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# Visual coherence of moving and stationary image changes

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## Abstract

Detection thresholds were compared for moving and stationary oscillations with equivalent contrast changes. Motion was more detectable than stationary oscillation, and the difference increased with size of the feature (a Gaussian blob). Phase discriminations between a center and two flanking features were much better for motion than for stationary oscillation. Motion phase discriminations were similar to motion detection and were robust over increases in spatial separation and temporal frequency, but not so for stationary oscillations. Separate visual motion signals were positively correlated, but visual signals for stationary oscillation were negatively correlated. Evidently, motion produces visually coherent changes in image structure, but stationary contrast oscillation does not. © 2002 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

Vision is very sensitive to the spatial structure of moving images (e.g., Epstein & Rogers, 1995; Jansson, Bergström, & Epstein, 1994; Lappin & Craft, 2000; Lappin, Norman, & Mowafy, 1991; Nakayama, 1985; Nakayama & Tyler, 1981; Regan, 2000; Watanabe, 1998). Spatial patterns of common motion and spatial changes produced by relative motion carry visible information about the shapes and locations of objects.

Gestalt psychologists proposed that the “common fate” of moving optical patterns defines intrinsically organized fields that are directly detected by the visual nervous system (e.g., Wertheimer, 1912; Köhler, 1930; Gibson, 1950; Lappin & van de Grind, in press). “Common fate” usually refers to image motion, but similar temporally synchronous changes also occur in other optical properties. Image motion involves changes in local contrast as well as changes in spatial position. If a luminous feature shifts its position within a homogeneous background, then the luminance increases at the new position and decreases at the initial position. Detectability of motion is limited by these contrast changes as well as by the spatial displacement (Nakayama &

Silverman, 1985). Some models of motion-sensitive mechanisms respond to such spatiotemporal patterns of contrast energy (e.g., Adelson & Bergen, 1985; Reichardt, 1961; van Santen & Sperling, 1985; Watson & Ahumada, 1985).

Several studies have found that hyperacutities for relative spatial position (e.g., for Vernier offset) often may be parsimoniously explained as contrast detections (e.g., Hu, Klein, & Carney, 1993; Klein, Casson, & Carney, 1990; Levi, McGraw, & Klein, 2000; Morgan & Aiba, 1985). The pattern of luminance changes produced by a shift in spatial position defines a local contrast *dipole*. The detectability of this local contrast difference often is equivalent to the acuity for discriminating a difference in spatial position. Motion detection might be amenable to the same analysis. Contrast change has been shown to determine detections and discriminations of displacements of sine-wave gratings (Nakayama & Silverman, 1985), though the dependence on contrast asymptoted at contrast values of only about 3%. Hock, Gilmore, and Harnett (2002) recently demonstrated that the perception of apparent motion is controlled by such dipole contrast changes—where the luminance at one location changes toward the background and subsequently the luminance at a neighboring location changes away from the background.

Suppose that local contrast changes occur without motion—without changing the positions of image

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features. If the local contrast change in a stationary image is equal to that produced by a given motion, are the stationary and moving image changes equally detectable? The present study addressed this question.

One way to produce such stationary contrast changes is to make them bilaterally symmetric. That is, the feature grows either brighter or darker, and larger or smaller, simultaneously on both sides, while the feature as a whole remains centered at the same position. Fig. 1 illustrates such stationary contrast changes in Gaussian features; and the Appendix gives the corresponding mathematical equations. The temporal variations in local contrast at fixed positions on either side of the initial blob centroid were the same for both moving and stationary patterns.

The purpose of this study was to compare the visibility of changes in moving and stationary images involving the same local contrast changes. Our first experiment compared the detectability of these two forms of image change applied to a single feature. Our primary interest, however, was the perceptual organization of multiple features, involving visual relations among features that were either moving or stationary. Such multi-local visual relations were evaluated by discriminations

of phase differences between multiple oscillating features, using methods similar to those of Lappin, Donnelly, and Kojima (2001). Sensitivities to these image changes were measured by both spatial acuities and contrast sensitivities.

Silverstein (1999), Silverstein and Klein (1994) and Lappin et al. (2001) found “hyperacuity” for relative motions. Indeed, the acuity for discriminating in-phase and anti-phase motions was lower than that for detecting motion (discriminating rigid oscillations vs. stationary patterns), even when features were separated by several degrees (Lappin et al., 2001). The impressive acuity for relative motion indicates that both (a) early visual mechanisms operate to effortlessly and efficiently “bind” commonly moving features, and (b) these mechanisms are very efficient in detecting deviations from common fate of even spatially separate features.

Perhaps similar perceptual binding occurs for other forms of common fate. Lee and Blake (1999, 2001) have found that the perceptual organization effected by common fate extends to a larger class of temporally synchronous image changes more general than common motion. Hyperacuities for relative motion might apply more generally to other forms of common fate.

