was greater when the gratings moved in opposite directions, than when they moved in the same direction, in the adaptation period, although what was presented in the center was identical through all the conditions. More precisely, the duration was longer for two subjects when the surround moved oppositely than when it was stationary; the duration was shorter for all the subjects when the surround moved in the same direction than when it was stationary. These data clearly indicate that the magnitude of MAE elicited within the region of one adapting stimulus was influenced by another adapting stimulus presented outside the former. MAE is 'facilitated' by the surround moving in the opposite direction and 'suppressed' by the surround moving in the same direction, if the condition of the stationary surround can be considered as 'base line'. We hereafter call these facilitatory and suppressive effects 'surround modulation'.

We also found some trends about effects of size and eccentricity such that MAE gradually increased with increasing size and with decreasing eccentricity. One could interpret such trends as merely reflecting the variability of the subject's criterion: increasing the size and decreasing the eccentricity of the test stimulus, it might become easier for the subject to judge the cessation time of a MAE. Alternatively, there might be some optimal size for the surround modulation of MAE at a given eccentricity. These issues are to be examined more systematically in Expt 2, employing a cancellation technique.

\*If the center grating in the test had just the same size as in the adaptation, the subject observed a peculiar MAE beside an ordinary one. It was seen confined along the contour of the center grating and appeared to drift along the curved contour. Such MAE was often in the direction predicted by surround direction, so we interpret this MAE as the result of small fixation errors during adaptation. To avoid this, the size of the center grating in the test was 80% in diameter. A similar manipulation was applied in Expt 2, where the width and height of the center grating in the test were 80% ( $0.8w \times 1.6w$ ) compared to those in the adaptation.

## Discussion

What is the underlying mechanism of the surround modulation? Like for the ordinary MAE (e.g. Mather, 1980), the most plausible explanation would be that a subset of directionally selective mechanisms tuned to the direction of an adapting stimulus are adapted and desensitized more strongly than others, and that this

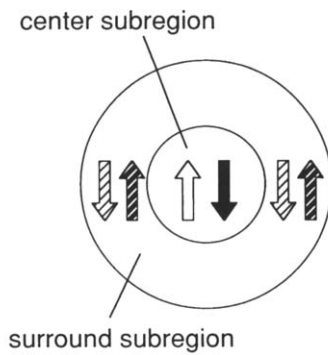


FIGURE 3. The RF property of a hypothetical motion contrast detector. The white and black arrows depict the preferred and null directions, respectively. The RF is subdivided into two subregions, center and surround. The center subregion has one directional selectivity such that the detector is excited by one direction (as indicated by the upward white arrow) and possibly inhibited by null direction (downward black arrow) inside of this subregion. The surround subregion has the directional selectivity opposite to the center subregion, as indicated by the hatched arrows.

temporary imbalance produces negative MAE. In the case of Expt 1, however, mechanisms sensitive to unidirectional motion such as Reichardt-type detectors (Reichardt, 1961) or directionally selective neurons in the area V1 (e.g. Hubel & Wiesel, 1968), cannot be responsible for the surround modulation of MAE, because they will show identical behavior with or without surrounding motion. Thus, it is reasonable to introduce the idea of some higher-order processing mechanism sensitive to the difference in motion signals from adjacent regions such as center and surround. As a most plausible model, let us describe the receptive field (RF) structure of 'a motion contrast detector' (see Fig. 3, see also Murakami & Shimojo, 1993b) and its relationship to our results.

Suppose the RF of this detector has a small center subregion and a larger surround subregion. The center subregion is selective to motion in one direction. The surround subregion is tuned antagonistically to the center subregion in a double-opponent way (*cf* Gorea & Papathomas, 1993). First, the detector's activity to the preferred direction in the center subregion is facilitated by a motion in the opposite direction in the surround subregion. This property is needed to explain the 'facilitatory' type of surround modulation of MAE. Second, the activity is suppressed when there is a stimulus in the same direction in the surround subregion. This property is needed to explain the 'suppressive' type of surround modulation of MAE. As a whole, these properties seem to be designed to detect motion contrast between the center and the surround, so that we call this mechanism a motion contrast detector.\*

\*Since this model describes the interaction between subunits tuned to opposite directions, the surround modulation might be abolished when the center and surround moved in orthogonal directions. Such a 'directional tuning' of the surround subregion, though an absolutely intriguing question, has been left to be investigated.

