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Modulation of perceived contrast by a moving surround

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Abstract

The apparent contrast of a center pattern depends on the contrast of its surround. To examine the suprathreshold perception of moving patterns, we measured the perceived contrast of a moving grating while the direction and speed of the surround patterns varied. Subjects matched the apparent contrast of a center patch embedded in surround patches to that of a patch with no surround pattern. Temporal frequency, Michelson contrast and movement direction of both center and surround patterns varied systematically. We found that: (1) contrast reduction is most prominent when the center and surround have the same velocity (velocity selectivity); (2) contrast enhancement occurs when the surround moves at a higher speed than the center, if the difference in temporal frequencies of center and surround exceeds 10–20, independent of the directional relationship between center and surround; (3) contrast reduction is stronger for higher surround contrasts with lower center contrasts; and (4) contrast enhancement is relatively unaffected by center and surround contrasts. We conclude that the contrast perception of moving patterns is influenced by directionally-selective mechanisms except at high temporal frequencies. Our results further suggest that there is not only the lateral inhibition often assumed to influence contrast gain control, but also an excitatory connection between motion encoding units.

Keywords: Motion; Contrast; Center and surround; Contrast reduction; Contrast enhancement

1. Introduction

Ejima and Takahashi (1985) first reported that the apparent contrast of a pattern is modulated by the contrast of its surround. When the contrast of a surround pattern is high, the perceived contrast of a stationary center pattern is lower than when it has no surround pattern (*contrast reduction*). Higher surround contrast with lower center contrast has been shown to induce greater contrast reduction (Cannon & Fullenkamp, 1991, 1993; Ellemberg, Wilkinson, Wilson & Arsenault, 1998; Snowden & Hammett, 1998). The opposite, *contrast enhancement*, has been reported when the surround is low in contrast (Ejima & Takahashi, 1985), though the effect is weak (Cannon & Fullenkamp, 1993). By examining the modulation of apparent contrast by its surround, we hope to understand how perceived contrast is determined by integrating contrast information from a spatially extended area.

Most previous studies of contrast modulation by a surround have used stationary stimuli. In fact, the perceived contrast of moving patterns has been largely ignored, although the effect of contrast on motion perception has been examined (e.g. Stone & Thompson, 1992). Therefore, we examined the perceived contrast of a center pattern (both stationary and moving) in the presence of a moving surround. It has been shown that when the center and surround have the same orientation or spatial frequency, contrast reduction is larger than when these stimulus attributes differ between the center and surround (Chubb, Sperling & Solomon, 1989; Solomon, Sperling & Chubb, 1989; Cannon & Fullenkamp, 1991; Ellemberg et al., 1998). Therefore, it is of interest to determine whether contrast modulation is larger when the direction and speed of center and surround are similar. These results may elucidate the mechanisms underlying contrast perception in a motion system.

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2. Methods

2.1. Subjects

Three subjects (AS, TA and TT) participated in most experimental sessions. AS and TA were paid subjects and were unaware of the purpose and ongoing results of the experiment. TT is one of the authors. Four additional paid naive subjects (MT, IS, RK and HT) participated in selected sessions to confirm the main conclusions. All had normal or corrected-to-normal vision.

2.2. Stimuli and apparatus

Stimuli were generated on a Pentium-based computer with VSG2/3 visual stimulus generator (Cambridge Research Systems) and displayed on a 21 in. RGB monitor (SONY multiscan 20se). The frame rate of the monitor was 120 Hz, with spatial resolution of 1000 × 1000 pixels and gray-level resolution of 13 bits. The monitor was calibrated with a TOPCON BM-5 colorimeter, and its output was linearized (gamma corrected) under software control. For all experiments using luminance-varying stimuli, the space-averaged chromaticity (CIE 1931) of the display was $x = 0.305$, $y = 0.323$. Subjects observed the display from a distance of 57 cm, with head position maintained by chin and head rests. The mean luminance of the display was 30 cd/m^2. The room was darkened and light shielded, with no other source of illumination present.

Both center and surround patterns were drifting vertical sine-wave gratings, presented in a square window centered in the display. Only the stimulus window was illuminated; the remainder of the screen was dark (< 0.01 cd/m^2). The center pattern subtended 2.0 × 2.0°, centered in a larger surround subtending 22.0 × 22.0°. On some intervals, the surround contained a grating; on other intervals, it contained a blank field matched to the center in space-averaged luminance. There was no gap between center and surround. Stimulus spatial frequency was 2.0 cycles/deg for both center and surround gratings. Temporal frequencies varied from 0.0 (stationary) to 48.0 Hz. Since velocity (deg/s) is defined as temporal frequency (Hz) divided by spatial frequency (c/deg), velocity varied from 0.0 to 24.0 deg/s. When the center or surround moved, the direction of motion was either leftward or rightward. Motion direction was randomized on each trial. Grating contrasts of center and surround defined according to the usual Michelson relationship varied from 0.0 to 96.0%. The spatial phase difference between center and surround was randomly chosen on each trial.

2.3. Procedure

We used a two-alternative, temporal forced-choice procedure to estimate the perceived contrast of a center pattern with a surround. In one interval, only the center pattern (*test pattern*) appeared, surrounded by the blank field equated in space-averaged luminance. In the other interval, both center and surround grating were presented (*reference pattern*). The presentation duration was 2.0 s for each interval. The two intervals were separated by a 1.0 s blank field of the same space-averaged luminance, and the onset of each interval was marked by an auditory cue. A small fixation cross was presented at the center of the display for 500 ms before the onset of each interval, and subjects were instructed to fixate the center of the display. Subjects judged which center pattern appeared higher in contrast. An adaptive staircase algorithm was used to measure the point of subjective equality (PSE) of the center patterns with and without surround patterns by changing the physical contrast of the test pattern (the center pattern with no surround grating) from trial to trial. When the test pattern was judged to be higher in contrast than the reference pattern, a decrement in the contrast of the test pattern followed; when the test pattern was judged lower in contrast than the reference pattern, its contrast was then increased. The size of the contrast increments or decrements decreased as the staircase depth increased, being 0.4 log unit in the beginning and falling to a terminal value of 0.1 log unit. The PSE for a given staircase run was computed as the mean of the contrasts of the final six out of 20 turning points. This provided an estimate of the perceived contrast of the center pattern in the presence of the surround. Each data point was calculated from five staircase runs. To prevent adaptation to a specific motion configuration, four staircases, in which different experimental variables were chosen, were interleaved in a single session.

3. Results

3.1. Stationary center and surround patterns

To determine whether the current stimulus configuration produced results comparable to those of previous studies, we first estimated the perceived contrast of the center with surround while both patterns were stationary. Fig. 1 shows the variation in perceived contrast of a center pattern with a surround when either the center contrast was fixed at 8.0% (Fig. 1A) or the surround contrast was fixed at 96.0% (Fig. 1B). The spatial phase relationship between center and surround was randomized on each trial.