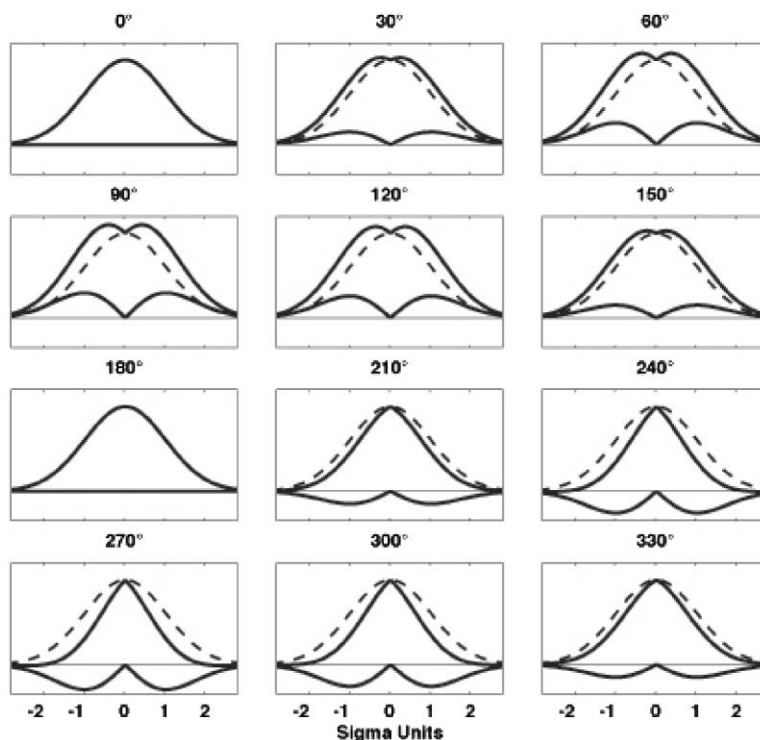


Fig. 1. Schematic illustration of the changing luminance distributions and local contrast changes in the stationary oscillations. A 1D profile of the initial Gaussian distribution is shown by the dotted line; and the pattern of local contrast change is shown by the lower curve in each panel. This local contrast change equals the difference between the initial Gaussian and the stationary luminance pattern in each panel. The amplitude of the oscillation illustrated here is  $0.5\sigma$ ; the oscillations in these experiments usually were much smaller. The contrast changes in these stationary oscillations matched those in the moving oscillations, which were directly proportional to the amplitudes of motion. Therefore, we can equally well specify detection thresholds for both moving and stationary oscillations either as spatial displacements (arcmin), contrast changes (%), or contrast sensitivities ( $1/\%$ ). The zero-crossing of the stationary change remained at the centroid of the stationary blob, but the zero-crossing shifted in the moving blobs (by  $1/2$  the amplitude of motion) (see Appendix A).

We found, however, that sensitivities to moving and stationary image changes differ both quantitatively and qualitatively. The differences were most striking when observers tried to discriminate phase differences in the oscillations of multiple features: this was an easy task for moving features, but was much more difficult for stationary oscillations, and these differences in difficulty increased with both spatial separation and temporal frequency. Moreover, when we evaluated detections of oscillations of single features, we found that for large features motions were more detectable than stationary contrast oscillations. In general, moving patterns provide more visible spatial information than stationary patterns with the same local contrast changes. Evidently, these two forms of common fate stimulate different visual mechanisms.

## 2. General method

The stimuli were circularly symmetric 2D Gaussian luminance patterns (“blobs”) added to a homogeneous background. These were displayed on a flat-screen video monitor (19 in. Sony GDM-F400), with a viewing area that subtended  $26.6^\circ \times 20^\circ$  visual angle ( $1600 \times 1200$  pixels). The display was viewed from a distance of 78 cm, and each pixel was  $1' \times 1'$ . The refresh rate was 85 Hz, and moving patterns were displaced slightly in each successive frame. The luminances were linearized by measuring each of the 256 gray-scale outputs with a Minolta luminance meter (model LS 110), and then fitting a gamma-correction function; and the values were then measured again and adjusted as necessary. Gray-scale resolution was expanded from 256 to 768 by a bit-stealing technique (Tyler, 1997), yielding a resolution of  $0.15 \text{ cd/m}^2$  for each step in gray-scale. The background luminance was  $35.3 \text{ cd/m}^2$ , including  $4.8 \text{ cd/m}^2$  ambient illumination at which the borders of the display screen and other objects in the room were fully visible. The peak luminance at the center of the blob was  $44.4 \text{ cd/m}^2$  (26% maximum contrast). Stimulus patterns were created with MatLab using the Psychophysics Toolbox (Brainard, 1997) and VideoToolbox (Pelli, 1997) on a Macintosh G4 computer.