For the next step, we intend to test whether these hypothetical detectors are really implemented in the human visual system. Wherever its physiological locus may be, the implementation should obey neuroanatomical and neurophysiological constraints in general. One of the simplest constraints is differences in 'scaling factor' across eccentricities. In visual areas organized topographically like V1 (Dow, Snyder, Vautin & Bauer, 1981) and MT (Maunsell & Van Essen, 1987), the cortical magnification (the cortical extent to represent 1 deg of the visual field) is gradually diminished with increasing eccentricity. Another feature apparently corresponding to this change is that the RF size of neurons gradually increases with increasing eccentricity. At any rate, these physiological characteristics lead to the idea that the mechanisms in a certain visual area are different across the visual field representation not in quality but only in scale; accordingly, the performance should be identical if stimulus size is the same not in physical terms but in terms of the extent of cortical representation or the normalized size relative to RF size.

A number of studies have successfully applied the concept of scaling factor to show that psychophysical performances across eccentricities are different only quantitatively and can be scaled to each other (see Drasdo, 1991 for review; as for motion, e.g. Levi, Klein & Aitsebaomo, 1984; McKee & Nakayama, 1984; Wright & Johnston, 1985). Indeed, Wright and Johnson (1985) applied this approach to MAE of unidirectional motion. They presented a drifting grating in a window with a blurred edge and measured the magnitude of MAE for predetermined stimulus size for each eccentricity according to an estimate of human cortical magnification factor of the primary visual cortex (Rovamo & Virsu, 1979). As a result, they found that any apparent differences across eccentricities were extinguished when the variables were expressed in millimeters of cortex activated.

Introducing a similar approach, we measured the amount of the surround modulation of MAE for various sizes at various eccentricities. If local processing units such as motion contrast detectors are responsible for the surround modulation, then the differences in MAE across various eccentricities could disappear by appropriately scaling the size according to some scaling factor. The duration of MAE seems less appropriate as a measure for such a quantitative analysis because the subject's criterion for the cessation of MAE might shift as a function of size and eccentricity. An alternative choice is the cancellation technique (to measure the physical velocity to just cancel a MAE, making the test stimulus appear stationary).

## EXPERIMENT 2

In this experiment, we examined the eccentricity- and size-dependence of the surround modulation effects using opposing motions between center and surround. The cancellation velocity (the physical velocity to just cancel the MAE) was measured.

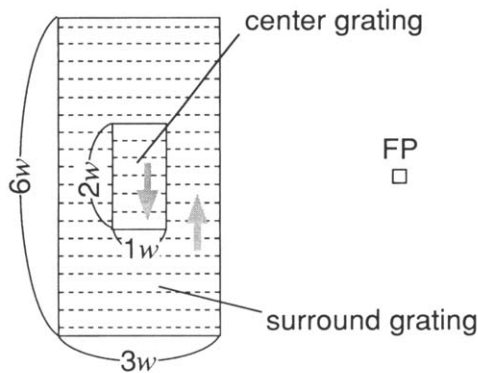


FIGURE 4. A schematic view of the stimulus configuration of Expt 2. The stripe with broken lines depicts a sinusoidal grating. 'FP' refers to the fixation point. See text for details.

### Methods

Four normal males (aged 23–36 yr; two were naive volunteers) participated. The subject IM (the first author) underwent the full stimulus set while the other subjects took a smaller subset. The equipment was identical to that used in Expt 1 except for the viewing distance, which were varied across sessions as described later.

Figure 4 shows a schematic view of the stimulus configuration. As in Expt 1, two achromatic sinusoidal gratings, center and surround, were used for adapting stimuli. The sizes of the gratings were controlled by one parameter  $w$ . Both gratings were oriented horizontally, with a spatial frequency of  $3/w$  c/deg; they had the same luminance contrast as in Expt 1. The center grating was presented within a rectangular region ( $1w \times 2w$ ) and drifted vertically ( $5w/3$  deg/sec). The surround grating was presented within another rectangular region ( $3w \times 6w$ ) surrounding the center grating and drifted in the opposite direction ( $-5w/3$  deg/sec). The stimuli were presented in the nasal visual field and were elongated vertically in an attempt to present effective adapting stimuli in a spatially confined region around each eccentricity.