In each figure, the vertical axis represents the contrast of the test pattern (a center pattern without surround) with respect to the physical contrast of the reference pattern (a center pattern with surround). A value of 1.0 means that the contrast of a center pattern with surround was veridically matched. Values lower than 1.0 indicate that the perceived contrast of the reference pattern (center with surround) is lower than that of a test pattern of the same physical contrast (*contrast reduction*). A value greater than 1.0 implies that the perceived contrast of the reference pattern is higher than that of a test pattern of the same physical contrast (*contrast enhancement*).

In Fig. 1A, the center contrast was fixed at 8.0% while the surround contrast varied from 2.0 to 96.0%. When the surround contrast was low (< 8.0%), subjects AS and TT made nearly veridical contrast matches. Contrast was underestimated by subject TA. There is an indication of contrast enhancement at the lowest surround contrast (2.0%) for subjects AS and TT, but the effect is weak. As the surround contrast increased, contrast reduction became noticeable. When the surround contrast was 96.0%, the perceived contrast of the center decreased to match test pattern contrasts from 70% (subject AS) to 50% (subject TA). The contrast reduction was even stronger when the center contrast was lower and surround contrast was 96.0% (Fig. 1B). These results are comparable to previous results in which higher surround contrasts in combination with lower center contrasts have been shown to induce larger contrast reduction in the center. They also agree with earlier reports that contrast enhancement is not prominent under similar conditions (Cannon & Fullenkamp, 1991, 1993; Snowden & Hammett, 1998).

3.2. Effect of a moving surround on the apparent contrast of a stationary center pattern

To examine the effect of a moving surround on the apparent contrast of the center pattern, we matched the perceived contrast of a stationary center grating while the velocity of a drifting surround, moving leftward or rightward, varied. Center and surround contrast were set at 8.0 and 96.0%, respectively, where strong contrast reduction is expected to be induced (Fig. 1). Fig. 2 shows results when the temporal frequency of the surround varied from 0.5 to 48.0 Hz (and velocity varied from 0.25 to 24.0 deg/s).

When the surround moves at less than 10.0 Hz, the contrast of a stationary center pattern was underestimated (*contrast reduction*). When the temporal frequency of the surround was 0.5 Hz, results were comparable to those when the surround was stationary (see data in Fig. 1 when center and surround contrasts were 8.0 and 96.0%). However, when the surround moved faster than 10.0 Hz, the center contrast was

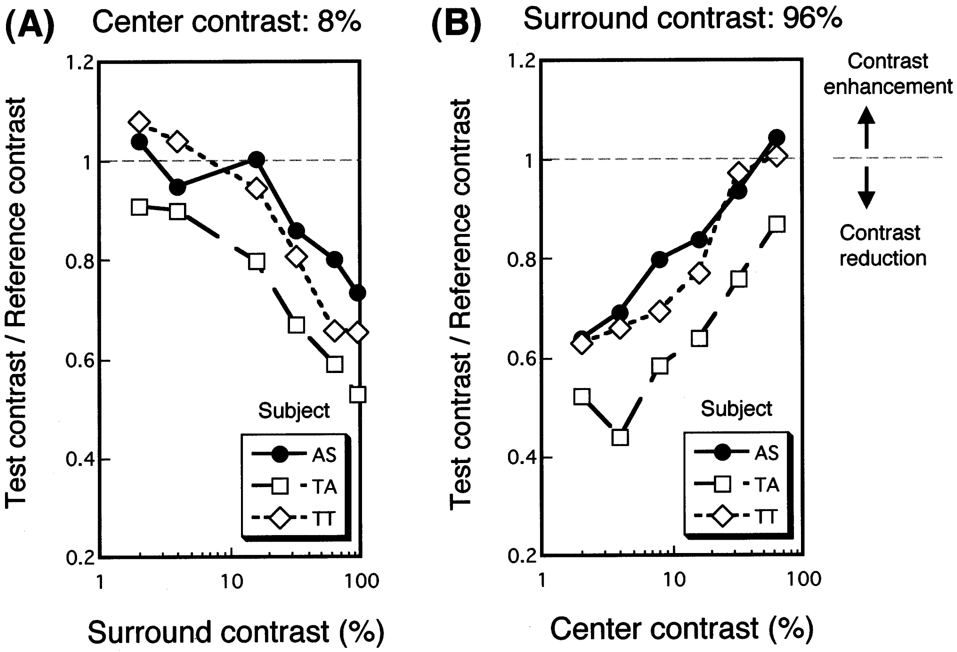

Fig. 1. (A) The ratio of the matching contrast of the test pattern (a center pattern without surround) to the contrast of the reference pattern (a center pattern with surround) is plotted as a function of surround contrast (%). The center contrast of the reference pattern was fixed at 8.0%. Different symbols identify individual subjects: AS (●), TA (□), TT (◇). Each point represents the average of five staircase runs. A value of 1.0 on the vertical axis indicates that the contrast of the reference pattern was veridically matched. Values lower than 1.0 indicate that the perceived contrast of the reference pattern is lower than that of a test pattern of the same physical contrast (contrast reduction). A value greater than 1.0 implies that the perceived contrast of the reference pattern is higher than that of a test pattern of the same physical contrast (*contrast enhancement*). (B) The ratio of test pattern contrast to a fixed reference pattern contrast is plotted as a function of the center contrast of the reference pattern (%). The surround contrast of the reference pattern was 96.0% in all cases. Other conditions were as in (A).

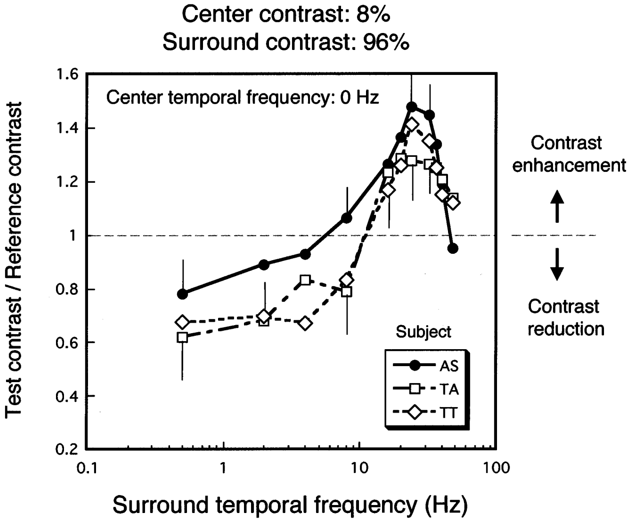

Fig. 2. The ratio of the matching contrast of the test pattern to the contrast of the reference pattern is plotted as a function of surround temporal frequency (Hz). The center grating was stationary; the surround grating drifted. Different symbols identify individual subjects: AS (●), TA (□), TT (◇). Each point represents the average of five staircase runs; error bars (shown for arbitrarily chosen points) represent ± 1 SD. Center and surround contrasts were 8.0 and 96.0%, respectively.