In Exp. 1, a single Gaussian blob, varying in size from  $\sigma = 3\text{--}60'$ , was presented in the center of the display. In Exps. 2–4, three blobs, all of size  $\sigma = 10'$ , were horizontally aligned. In Exps. 2 and 4, the center-to-center separation was  $100'$ ; and in Exp. 3, the separation was  $80'$  or  $240'$  in different conditions. These stimulus patterns were displayed for 2 s. The temporal frequency of oscillation was 3 Hz in Exps. 1 and 4, 2.24 Hz in Exp. 2, and varied from 1 to 8.5 Hz in Exp. 3. The initial phase position was randomized between trials.

Moving patterns oscillated horizontally by small amplitudes, usually smaller than a single pixel, involving

small changes in gray-level of some of the pixels within the blob. Stationary oscillations were derived from the contrast changes produced by motion as described in Fig. 1 and in the Appendix. The local luminance changes produced by a given amplitude of oscillation were exactly the same for both moving and stationary blobs. The global luminance change in the stationary oscillations differed from that in the moving patterns in two respects: first, the stationary contrast changes had the same sign on both sides of the central zero-crossing, both positive or both negative, whereas the moving difference pattern always had opposite signs on the right and left sides of the zero-crossing. Second, the central zero-crossing of the stationary contrast change was positioned at the blob’s centroid, whereas the zero-crossing of the moving difference pattern oscillated with the moving blob (at half the amplitude of the motions of the blob’s centroid). In both moving and stationary patterns, the magnitude of the contrast change integrated over the whole blob was proportional to the actual or simulated displacement distance.

Two different discrimination tasks were used to evaluate the visibility of these oscillations: detection and phase discrimination. Both tasks were 2IFC discriminations, with oscillation amplitudes adjusted by a Quest adaptive staircase (Watson & Pelli, 1983), converging on a threshold accuracy of 76% (where  $d' = 1.0$ ). Thresholds were estimated by averages of three or four 25-trial Quest staircases. In detection tasks, an oscillating pattern and a constant pattern (one frame randomly chosen from the oscillation sequence) appeared on each trial.

In phase discrimination tasks, the center blob oscillated either in-phase or out-of-phase relative to the two flanking blobs, which always oscillated in phase with one another. The magnitude of the phase difference was  $60^\circ$  in Exp. 2, and  $180^\circ$  in Exps. 3 and 4. Thus, in moving patterns, the three blobs oscillated either rigidly or the position of the central blob oscillated relative to the two flankers. In stationary patterns, the contrasts of the three blobs were either equal and oscillating in phase, or the contrast of the center blob oscillated out of phase with the two flankers. Sensitivities were measured by the minimum oscillation amplitudes at which phase discrimination was possible.

## 3. Experiment 1: detecting moving and stationary contrast oscillations

The purpose was to compare detectabilities of the image changes produced by motion and by stationary contrast oscillations of features of varying size. Initially, we expected no difference in detectability of these two forms of image change, and this expectation was

supported by an earlier experiment. In this previous experiment, which was similar to Exp. 2 in the present study, the oscillating features were Gaussian blobs (three of them, as in Exp. 2) of a single size,  $\sigma = 7'$ . The assumption that these two forms of image change were equally detectable was questioned later when we happened to use a larger blob, found that moving oscillations were more detectable than stationary ones, and suspected that the difference might depend on size of the blob. Additional pilot work indicated that size has an important effect, so the present experiment quantified these effects.

As the size of these Gaussian features increases, their contrast gradients decrease, and the local contrast changes produced by a given spatial shift also decrease. Thus, detection thresholds may be expected to increase with size of the blob, whether the oscillations are moving or stationary. Three basic questions concern (a) the effects of blob size on oscillation thresholds, (b) how detection thresholds depend on the local contrast changes, and (c) whether blob size has different effects on the moving and stationary oscillations.

### 3.1. Method

Detection thresholds were evaluated for two well-practiced observers, one of whom was the second author. Size of the blobs varied from  $\sigma = 3$ – $60'$ . Observer DT obtained thresholds for seven different sizes ( $\sigma = 3', 6', 10', 14', 20', 30', 60'$ ), and observer BM obtained thresholds for six sizes ( $\sigma = 3', 6', 12', 20', 30', 60'$ ). Detection thresholds were evaluated for both moving and stationary oscillations at each size. Threshold oscillation amplitudes were estimated by the means of the thresholds obtained from three Quest staircases. Observer DT obtained thresholds for each of the 14 different conditions in three randomly permuted sequences, and observer BM did the same for random sequences of 12 conditions.