The magnitude of MAE does not depend on spatial frequency or speed (when the adapting and test stimuli have the same spatial frequency like in the present study) but depends on temporal frequency of an adapting stimulus (Over & Lovegrove, 1973; Pantle, 1974; Wright, 1986; Wright & Johnston, 1985). Accordingly, the spatial frequency and speed of both gratings were varied contingently with varying the size parameter  $w$ , while the temporal frequency was fixed to 5 Hz (this frequency is nearly optimal to elicit strong MAE; see Pantle, 1974; Wright & Johnston, 1985)\*. The size parameter  $w$  was varied in seven steps (40, 60, 75, 90, 105, 120 and 140') by changing the distance from the chin rest to the monitor. The eccentricity was varied in six steps (2, 3, 4.5, 6, 8, 10°) by changing the position of the fixation point.

\*Quantitatively similar results were obtained for the subject IM when the spatial frequencies were doubled ( $6/w$  c/deg) and the speeds were halved ( $5w/6$  deg/sec) in a control experiment.

One trial consisted of three stages: the initial adaptation, the repeated pairs of test and re-adaptation and the recovery.

At first, the two gratings of one of the seven sizes appeared at one of the six eccentricities. The center grating drifted upward, say, while the surround grating drifted in the opposite direction. The subject just observed them for 30 sec.

In the next stage, adjustment (1 sec) and re-adaptation (5 sec) were alternated. In the adjustment period, only the fixation point and the center grating remained on the display. Downward MAE would be observed in the center grating if it were physically stationary. The physical velocity of the grating was adjustable by dragging the computer mouse smoothly back and forth. Thus, what the subject perceived was the sum of the MAE component and the physical motion component. The subject's task in this period was to drift the grating upward at an appropriate physical velocity so as to 'cancel' the MAE (see Wright & Johnston, 1985 for the cancellation technique). The physical velocity at the first adjustment period was chosen randomly from range of  $\pm 2w/3$  deg/sec, hence the subject was totally blind to the magnitude of MAE component in the perceived motion from beginning to end. Since MAE is known to deteriorate quickly, an adjustment period was coupled with a following re-adaptation period (5 sec). In this period, the stimuli were just the same as that in the initial adaptation. Immediately after this re-adaptation period a next adjustment period came, when the center grating drifted initially at the velocity set at the end of the last adjustment period. The adjustment period followed by a readaptation period was repeated as many (at least four) times as the subject required until the grating appeared stationary. When the subject was satisfied with his adjustment and pushed a button after several times of adjustment periods, the 'cancellation velocity' was recorded and the recovery period was triggered. It was identical to that in Expt 1 and lasted for 40 sec.

The center grating drifted upward in five trials and downward in six trials, and the data were combined in the analysis.

### Results and discussion

Figure 5(a) shows the results for one subject IM (the first author). In Fig. 5(a), the cancellation velocity is plotted as a function of physical stimulus size (the width of the center grating). The profiles for various eccentricities are overlaid. Plus cancellation velocities indicate the same direction as the center grating in the adaptation (and thus indicate the magnitude of MAE). As clearly seen, the strength of MAE varied with the size and eccentricity, and the profiles show a strong interaction between these parameters: at smaller eccentricities, MAE was weakened with increasing size; at larger eccentricities, MAE was increased with increasing size and then decreased in most cases.

Here we attempt to rescale the physical size into some 'cortical' size for the data shown in Fig. 5(a) (see Watson, 1987 for the idea of rescaling data). This analysis is based

on the concept that mechanisms underlying this type of MAE are homogeneous across eccentricities except for a variation of scale (RF size, cortical magnification, etc.). Since we do not know what kind of fitting function or physiological knowledge is appropriate, we apply a knowledge-free procedure introduced by Whitaker, Rovamo, Macveigh and Mäkelä (1992). Using the least square method iteratively, it calculates out the scaling

factor such that profiles for different eccentricities agree best with each other (see *Appendix*). Assuming that the scaling factor should be a linear function of eccentricity, the factors estimated for individual eccentricities were fitted with a linear regression line.