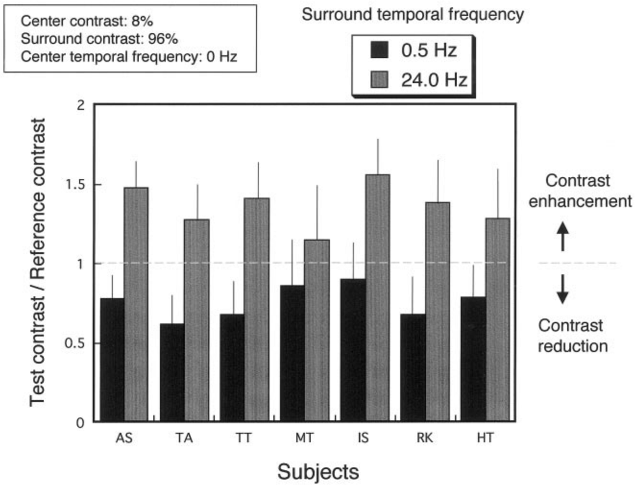

Fig. 3. The ratio of test pattern matching contrast to reference pattern contrast at two conditions (surround temporal frequencies 0.5 and 24.0 Hz, respectively) for seven subjects. Error bars represent ± 1 SD. Center and surround contrasts were 8.0 and 96.0%, respectively. The center grating was stationary; the surround grating drifted.

consistently overestimated (*contrast enhancement*) by a factor of nearly 1.4 at maximum for subjects AS and TT at a temporal frequency 24.0 Hz. Subject TA also showed constant contrast enhancement when the surround temporal frequency was greater than 10 Hz, though the magnitude of the enhancement was somewhat smaller. At the higher temporal frequencies examined (> 40 Hz), contrast enhancement became weak (subjects TA and TT) or disappeared entirely (subject AS). The impression of surround motion is very weak at these high temporal frequencies.

Cannon and Fullenkamp (1993) showed that the magnitude of contrast enhancement in a stationary pattern differs significantly between subjects. Some subjects showed both contrast reduction and contrast enhancement, while other subjects showed only contrast reduction. To determine the robustness of the results shown in Fig. 2, thus, four additional subjects participated in sessions in which the surround grating moved at either 0.5 or 24.0 Hz and the center was stationary. Center and surround contrasts were set at 8.0 and 96.0%, respectively. Each subject completed five staircases for each experimental condition. Fig. 3 shows the results from four subjects (MT, IS, RK and HT), as well as the original three subjects (AS, TA and TT) whose data are also shown in Fig. 2.

In Fig. 3, note that the all of the subjects showed contrast reduction when the surround moved at 0.5 Hz, and contrast enhancement when the surround moved at 24.0 Hz. A stationary surround has not previously been reported to induce strong contrast enhancement, especially when its contrast is as high as 96% (Snowden & Hammett, 1998). These results imply that the velocity of the surround has an important effect on the perceived contrast of a stationary center pattern. A surround grating moving at a low velocity induces *contrast reduction*, while a high-velocity surround grating produces *contrast enhancement*.

3.3. *Effect of a moving surround on the apparent contrast of a moving center pattern*

In the next experiment, we matched the perceived contrast of the center with a surround while both center and surround gratings were moving. Center and surround contrasts were set at 8.0 and 96.0%, respectively, as in the previous experiment. The temporal frequency of the center grating was either 2.0, 4.0 or 8.0 Hz. The temporal frequency of the surround grating varied from 2.0 to 32.0 Hz (velocity thus varied from 1.0 to 16.0 deg/s). To prevent adaptation to a specific motion configuration, the direction of the center grating, either leftward or rightward, was pseudorandomly chosen on each trial. From trial to trial, the surround grating moved in either the same or the opposite direction as that of the center grating, with equal numbers of trials in each case.

In Fig. 4, the ratio of the matching contrast of the test pattern with respect to the fixed contrast of the reference pattern is plotted as a function of surround temporal frequency. Fig. 4A–C are data from subject AS, and Fig. 4D–F are from subject TT. The temporal frequencies of the center grating were 2.0 Hz in Fig. 4A,D, 4.0 Hz in Fig. 4B,E and 8.0 Hz in Fig. 4C,F. The temporal frequency of the center grating is specified in the legend inset in each figure. On the vertical axis of each figure, values lower than 1.0 indicate contrast reduction, while values greater than 1.0 indicate contrast enhancement. Filled circles in the figure denote trials on which the center and surround gratings moved in the same direction, and blank squares denote trials on which the directions of center and surround gratings were opposite.

The amount of contrast modulation depends on the temporal frequencies of center and surround, combined with the directional relationship between center and surround. When the surround velocity was low, reference pattern contrast was underestimated (*contrast reduction*). The amount of contrast reduction depended on the relative motion directions of center and surround. The maximum contrast reduction was obtained when center and surround velocities were the same (shown by arrows in each panel). For example, for the data of subject AS shown in Fig. 4B, the ratio of test and reference pattern contrasts was 0.66, which implies contrast reduction, when the center and surround motion directions were identical. When the center and the surround moved in the opposite direction, however, the ratio was 1.02, indicating veridical contrast perception. Furthermore, when the center temporal frequency was either 2.0 or 4.0 Hz (Fig. 4A,B,D and E), contrast reduction was quite weak or nonexistent if the center and surround moved in the opposite direction, except