### 3.2. Results

The results are shown in Fig. 2. Detection thresholds are expressed both as spatial amplitudes (arcmin) and as contrast changes (percentages of the total luminance in the visible area of the blob). (Amplitudes of even the stationary oscillations may be scaled spatially, since magnitude of the contrast change corresponded to the spatial displacement in the moving patterns.) The effects of blob size (arcmin/ $\sigma$ ) on detection thresholds are shown for both moving and stationary oscillations for both observers.

As may be seen, the spatial oscillation thresholds increased linearly with blob size. Furthermore, the slope of this increase was smaller for the moving patterns than

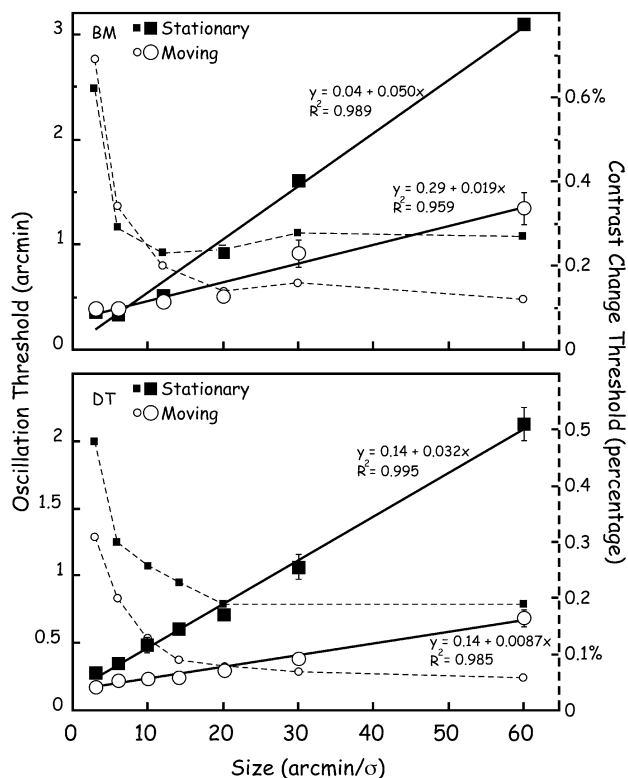


Fig. 2. Thresholds for detecting moving and stationary oscillations of a single Gaussian blob as a function of its size. The oscillation thresholds were approximately linear functions of the size. These linear functions refer to the left vertical axis. The nonlinear functions shown in small symbols with dashed lines are the same data measured as contrast change thresholds, and these refer to the values on the right vertical axis. (The stationary and moving oscillations are both given as amplitudes of spatial displacement, since the stationary contrast changes were matched to those produced by the moving patterns.) The error bars are the standard errors of the mean for the designated data points; those that are not visible were smaller than the plotting symbol.

for the stationary patterns. For the moving patterns, the average threshold increase was just 1.3% of the increase in feature size (0.9% for DT, and 1.9% for BM); but for the stationary patterns, the threshold increase averaged 4.1% of the increase in feature size (3.2% for DT, and 5.0% for BM). Thus, the moving and stationary thresholds were very similar when the blobs were small, but moving oscillations were much more visible than stationary oscillations when the blobs were large. On average, the threshold/size slope was 3.3 times greater for the stationary than for the moving oscillations (3.7 for DT, and 2.8 for BM). Quantitative details differ for the two observers, but the qualitative results were very similar.

Thresholds for these image changes also may be expressed as contrast changes—as ratios of the luminance difference to the integrated luminance over the whole area of the blob. (For the stimuli in this experiment, Gaussian blobs, the measures of contrast change and spatial acuity are redundant. The luminance change is

directly proportional to the spatial shift.)<sup>1</sup> The contrast change thresholds are given on the right vertical axis, and the functions relating these thresholds to blob size are given by the dashed curves (small symbols) in Fig. 2.

As may be seen, the contrast sensitivities implicit in these oscillation thresholds are impressive, particularly for the moving patterns. The asymptotic contrast change threshold for moving oscillations of the largest blob was only 0.06% for DT and 0.12% for BM (contrast sensitivities over 1600 and 800)! Corresponding values for the stationary oscillations were 0.19% for DT and 0.27% for BM. (Note that these values depend on the area over which the blob luminance is integrated. The present computation was based on the visible area of the blob—where it could be discriminated from the background—but the visual integration area might be different.) The near constancy of these contrast thresholds for larger blobs suggests that the effective visual integration area changed with the area of the blobs. Research is needed, however, to determine the relative roles of contrast change and spatial acuity in detecting motion.