The above analysis resulted in an estimated scaling function in the form of  $(F - 1) = 0.142 (E - 6)$ , or equivalently,  $F = 0.148 + 0.142 E$  [Fig. 5(b)]. Dividing the physical size and physical velocity by the estimated scaling factor,  $F$ , we obtain the scaled size ( $\text{deg}_6$ ) and scaled velocity ( $\text{deg}_6/\text{sec}$ ), where the unit 'deg<sub>6</sub>' denotes one degree at 6° eccentricity. When the data are plotted using these scaled values, a remarkable (though imperfect) agreement across eccentricities is obvious [Fig. 5(c)]. The residual disagreement would be interpreted as a noise, since no systematic deviation is found and most of the standard errors overlap.

The agreement to a reasonable extent suggests that the underlying mechanisms for the surround modulation of MAE are qualitatively similar across the visual field, their eccentricity dependence being only the matter of scale. Also, the agreed curve shows an inverted-U-shaped function, suggesting a band-pass characteristic of the underlying mechanism. Both the reasonable agreement by scaling and the inverted-U-shaped function are altogether consistent with the idea of the motion contrast detector, as far as IM's data are concerned.

These seemingly straightforward characteristics, however, could not apply very well to the data for other subjects. Figure 6 shows their data before and after scaling. Estimating a scaling function on the basis of their own data, if possible, seemed unreliable, considering their larger variances or fewer data points. Alternatively, they were scaled according to the scaling function estimated for IM's data. It is obvious for the subjects HO and SS that the scaled data showed *at least* a better agreement than the raw data. However, it is unclear whether the particular scaling function for IM's data is best, since any arbitrary scaling factor over a wide range would lead to at least better agreement than the raw data. The subject MK seemed to be exceptional, but his data are unreliable because MAE is very feeble (see the ordinate) and noisy.

The better agreement of the scaled data for three of the four subjects suggests that the underlying mechanisms are different across eccentricities not in quality but only in scale. However, it is still uncertain whether the eccentricity-dependence obey a single linear scaling function.

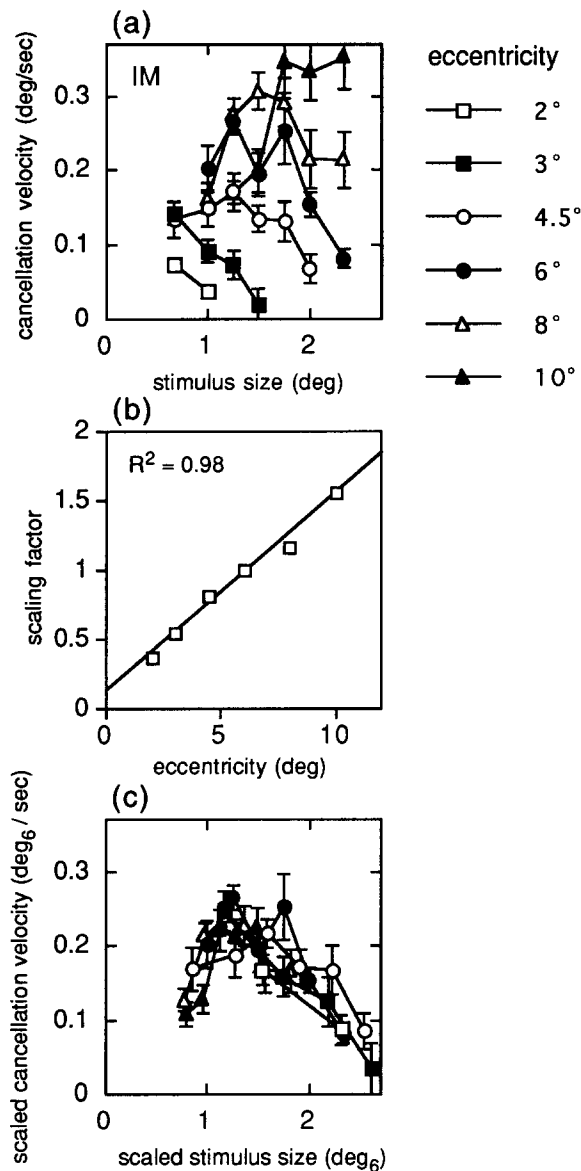


FIGURE 5. Results of Expt 2, for the subject IM. (a) Cancellation velocity refers to the physical velocity of the test grating to just cancel the MAE. Stimulus size refers to the size parameter  $w$ . The data for various eccentricities are superimposed. Each point is based on 11 repeated measurements. The bars indicate SEs. (b) The scaling factor measured for each eccentricity and the result of linear regression analysis. The data for each eccentricity  $x^\circ$  were tentatively scaled with various scaling factors and were superimposed on the data at 6° eccentricity, and then the factor that yields the best agreement between  $x^\circ$  data and 6° data was defined as an estimated scaling factor for  $x^\circ$ . These factors are plotted against eccentricity with a regression line. See *Appendix* for details. (c) The data at each eccentricity in (a) are divided by the scaling factor and replotted. The stimulus size is expressed in terms of degrees at 6° eccentricity ( $\text{deg}_6$ ) and the velocity is expressed in terms of  $\text{deg}_6/\text{sec}$ , for convenience.