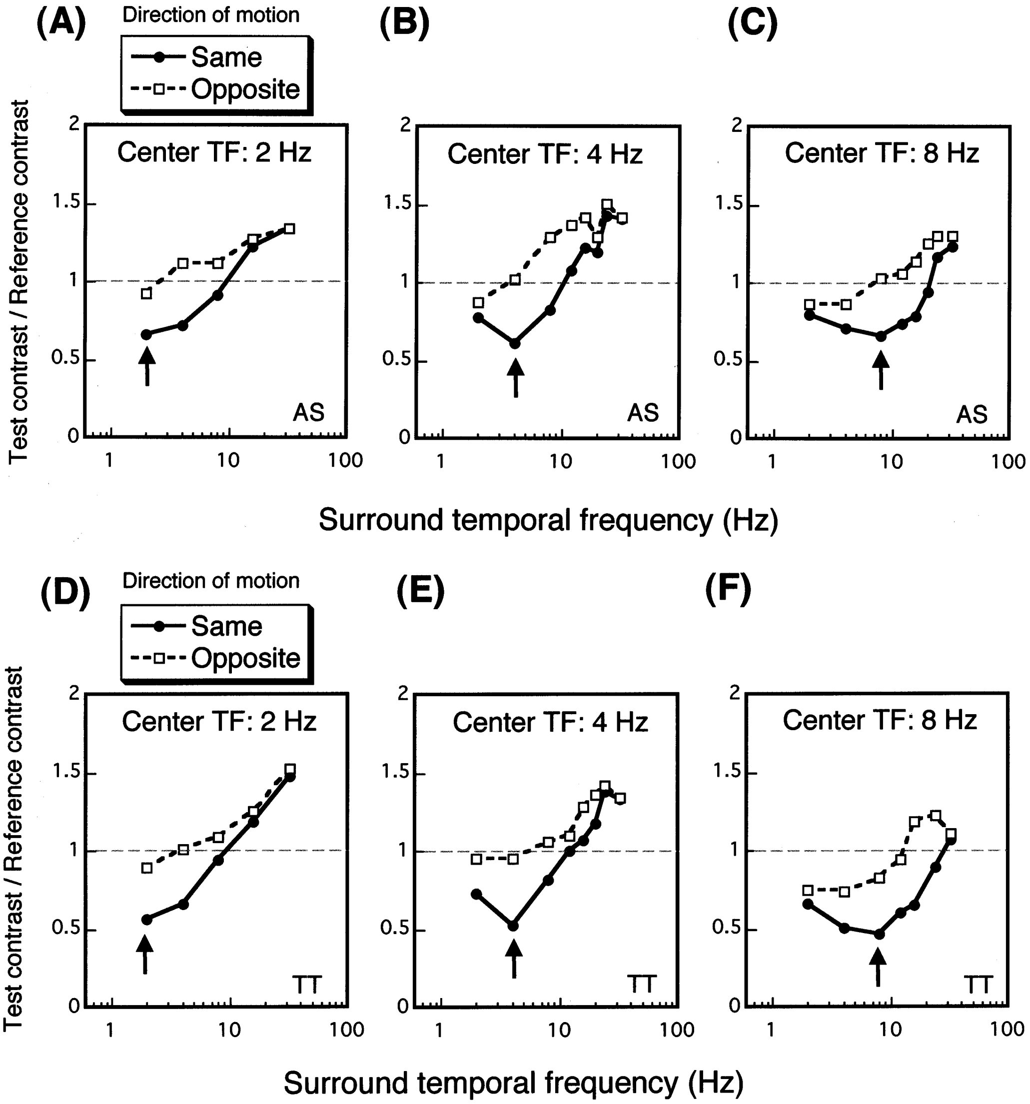

Fig. 4. The ratio of the test pattern matching contrast to the contrast of the reference pattern is plotted as a function of surround temporal frequency (Hz). The center and surround gratings moved either in the same (●) or opposite (□) directions. Each point represents the average of five staircase runs. The arrow on each graph indicates the point at which the center and surround have the same temporal frequency. The contrasts of center and surround were 8 and 96%, respectively. Graphs A, B, and C show data from Subject AS. D, E, and F show data from Subject TT. In A and D, the center temporal frequency was 2.0 Hz; in B and E, the center temporal frequency was 4.0 Hz; in C and F, the center temporal frequency was 8.0 Hz.

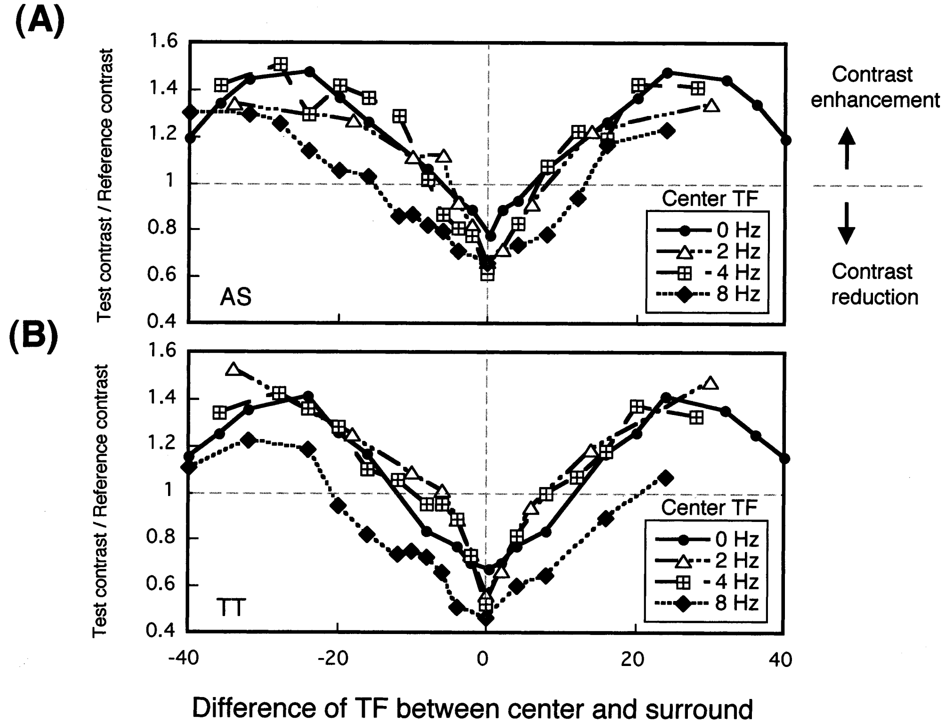

Fig. 5. The ratio of the matching contrast of the test pattern to the contrast of the reference pattern is plotted as a function of the difference between the temporal frequencies of the center and surround for two subjects, AS (A) and TT (B). The various functions in the figure show data corresponding to different center temporal frequencies: 0 Hz (filled circles), 2 Hz (open triangles), 4.0 Hz (open squares with cross), and 8.0 Hz (filled diamonds). Positive values on the horizontal axis correspond to center and surround movement in the same direction; negative values indicate that the center and surround moved in opposite directions.

at the lowest surround temporal frequency (2.0 Hz). Therefore, contrast reduction is selective for velocity (both direction of motion and speed) when the temporal frequency of the center pattern is low. However, when the center temporal frequency was 8.0 Hz (Fig. 4C and D), small but consistent contrast reduction was found even when the directions of motion of center and surround were opposite. Though we can conclude that the contrast reduction is velocity selective, therefore, the degree of selectivity depends on stimulus temporal frequency.

As the surround temporal frequency increased, contrast enhancement became prominent. The amount of contrast enhancement depended on the directional relationship and temporal frequencies of center and surround. Contrast enhancement was generally larger at intermediate temporal frequencies when the center and surround motion directions were opposite. At some intermediate temporal frequencies, there were cases in which contrast enhancement was observed when the motion direction was opposite and contrast reduction was observed when the motion direction was the same (for example, see Fig. 4B at a surround frequency of 8.0 Hz or Fig. 4F at 16.0 Hz).

We found that at high surround temporal frequencies (around 20–30 Hz), where the largest contrast enhancement was obtained, the amount of contrast enhancement was nearly independent of the relative motion directions of center and surround. The solid lines (‘same condition’) and dashed lines (‘opposite condition’) converge at the high temporal frequencies in all of the panels in Fig. 4.

The next question is whether the temporal frequency difference between center and surround can adequately predict the modulation of apparent contrast. For this purpose, we replotted Fig. 2 (where the center temporal frequency is 0 Hz) and Fig. 4 (where center temporal frequencies are 2, 4 or 8 Hz) to show the amount of apparent contrast modulation as a function of the difference between the temporal frequencies of the center and surround for two subjects, AS (Fig. 5A) and TT (Fig. 5B). The temporal frequency difference was calculated by subtracting the temporal frequency of the surround from the temporal frequency of the center. For example, if the center and surround moved in the same direction with temporal frequencies of 4.0 and 8.0 Hz, the difference is 4 $(=8.0-4.0)$. If they moved in the opposite direction, the difference is -12 $(=(-8.0)-4.0)$. Therefore, positive values on the horizontal axis of Fig. 5 denote that the center and surround moved in the same direction, and negative values indicate that the center and surround moved in opposite directions. The various functions in Fig. 5 show data corresponding to different center temporal frequencies (from 0.0 to 8.0 Hz). For the case of zero center temporal frequency (filled circles with solid line in Fig. 5), the curve is symmetrically drawn with respect to the center vertical axis.