The linear relation between the spatial oscillation thresholds and size of the Gaussian blobs is compelling, but this linearity could change for larger sizes. In more recent experiments on motion discrimination with Gabor patches, we have found clear inhibitory effects when the diameter of the patch exceeds about  $4^\circ$  (Tadin & Lappin, 2001)—resembling those observed for single neurons in cortical area MT. Electrophysiological studies (e.g., Allman, Miezin, & McGuinness, 1985; Born & Tootell, 1992; Raiguel, van Hulle, Xiao, Marcicar, & Orban, 1995) have found that MT responses to motion often are altered by motion outside the classical receptive field—facilitated by opposite-direction and inhibited by same-direction motions. Raiguel et al. (1995) found that the average radius of foveal receptive fields in macaque area MT is about  $2.3^\circ$ —exceeding the largest stimuli in the present experiment. If performance

of this motion detection task depends on such MT cells, then detection thresholds might rise more sharply for larger stimuli.

#### 4. Experiment 2: discriminating phase relations among moving and stationary oscillations of separate features

The next three experiments investigated visual efficiencies in discriminating oscillation *phase* differences between separate features. Three blobs were horizontally aligned, and the center blob oscillated either in phase or out of phase relative to the two flanking blobs. Thresholds for these phase discriminations were compared with those for detecting rigid oscillations of all three blobs. Lappin et al. (2001) found that thresholds for discriminating motion phase differences of  $0^\circ$  vs.  $180^\circ$  were even lower than those for detecting rigid oscillations. Now we evaluated phase discriminations for stationary oscillations.<sup>2</sup>

##### 4.1. Method

Three horizontally aligned Gaussian blobs ( $\sigma = 10'$ ) were separated by  $100'$  center to center. Detection and phase discrimination thresholds were evaluated for moving and stationary oscillations of 2.25 Hz. Thresholds were evaluated for four discrimination tasks: motion detection, stationary detection, motion phase discrimination, and stationary phase discrimination.

In the motion detection task, all three blobs were either moving or stationary. When the blobs moved, they moved rigidly in phase with one another. In the motion phase discrimination task, all three blobs oscillated horizontally, and the center blob was either in-phase or out-of-phase by  $60^\circ$  relative to the two flanking blobs (which always oscillated rigidly in phase with one another). When the center blob was  $60^\circ$  out of phase, the relative motion of center and flanking blobs was the same as in the motion detection task.

The stationary detection and stationary phase discrimination tasks were similar to their motion counterparts. In the stationary detection task, all three blobs either remained unchanged or the contrast of all three oscillated in phase. In the stationary phase discrimination task, the contrast of the center blob oscillated in phase or  $60^\circ$  out of phase relative to the two flankers.

Thresholds were estimated from four Quest staircases. The four discrimination tasks were evaluated in separate

<sup>1</sup> For Gaussian blobs, the measures of contrast change and spatial acuity are redundant. The luminance change is directly proportional to the spatial shift (for all spatial shifts less than the radius of the blob). Moreover, the percentage of the total blob luminance that changes with a given spatial shift is directly proportional to the ratio of the spatial shift divided by the linear size,  $\sigma$ , of the blob. Thus, if the spatial acuity thresholds shown on the left vertical axis of Fig. 2 were directly proportional to the linear size,  $\sigma$ , with a zero intercept, then the ratio of the acuity threshold to the blob size would be constant, and the same would be true for the contrast change thresholds. The function relating contrast change threshold to blob size is determined by the function relating acuity threshold to blob size. The initial decrease in contrast change with blob size is determined by the vertical axis intercept of the linear function relating acuity threshold to blob size. With increasing blob size, the influence of this small intercept becomes smaller, and the function approaches a constant. The stimuli used in this study do not allow us to determine whether performance was limited by spatial acuity or by contrast change.

<sup>2</sup> Exps. 2–4 are replications of similar experiments conducted earlier. Several methodological details were slightly different in the previous experiments, and there were two other observers. The present results were essentially the same as those in the previous experiments, though here we report only the more recent results.

blocks of trials in a randomly permuted order, in four independently ordered sequences of the four tasks. Data were collected for three well-practiced observers, including two of the authors and two who participated in Exp. 1.

#### 4.2. Results

The results are described in Fig. 3, which shows oscillation thresholds (as spatial amplitudes) for each of the three observers in each of the four conditions. The principal result was that thresholds were much higher for the stationary phase discrimination task than for either the motion phase discrimination or stationary detection tasks. These threshold values quantify the subjective impression that phase relations among the stationary oscillations were poorly perceived. One could see the changing contrasts, but the phase relations between features were inconspicuous and confusable. By comparison, phase differences in the moving patterns were salient and effortlessly visible. Evidently, the moving oscillations are visually coherent, with spontaneously visible phase relations (Lappin et al., 2001). Such visual organization did not occur for the stationary contrast oscillations.<sup>3</sup>