## GENERAL DISCUSSION

In Expt 1, we have demonstrated two points, which we would call surround modulation effects. First, stronger MAE was elicited in the center when there were opposite directions of motion between the center and the surround than when the surround was stationary (for two of three subjects). This finding is consistent with Anstis and Reinhardt-Rutland (1976). They observed that the presence of a moving stimulus adjacent to a stationary

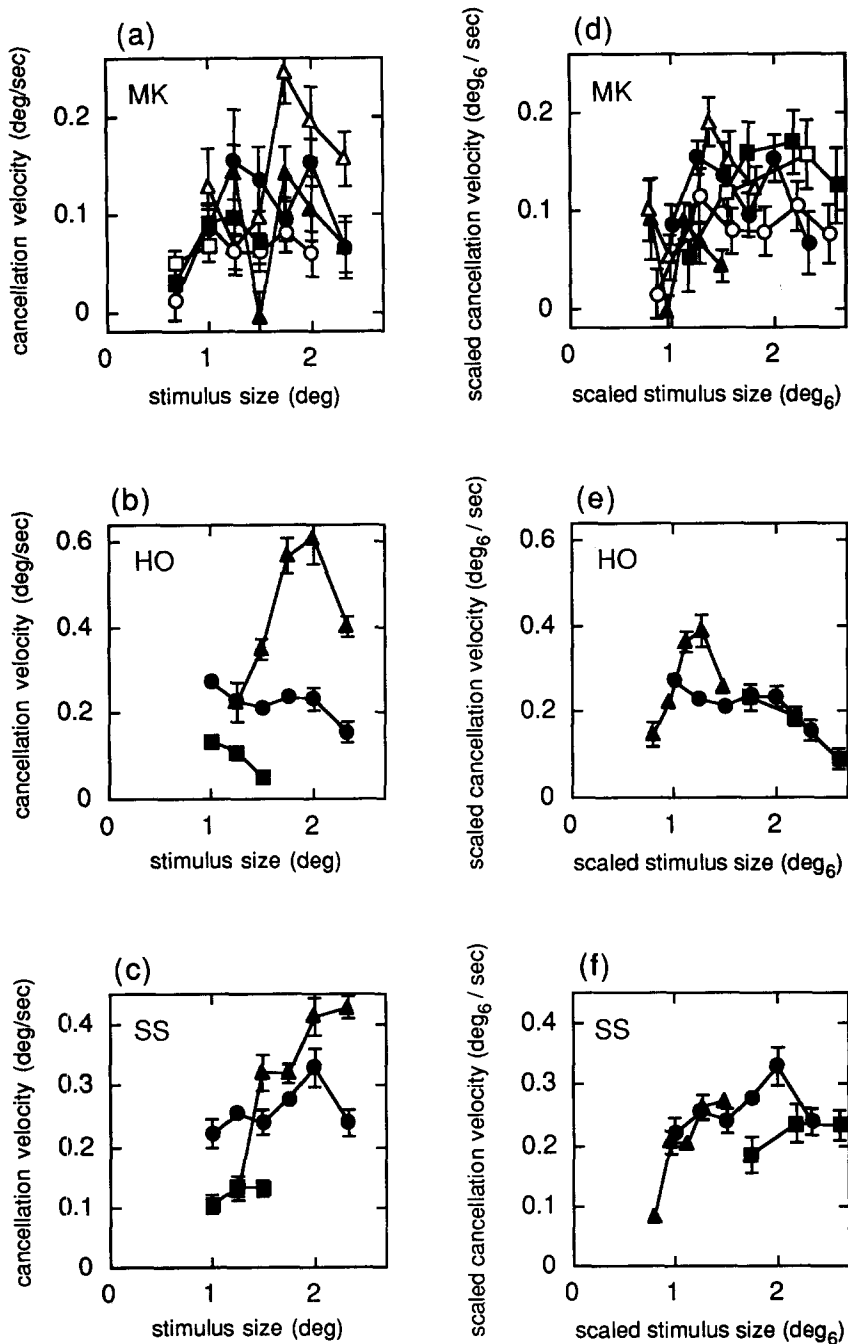


FIGURE 6. Results for other subjects. (a-c) Subject's original data before scaling. (d-f) The scaled data according to the scaling factor estimated using IM's data. Other conventions are the same as Fig. 5.