Since the curves representing data from center frequencies of 0.0, 2.0 and 4.0 Hz, respectively, are virtually superimposed, the temporal frequency difference between center and surround can well predict contrast modulation under these conditions. However, the data from the 8.0 Hz center frequency are different. When the center-surround speed difference is zero, the contrast reduction is maximum, implying velocity selectivity of contrast reduction, as already noted. The bandwidth of the contrast-reduction portion of each curve represents the temporal frequency tuning characteristics of the contrast reduction. This indicates how similar the center and surround temporal frequency must be to produce strong contrast induction. The bandwidth of the contrast reduction portion of the curve is wider at a center temporal frequency of 8.0 Hz (filled diamonds with dashed lines in Fig. 5) than at the other center temporal frequencies. This implies that velocity selectivity is weaker when the center moves at 8 Hz than when it moves more slowly. For subject AS (Fig. 5A), the tuning curves at 0.0, 2.0 and 4.0 Hz are nearly identical, which suggests that the tuning characteristics are approximately the same at these lower temporal frequencies. For subject TT (Fig. 5B), velocity selectivity at 8.0 Hz was also weak compared to the other temporal frequencies. Therefore, since the velocity tuning characteristics of contrast reduction depend on the center temporal frequency, the temporal frequency difference between center and surround is not the only factor that determines the strength of contrast reduction.

Contrast enhancement was prominent where the center-surround temporal frequency difference is larger. The amount of contrast enhancement increased as the difference of center-surround temporal frequencies increased. For both subjects, the curves from 0.0, 2.0 and 4.0 Hz center temporal frequencies can be approximately superimposed. At these center temporal frequencies, the contrast reduction changes to contrast enhancement when the temporal frequency difference is greater than about 10 (same direction) or -10 (opposite direction), where each curve crosses the horizontal line of 1.0, which represents veridical contrast matching. However, when the center temporal frequency was 8.0 Hz, the point at which contrast reduction changed to contrast enhancement occurred at a higher temporal frequency difference. Temporal frequency differences of about 20 or -20 were required for contrast enhancement for subject TT (Fig. 5B), and 15 or -20 for subject AS (Fig. 5A). Therefore, though the temporal frequency difference between center and surround can predict the contrast modulation for each center temporal frequency, the magnitude of change in apparent contrast is a function of the center temporal frequency.

3.4. Effect of contrast on modulation of apparent contrast

In our experiments (Figs. 2–5), the contrasts of center and surround were fixed at 8.0 and 96.0%, respectively, since this combination had earlier been shown to induce a large contrast reduction in stationary patterns (e.g. Snowden & Hammett, 1998; see also our Fig. 1). Our experiments showed that contrast enhancement could also be induced at this contrast. However, since contrast reduction depends primarily on the contrast in a stationary pattern, it is of interest to see whether the amount of contrast enhancement also varies with the contrasts of center and surround. Therefore, in our next experiment, we systematically varied the contrasts of center and surround, and examined contrast modulation by comparing two conditions. In one, contrast reduction is prominent (center and surround temporal frequencies were fixed at 4 Hz); in the other, contrast enhancement is prominent (center temporal frequency was 4 Hz and surround temporal frequency was 24 Hz).

Fig. 6A shows the data recorded when the center contrast was fixed at 8% and the surround contrast varied from 2.0 to 96.0% for three subjects. Fig. 6B shows the data collected when the surround contrast was fixed at 96% while the center contrast varied from 8.0 to 64.0% for three subjects. Center and surround temporal frequencies were fixed at 4.0 Hz in both cases. Filled circles represent the conditions in which the center and surround moved in the same direction, and blank squares represent those in which the motion directions of center and surround were opposite.

We found that contrast reduction depends strongly on both direction and contrast of center and surround. Contrast reduction is directionally selective, since it appeared unambiguously only when the center and surround moved in the same direction. In addition, both center and surround contrasts have a strong effect on the amount of contrast reduction. When the directions of motion are the same, perceived contrast is a monotonically decreasing function of surround contrast (Fig. 6A). When the surround contrast is fixed at 96% (Fig. 6B), perceived contrast increases monotonically as center contrast increases. Therefore, as with stationary patterns (Fig. 1), contrast reduction is stronger for higher surround contrasts (Fig. 6A) and for lower center contrasts (Fig. 6B) when the two directions of motion are the same. When the two motion directions differed, contrast modulation was small, though it depended upon center and surround contrasts in the same manner. Strong contrast enhancement was not seen under any of these conditions.

Fig. 7A and B show data from conditions in which the center and surround temporal frequencies were fixed at 4.0 and 24.0 Hz, respectively. Significant contrast enhancement was induced under all stimulus conditions examined. When the directions of motion of the center and surround were opposite, contrast enhancement was constantly greater than when the directions were the same, though this 'directional selectivity' was weak (see also Fig. 4). Moreover, the effect of contrast variation of center and surround was also found to be weak. Higher surround contrasts with lower center contrasts tend to induce a stronger contrast enhancement, but the correlation is not strong. This relative immunity of contrast enhancement to the effects of contrast variation in center or surround is quite different from that of the characteristics of contrast reduction (Fig. 6).