Relative threshold values for the motion detection and motion phase discrimination replicate the qualitative results of Lappin et al. (2001). Quantitatively, phase discrimination thresholds were higher in the present study than in that of Lappin et al.—averaging 0.43' and 0.14' for the present and previous experiments, respectively. The higher thresholds in the present study resulted from two differences in the stimuli: the present blobs had lower contrast—26% at the blob peak relative to the background, as compared to 78% in the previous study—and the phase difference was smaller in the present experiment—60° as compared to the previous 180° difference. Despite the significantly larger spatial thresholds in the present experiment, motion phase discrimination thresholds were similar to those found previously when they are expressed in terms of contrast

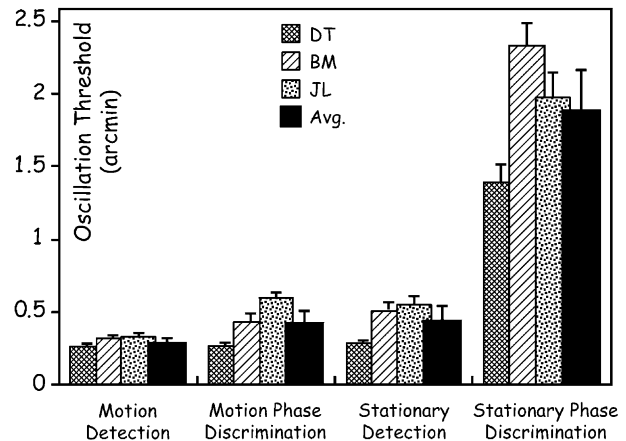


Fig. 3. Detection thresholds and phase discrimination (60° phase difference) thresholds for moving and stationary oscillations of three Gaussian blobs.

change—averaging 0.23% and 0.24% in the present and previous experiments, respectively.

The next two experiments explore additional aspects of the apparently poor perceptual organization of stationary contrast oscillations.

#### 5. Experiment 3: effects of spatial separation and temporal frequency on phase discriminations

Lappin et al. (2001) found that motion phase discriminations were robust over increases in temporal frequency and spatial separation between features. The present experiment investigated effects of these variables on perception of stationary oscillations.

The effect of temporal frequency on phase discrimination offers an index of the strength of the visual relationships among these features. If phase differences remain well discriminated when oscillation frequency is increased, this suggests that these changing features are perceptually coherent, unified. If phase discriminations deteriorate with increased oscillation frequency, this indicates that visual relations among the changing features emerge more slowly than the oscillation rate. Perhaps this visual organization requires attentional comparison.

Similarly, the effects of spatial separation depend on the mechanisms that combine information from retinally separate locations. Increased spatial separation might involve increased neural noise, and spatial resolution may also decrease with greater eccentricity. Thus, thresholds for multi-local discriminations might degrade systematically with spatial separation, as found in bisection and vernier acuities for stationary features (e.g., Levi & Klein, 1992). Lappin et al. (2001) found only small effects of spatial separation on motion phase dis-

<sup>3</sup> In the motion phase discrimination task, the center blob changed its relative position between the two flankers, and these changes in relative position were readily visible. One might wonder whether these changes in relative position could have been detected without perceiving motion at all. In fact, this was not possible; static offsets of this amplitude and contrast change were not visible without motion. Lappin et al. (2001) found that bisection acuity thresholds for static offsets were much higher than those for motion phase discriminations; and Toet, Eekhout, Simons, and Koenderink (1987) found thresholds for static Vernier alignment and bisection of approximately  $\sigma/10$ , whereas our acuity thresholds for relative motion were about  $\sigma/100$ . Decreases in temporal frequency below about 1.5 Hz produce increases in thresholds for detecting changes in relative position (Lappin et al., 2001; Exp. 3).

crimination, although these effects were tested at only a single temporal frequency (1.5 Hz).

In the present experiment, spatial separation and temporal frequency varied independently, and their effects were examined for both motion phase and stationary phase discriminations. The center blob oscillated either in-phase or anti-phase (180°) relative to the two flanking blobs. The phase difference was increased from that in Exp. 2 in order to improve phase discrimination for stationary contrast oscillation.

5.1. Method

Spatial separations between adjacent Gaussian blobs ( $\sigma = 10'$ ) were either 80' or 240', and the temporal frequency was 1.0, 3.0 or 8.5 Hz. The six combinations of these two factors were tested for both motion phase and stationary phase discrimination tasks. Two well-practiced observers, both of whom served in the other experiments, collected data for these 12 conditions in randomly permuted sequences. Thresholds for observer BM were estimated from four Quest staircases, and for DT there were three staircases for each condition.