stimulus caused the latter to appear to move oppositely (i.e. induced motion) and in turn to yield MAE in the opposite direction to this induced motion. If such a component of MAE caused by induced motion and another component of MAE caused by real motion are additive, it is naturally expected that the MAE in the present study is stronger when the surround moved oppositely than when it was stationary. Indeed it was the case. Second, stronger MAE was elicited in the center when the surround was stationary than when it moved in the same direction as the center. This finding may have a bearing on the study by Day and Strelow (1971). They found that the adapting stimulus presented in a vacant background yielded very poor MAE and argued for the

importance of the visibility of the surround. Putting their finding and our results together, what is important for MAE to occur seems the visibility of the surround that is not moving together with the center. This is also consistent with the notion of zero velocity as a special kind of motion information, which was demonstrated by 'position capture' (see Murakami & Shimojo, 1993b).

Swanston and Wade (1992) also found that a stationary stimulus adjacent to moving surrounds in an otherwise dark background (except for the fixation point) gave rise to induced motion and successive MAE in the opposite direction. To account for this, they argued the importance of the frame of reference, with respect to which the relative motion should be computed and allocated to other

objects. According to their theory, the relative motion of the stationary center is computed with respect to the frame of reference, namely the moving surround. As a result, the center appears to move during adaptation and gives rise to successive MAE. Our finding could be described in relation to their theory, in that our surround grating totally enclosed the center and thus would be easily become the frame of reference. What could be the mechanism to make this scheme possible?

As a responsible mechanism of the surround modulation effects, we propose a hypothetical processing unit, 'a motion contrast detector', whose RF is organized in center-surround antagonistic fashion with respect to preferred direction. A physiological basis of our hypothesis is that a subpopulation of neurons in the area MT have been reported to show qualitatively the same response property as our motion contrast detectors (Allman, Miezin & McGuinness, 1985; Born & Tootell, 1992; Komatsu & Wurtz, 1988; Lagae, Gulyás, Raiguel & Orban, 1989; Tanaka, Hikosaka, Saito, Yukié, Fukada & Iwai, 1986).

In Expt 2, we have found that the surround modulation is dependent on stimulus size. The size-dependent profiles obtained for different eccentricities showed a better agreement with each other for three of the four subjects, once spatial parameters are scaled according to the scaling technique developed by Whitaker *et al.* (1992). The inverted-U-shaped function obtained after scaling suggests that there is an optimal size for surround modulation. Since eye movement was not monitored, there is some possibility of artifact from fixation error, which would be constant across eccentricities and would lead to a more serious underestimation of MAE as the size becomes smaller. This could be a part of the cause for the residual disagreement.

Even though the scaling was not perfect for all the subjects, it is worth while to compare the estimated scaling factor to the previous studies. In Fig. 7, the scaling factor estimated in the present study is plotted together with that used by Wright and Johnston (1985) in scaling the MAE of absolute motion. Both lines are normalized so as to pass (0, 1). Obviously our scaling factor is steeper than Wright and Johnston's. It may raise the possibility that absolute motion and relative motion are processed in distinct physiological stages. The eccentricity-dependences of RF sizes of the macaque's V1 (Dow *et al.*, 1981) and MT (Albright & Desimone, 1987) neurons are normalized and plotted together for comparison. The slope for absolute motion is between the slope of V1 and MT factors. It might be that MAE of absolute motion is constrained by both loci, since there are many neurons having strong directionality both in V1 and in MT. On the other hand, the scaling factor of relative motion is even steeper than MT's. They should be identical if our motion contrast detectors are located in MT and the eccentricity-dependence of the RF sizes of the human MT-homologue neurons are comparable to the macaque's. One possibility to interpret this discrepancy is the contribution of other, possibly higher, loci such as MST. Another possibility is interspecies difference in RF