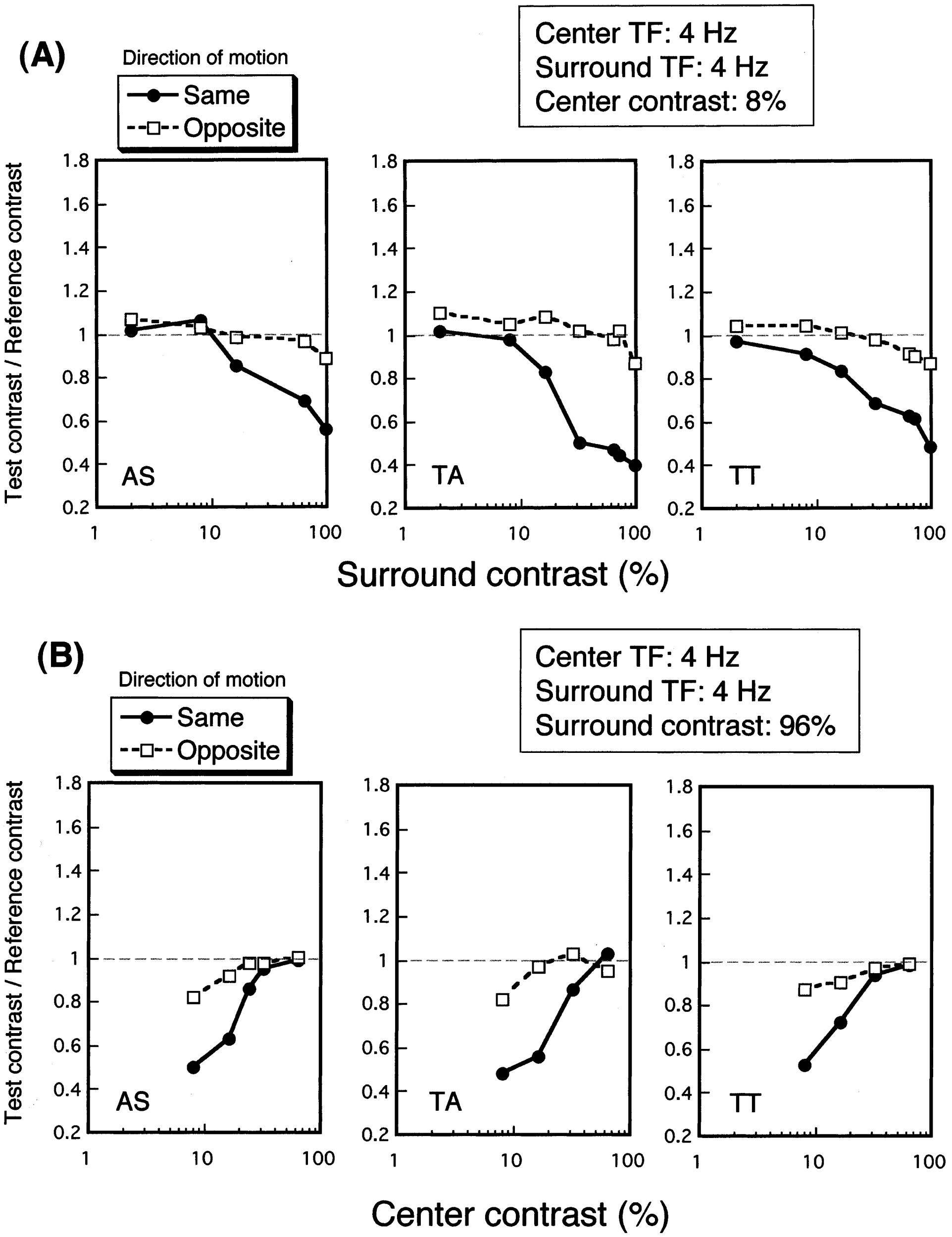

Fig. 6. (A) The ratio of the matching contrast of the test pattern to the contrast of the reference pattern is plotted as a function of surround contrast (%). The directions of motion of the center and surround were the same (●) or opposite (□). Each point represents the average of five staircase runs. The left panel shows the data for subject AS, the middle panel for subject TA, and the right panel for subject TT. The temporal frequencies of center and surround were both 4.0 Hz. The center contrast was 8%. (B) The ratio of the matching contrast of the test pattern to the contrast of the reference pattern is plotted as a function of center contrast (%). The surround contrast was 96%. Other conditions were as in (A).

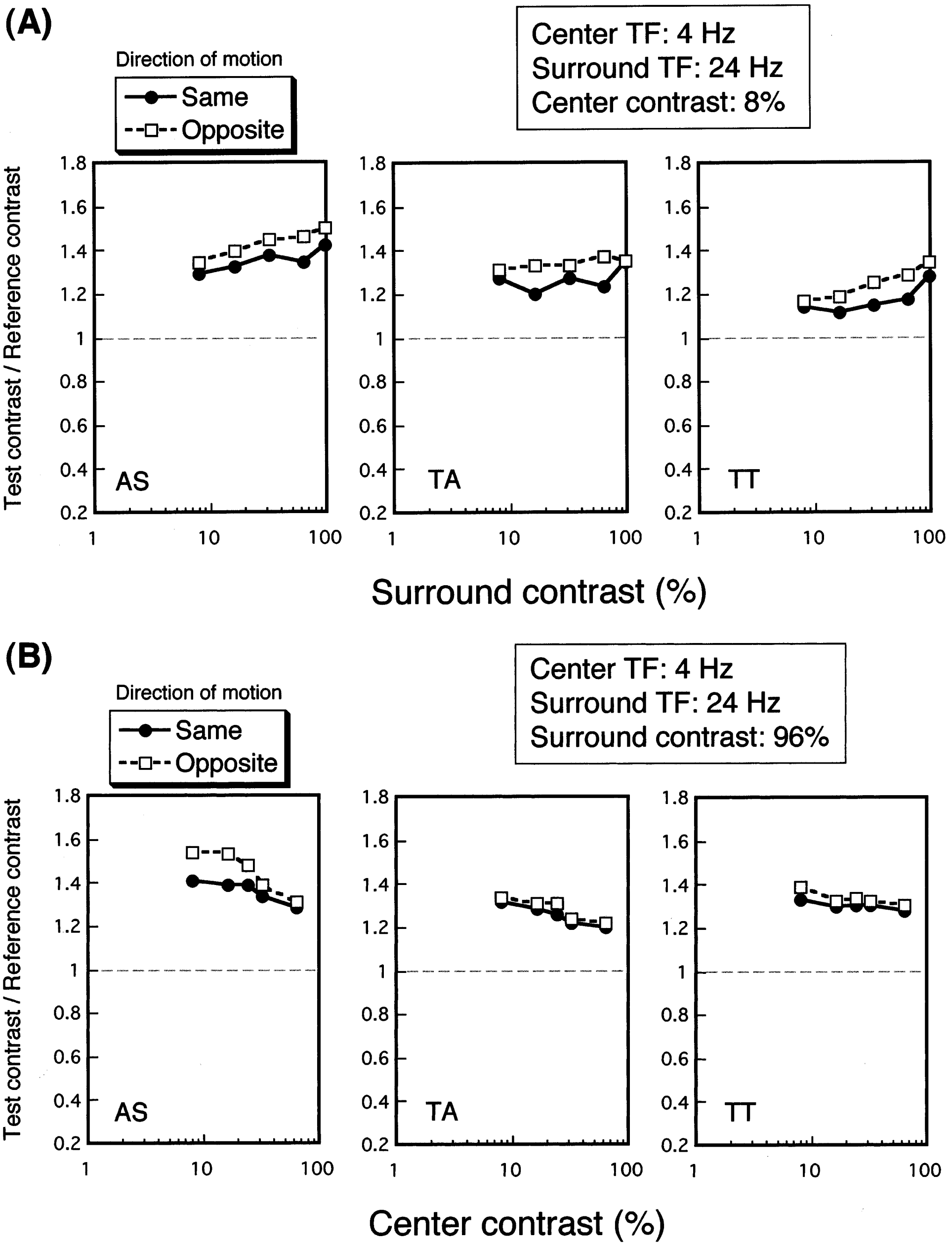

Fig. 7. (A) The ratio of the matching contrast of the test pattern to the contrast of the reference pattern is plotted as a function of surround contrast (%). The directions of motion of the center and surround were either the same (●) or opposite (□). Each point represents the average of five staircase runs. The left panel shows the data for subject AS, the middle panel for subject TA, and the right panel for subject TT. The temporal frequencies of center and surround were 4.0 and 24.0 Hz. The center contrast was 8%. (B) The ratio of the matching contrast of the test pattern to the contrast of the reference pattern is plotted as a function of center contrast (%). The surround contrast was 96%. Other conditions were as in (A).