5.2. Results

The oscillation thresholds are shown for each observer in Fig. 4 and Table 1. As may be seen, phase discrimination was more difficult for stationary than for moving oscillations, and the difference increased with temporal frequency and spatial separation. Table 1 offers a different description of the same results in terms of contrast sensitivities (reciprocal of the contrast change threshold). Motion phase discriminations at 3 Hz were particularly impressive, involving contrast change sensitivities of more than 1000 (one part per thousand) at 80' separation and above 800 at 240' separation. Remarkably, these small contrast changes were sufficient for discriminating oscillation phase differences between separate features. At the other extreme, contrast change sensitivities for stationary phase discriminations at 8.5 Hz were just 56 and 26 for the two separations.

Both temporal frequency and spatial separation had different effects on stationary and moving phase discriminations. Phase discriminations of the stationary patterns were more vulnerable to increases in either temporal frequency or spatial separation. Increasing temporal frequency from 1 to 3 Hz lowered phase discrimination thresholds for motion but slightly increased thresholds for stationary oscillations, and the increase in thresholds between 1 and 8.5 Hz was smaller for the moving patterns. We found the same interactive effects of these variables in an earlier version of this experiment with two other observers, different stimulus contrasts, and spatial separations of 30', 90', and 270'.

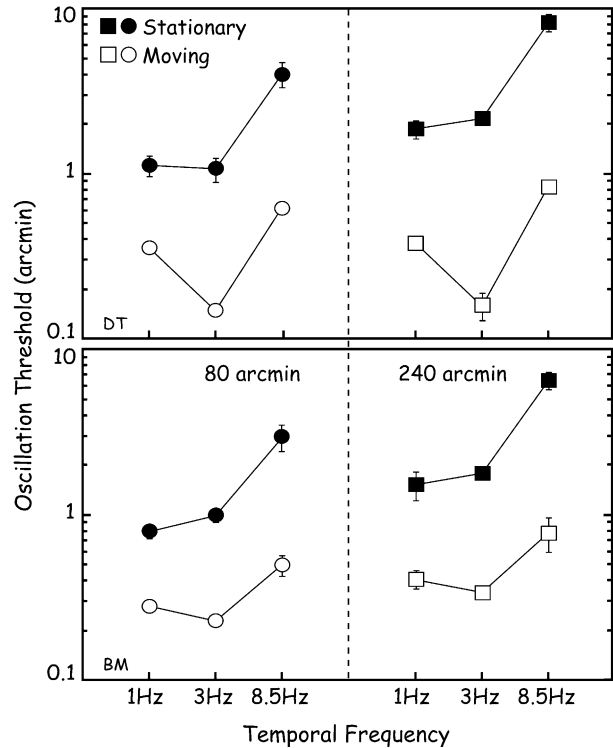


Fig. 4. Phase discrimination (180° phase difference) thresholds for moving and stationary oscillations of three Gaussian blobs, as a function of the temporal frequency and spatial separation between blobs.

Table 1 Contrast change sensitivities (reciprocals of contrast change thresholds) for each task condition and observer in Exp. 3

|                   | 80'  |      |        | 240' |      |        |
|-------------------|------|------|--------|------|------|--------|
|                   | 1 Hz | 3 Hz | 8.5 Hz | 1 Hz | 3 Hz | 8.5 Hz |
| <i>Moving</i>     |      |      |        |      |      |        |
| BM                | 684  | 851  | 387    | 467  | 571  | 245    |
| DT                | 532  | 1273 | 305    | 508  | 1195 | 228    |
| Average           | 608  | 1062 | 346    | 488  | 883  | 237    |
| <i>Stationary</i> |      |      |        |      |      |        |
| BM                | 241  | 191  | 65     | 126  | 106  | 29     |
| DT                | 171  | 179  | 47     | 102  | 88   | 23     |
| Average           | 206  | 185  | 56     | 114  | 97   | 26     |

Contrast change thresholds were directly proportional to spatial oscillation thresholds, with  $1' = 0.5224\%$ .

6. Experiment 4: correlations of visual signals

In Exp. 2 and in Lappin et al. (2001), motion phase discrimination thresholds were similar to motion detection thresholds. The small difference in these thresholds implies that visual signals for multiple moving features are positively correlated, as noted by Lappin et al. (2001). The present experiment estimated this visual correlation more directly by measuring thresholds for detecting oscillations of the center alone and the two

flankers alone as well as the phase discrimination threshold for the difference between these two signals.