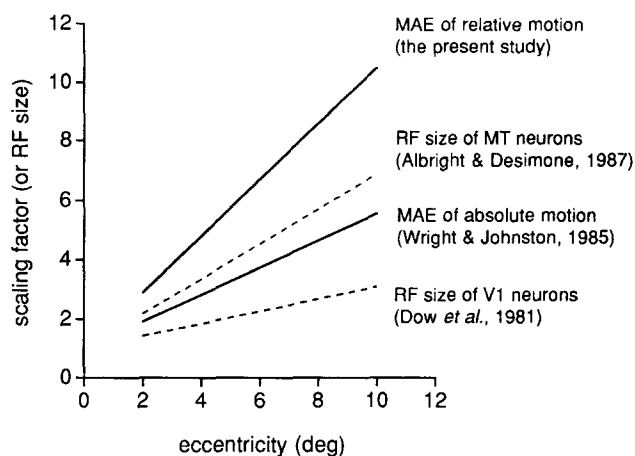


FIGURE 7. The scaling factor for IM is normalized to pass (0, 1) and plotted in the range of  $2^{\circ}$ – $10^{\circ}$  used in the present study. Also plotted is the scaling factor used in the study by Wright and Johnston (1985) (scaling factor =  $1 + 0.42 E + 0.00012 E^2$ ), approximated to a linear function (scaling factor =  $0.953 + 0.434 E$ ) for this range and then normalized. The eccentricity-dependence of RF size of the macaque's V1 (Dow *et al.*, 1981) [ $\log_{10}(RF \times 60) = 1.1438 + 0.1920 x + 0.0712 x^2 + 0.0619 x^3$ , where  $x = \log_{10}(E \times 60) - 1.5$ ] is approximated to a linear function ( $RF = 0.232 + 0.0488 E$ ) for this range, normalized and plotted together. Also, the eccentricity-dependence of RF size of the macaque's MT (Albright & Desimone, 1987) ( $RF = 1.04 + 0.61 E$ ) are normalized and plotted together. The symbols  $RF$  and  $E$  in the equations refer to RF size (deg) and eccentricity (deg), respectively.

sizes between the human and the macaque. Still another possibility is that it is not very adequate for the present purpose to use the RF size reported by Albright and Desimone (1987). Their data were based on the area MT as a whole, while there has been a report to show that the neurons having surround inhibition are clustered in distinct columns (Born & Tootell, 1992).

So far, psychophysical evidence for the motion contrast detector has been collected only in suprathreshold domain (Murakami & Shimojo, 1993b and the present study). Now, an interesting question would be whether the motion detection threshold also shows similar surround modulation effects. We are preliminarily obtaining positive results (Murakami & Shimojo, 1993a).

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## APPENDIX

In an attempt to rescale the physical size into some 'cortical' size, we apply a knowledge-free procedure introduced by Whitaker *et al.* (1992). In the analysis for the present study, the data at an intermediate eccentricity,  $6^\circ$ , was taken as the 'master', to which the data at other eccentricities were to be scaled. Since both the ordinate and the abscissa had a spatial parameter, they were scaled by the same scaling factor. First, the profiles for  $6^\circ$  and for another eccentricity  $x^\circ$  were superimposed. Second, an approximation to the scaling factor was estimated by eye, while the data at  $x^\circ$  were scaled and replotted using various factors. Third, a more precise setting of the factor was done by using polynomial regression. The  $6^\circ$  and  $x^\circ$  data were merged and fitted with a single third-order polynomial regression curve (the choice of this particular regression would not be crucial) and the sum of squares of residuals were calculated. Then the  $x^\circ$  data were scaled with a slightly different factor and the same procedure was repeated to find a scaling factor that minimized the sum of squares of residuals. This factor was taken as the scaling factor estimated empirically at  $x^\circ$  eccentricity. The data at 2, 3, 4.5, 9 and  $12^\circ$  eccentricities underwent this procedure, whereas the master data of  $6^\circ$  eccentricity are to be scaled to themselves

by a factor of 1 by definition. The obtained scaling factors at various eccentricities were then fitted to the linear regression line constrained to go through 1 at  $6^\circ$  eccentricity:  $(F - 1) = S(E - 6)$ , where  $F$  and  $E$  denote scaling factor and eccentricity, respectively, and  $S$  is the regression coefficient. The above analysis yielded  $S = 0.142$  for the subject IM.