3.5. Effect of the spatial distance between center and surround

In the all of experiments reported, the center and surround patterns were spatially contiguous. Therefore, the local edge at the immediate boundary of the center and surround might conceivably influence the results of these experiments. To determine whether the main conclusions described above depended upon the contiguity of center and surround, we spatially separated them by 0.2 or 0.4° and replicated several experimental conditions that had been shown to induce contrast reduction or contrast enhancement. The gap between center and surround was equated in luminance to the space-averaged luminance of center and surround. Fig. 8 shows the results for three gap conditions. Though the amount of contrast modulation decreased as the gap between center and surround increased, both contrast reduction and contrast enhancement were induced in the presence of a 0.4° gap between center and surround.

Thus, the contrast enhancement described above (Figs. 2–4) is not an artifact induced by interactions at the edge between the center and the surround.

4. Discussion

The present study examined the effect of a moving surround on the perception of the contrast of a center pattern. We found that the modulation of contrast depends on both the velocity and the contrast of both center and surround patterns. Specifically: (1) contrast reduction is prominent when the center and surround have the same velocity (velocity selectivity). (2) Contrast enhancement occurs when the surround moves at a higher speed than the center, when the temporal frequency difference between center and surround exceeds 10–20, independent of the directional relationship between center and surround. (3) Contrast reduction is stronger for higher surround contrasts with lower cen-

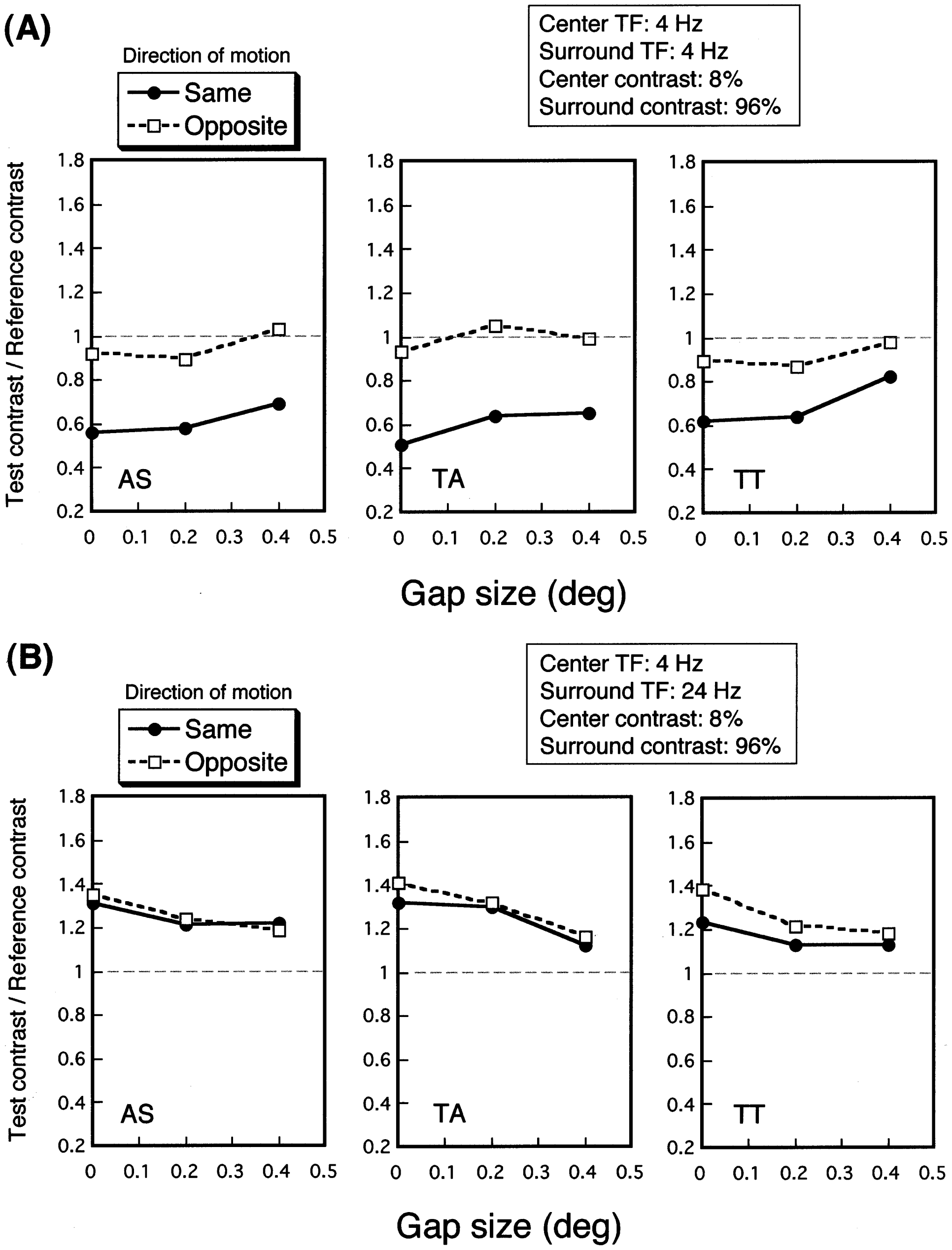

Fig. 8. (A) The ratio of the matching contrast of the test pattern to the contrast of the reference pattern is plotted as a function of the gap size (°) between the center and surround. The gap was equal in luminance to the space-averaged luminance of the grating patterns. Different symbols identify individual subjects: AS (●), TA (□), TT (◇). The temporal frequencies of center and surround were both 4.0 Hz. Center and surround contrasts were 8 and 96%, respectively. (B) Conditions were as in (A), except that the temporal frequencies of center and surround were 4.0 and 24.0 Hz.

ter contrasts. (4) Contrast enhancement is relatively unaffected by center and surround contrasts. Those results suggest that the modulation of the perceived contrast of a moving pattern by its moving surround is a complex phenomenon in which multiple mechanisms are involved.

Solomon et al. (1989) formalized a model of contrast reduction based on lateral inhibition between neighboring neural units. In their model, the lateral inhibition is accomplished by a divisive gain control network. The units that respond to the surround produce divisive inhibition on the units that respond to the center, while those that respond to the center also send a divisive inhibitory signal to the units responding to the surround. Ejima and Takahashi (1985) and Cannon and Fullenkamp (1993) also suggested a role for lateral inhibition in contrast reduction. Snowden and Hammett (1998) argued that the effect of the surround can be considered as simple lateral masking and showed that a divisive inhibitory model (Foley, 1994) can capture the characteristics of the contrast reduction. Singer and D'Zmura (1994, 1995) proposed a model for contrast gain control as a feed-forward multiplicative interaction rather than as divisive inhibition to explain the perceived reduction of contrast in isoluminant stimuli. Though how contrast gain control in the human visual system is accomplished is still not fully understood, our results imply that the mechanism that induces reduction in apparent contrast is selective for both direction and speed.

Except for the work of Ejima and Takahashi (1985), most earlier studies examining the contrast modulation of stationary patterns have reported that contrast enhancement is weak and that there are large individual differences (Cannon & Fullenkamp, 1993). Under peripheral viewing, contrast enhancement was not observed at all (Ellemberg et al., 1998). Our results have shown that this is not the case when the patterns are moving. Contrast enhancement was induced when the surround moved at a high temporal frequency. Our results are consistent with the suggestion of Cannon and Fullenkamp (1993) that the units tuned to the moving surround send an excitatory signal to the units tuned to the center. Polat and Sagi (1993, 1994) found that surround stimuli could either increase or decrease the detection threshold of a center pattern, depending on the distance of the surround pattern from the center. They suggested that there is a direct relationship between the perceived contrast of a pattern and the modulation of its detection threshold by its surround. If so, a surround moving at high speed should decrease the contrast detection threshold of a center stimulus.

The perceived contrast of a temporally-varying pattern decreases as the temporal frequency increases, even when the physical contrast is invariant (Georgeson, 1987). With our stimuli, when the surround moves at a temporal frequency of 20–40 Hz, its perceived contrast is lower than when it moves at lower temporal frequency. One might thus argue that this apparent reduction of contrast in the surround was responsible for the apparent enhancement of contrast at the center. However, as shown in Fig. 1 as well as in previous studies (e.g. Cannon & Fullenkamp, 1991), a stationary surround of low contrast does not necessarily induce contrast enhancement in a center pattern. Furthermore, when the surround contrast is physically reduced, the amount of contrast enhancement also decreases (Fig. 7A). An explanation based on the perceived reduction of contrast in the moving surround thus seems inadequate for the contrast enhancement observed here. This further suggests that the mechanism that produces contrast reduction and that that produces contrast enhancement are different.

Previous studies have shown that the contrast reduction in a stationary pattern is stimulus specific. The perceived contrast of a center pattern is reduced more when the center and surround are similar in spatial frequency, orientation or color axis (Chubb et al., 1989; Solomon et al., 1989; Cannon & Fullenkamp, 1991; Singer & D'Zmura, 1994; Ellemberg et al., 1998). The velocity selectivity we found (Fig. 4) further supports the idea that apparent contrast reduction is highly specific to stimulus attributes. It has been argued that a possible neural site for the induction of contrast reduction is an early level in visual cortex, conceivably even in V1 (Solomon et al., 1989), where many neurons are selective for such stimulus attributes. The emergence of velocity selectivity in contrast reduction is consistent with this suggestion, since the first neurons known to show directional selectivity in primates are found in V1 (e.g. Hubel & Weisel, 1968). It is of interest to see whether the contrast modulation seen with moving center-surround patterns is also selective to the other stimulus attributes previously studied.

We showed that contrast enhancement varies little as the contrast of center and surround patterns changes (Fig. 7B), while contrast reduction depends strongly on the contrasts of center and surround (Fig. 7A). This suggests that the neural mechanisms underlying the induction of these two types of contrast modulation differ. In many psychophysical tasks, visual performance is largely contrast invariant (e.g. Keck, Palella & Pantle, 1976; Nakayama & Silverman, 1985). It has been shown that neurons in MT (which is widely considered to be an important neural site for motion coding) are activated at low contrasts and show constant responses over a broad contrast range in macaque (Sclar, Maunsell & Lennie, 1990). It has also been shown that larger-scale responses recorded from a presumed human homologue of MT show similar contrast dependence (Tootell, Reppas & Kwong, 1995; Anderson, Holliday, Singh & Harding, 1996). Since the strength of contrast enhancement is largely independent of contrast (Fig. 6), it is tempting to suggest that the phenomenon might be related to the output of neurons in this pathway. The contrast dependent characteristics of contrast reduction are significantly different and might therefore reflect activity in a different mechanism or pathway in which the contrast response is not as steep as that seen in MT (Sclar et al., 1990). We note, however, that the relationship between the strength of perceived contrast and the response of selected neurons is not clear. We urge caution, therefore, in attributing the perception of contrast to any particular neural substrate.

There are many reports that directionally-selective neurons are inhibited by a surround stimulus moving in the same direction as a stimulus moving in the receptive field (RF) center, and their response is facilitated by a surround stimulus moving in the opposite direction. Such neurons are found in area 17 (Orban, Gulyás & Vogels, 1987) and area 18 of cat (Orban, Gulyás & Spileers, 1988) and in areas MT and MST in macaque monkey (Allman, Miezin & McGuinness, 1985; Tanaka, Hikosaka, Saito, Yukie, Fukada & Iwai, 1986; Born & Tootell, 1992). In V1 in macaque monkey, it has been found that some neurons respond better to a center moving pattern when its surround moves in the opposite direction, irrespective of the direction of motion of the center stimulus itself (Lamme, 1995; Kastner, Nothdurft & Pigarev, 1997). Such center-surround antagonism of directionally-selective neurons may be related to motion contrast, or induced motion in which the perceived direction of a center stimulus is modified by the motion of its surround (e.g. Reinhardt-Rutland, 1988; Nawrot & Sekuler, 1990), or rapid texture segregation by motion (e.g. Julesz & Hesse, 1970; Nothdurft, 1993).

The significance of the center-surround organization of directionally-selective neurons in contrast modulation is not clear. At least qualitatively, the velocity selectivity of contrast reduction can be explained if we simply assume that an increase (or a decrease) in the response of those directionally-selective neurons with a center-surround antagonism induces an increase (or a decrease) in the perceived contrast of a center stimulus. The increase of perceived contrast at middle temporal frequencies when center and surround motion directions are different (Fig. 4) also corresponds to the characteristics of those neurons which are activated by a background moving opposite to its center. However, we know of no physiological reports describing neurons whose characteristics could predict the emergence of contrast enhancement at higher temporal frequencies of the surround irrespective of the direction of motion (Fig. 4). There could be a mechanism that calculates and represents the relative temporal frequencies of two spatially contiguous regions, or there might be a mechanism that is less directionally-selective at higher temporal frequencies. Several psychophysical studies suggest that directional selectivity is not strong at high temporal frequencies (Kelly & Burbeck, 1987; Smith & Edgar, 1994), which might be related.

How moving stimuli are perceived is not well understood (e.g. Nishida, Motoyoshi & Takeuchi, 1999). For example, the perceived spatial frequency of a drifting grating is increased more than 30% (Parker, 1983) compared to a stationary grating. In spite of a rather sluggish temporal impulse response, the moving images are not perceived as blurred (Burr, 1980). In fact, a blurred image may appear even sharper when it is moving (Ramachandran, Rao & Vidyasagar, 1974; Bex, Edgar & Smith, 1995). This sharpening process should be very important from a functional point of view. Our experiments have shown that the perceived contrast of moving patterns is largely enhanced by a fast moving surround. We speculate that the functional role of contrast enhancement is related to the task of tracking moving objects. If a surround pattern moving at high speed enhances the perceived contrast of a center pattern, then the perceived contrast of eye-tracked objects may be enhanced when the image of the background moves faster on the retina than the tracked object during eye movements. Since subjects were instructed to fixate the stimulus in the present study, it might be interesting to examine how perceived contrast is modulated while tracking the moving stimuli.

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