The rationale for estimating this correlation is based on the statistical formula for the variance of a difference between two random variables. The oscillation thresholds in these experiments estimate standard deviations of the visual signals; and the phase discrimination thresholds estimate the standard deviation of a difference between two such signals. The following statistical formula describes the relation between these quantities and the correlation coefficient. Let  $\sigma_C$  and  $\sigma_F$  represent the thresholds for detecting oscillations of the center and flanking features, respectively, and let  $\sigma_{(C-F)}$  be the phase discrimination threshold for these two oscillations. Then

$$\sigma_{(C-F)}^2 = \sigma_C^2 + \sigma_F^2 - 2r\sigma_C\sigma_F, \quad \text{and} \\ r = [\sigma_C^2 + \sigma_F^2 - \sigma_{(C-F)}^2] / [2\sigma_C\sigma_F]. \quad (1)$$

If signals for the center and flanking features were visually independent—if  $r = 0$ —then the squared threshold for the difference between the two signals would equal the sum of the squares of thresholds for the two components—i.e.,  $\sigma_{(C-F)}^2 = \sigma_C^2 + \sigma_F^2$ , and the numerator of Eq. (1) would be zero. As the phase discrimination threshold,  $\sigma_{(C-F)}$ , becomes smaller, the correlation between the two signals becomes larger. Thus, the finding of Exp. 1 and of Lappin et al. (2001) that motion phase discrimination thresholds were comparable to those for detecting motion indicates that the underlying visual signals were positively correlated.<sup>4</sup>

<sup>4</sup> Note that this method for estimating a correlation differs from the standard statistical situation involving distributions of pairs of values of two variables—from which the quantities  $\sigma_C^2$ ,  $\sigma_F^2$ , and  $\sigma_{(C-F)}^2$  can be computed. In the standard situation, the values for a difference (or sum or product) between the two variables can be computed from the paired values of the two variables; and there are intrinsic upper and lower bounds on the variance of this difference (or sum or product). In the present situation, however, we have three independent estimates of these three variances, and it is quite possible for these three values to violate the constraints that ordinarily hold for a difference (sum, product) between two other variables. The statistical formula in Eq. (1) is a version of the trigonometric formula known as the *law of cosines*, where the quantity  $\cos \delta$  is equivalent to the correlation coefficient  $r$ , and the standard deviations are geometrically interpreted as lengths of vectors. Thus, in both the trigonometric model and in the standard statistical application, lower and upper bounds on the length of the difference vector,  $\sigma_{(C-F)}$ , are given by the difference and sum of the lengths of the other two variables,  $|\sigma_C - \sigma_F| \leq \sigma_{(C-F)} \leq \sigma_C + \sigma_F$ . In the present application, however, where the length of the difference vector,  $\sigma_{(C-F)}$ , is independently estimated, these boundary constraints can be violated. Indeed, this violation occurred in the stationary conditions of Exp. 4. Even though the obtained values for the stationary phase discriminations violated the statistical and trigonometric models for a correlation between two vectors, the relation between these three thresholds is still informative about the underlying mechanism. We report the resulting “correlation coefficient” with the understanding that the results do fit the model of two negatively correlated vectors. This violation is probably due to limitations of perceptual organization and attention beyond those associated with a negative correlation between variables.

## 6.1. Method

Thresholds were estimated for six conditions—two detection tasks and a phase discrimination task for both moving and stationary oscillations. In the center detection task, only the center blob was displayed, and on each trial this either oscillated or was stationary and constant. In the flanks detection task, only the two flanking blobs were displayed, and the observer discriminated between an oscillating pattern and one that was stationary and constant. In the phase discrimination task, the center and flanking blobs all oscillated in-phase or the center blob oscillated in anti-phase relative to the two flankers, with the oscillation amplitude constant for the block of trials.

The stimuli were Gaussian blobs ( $\sigma = 10'$ ). The oscillation frequency was 3 Hz. In the phase discrimination task, the center-to-center separation was  $100'$ ; and in the flanks detection task the two blobs were separated by  $200'$ .

Data were collected for three well-practiced observers, including two of the authors; all had participated in one or more of the previous experiments. Thresholds were estimated from four Quest staircases for each condition. The six conditions were scheduled in four independent random permutations for each observer.

## 6.2. Results

The thresholds for each observer in each condition are given in Table 2, along with the estimated correlation coefficients between the center and flanker signals in the moving and stationary conditions. For all three observers, the low thresholds for the motion phase discrimination tasks resulted in an estimated positive correlation between the Center and Flanker signals.

Table 2  
Oscillation threshold estimates (arcmin) for each of the six conditions in Exp. 4, plus the estimated visual correlation of the center and flanking signals computed by Eq. (1)

|                                      | JL    | BM    | DT    | Average |
|--------------------------------------|-------|-------|-------|---------|
| <i>Moving oscillations</i>           |       |       |       |         |
| Center detection                     | 0.30  | 0.42  | 0.27  | 0.33    |
| Flanks detection                     | 0.27  | 0.43  | 0.32  | 0.34    |
| Phase discrimination                 | 0.22  | 0.27  | 0.21  | 0.23    |
| Estimated visual correlation ( $r$ ) | +0.72 | +0.80 | +0.76 | +0.76   |
| <i>Stationary oscillations</i>       |       |       |       |         |
| Center detection                     | 0.59  | 0.52  | 0.40  | 0.50    |
| Flanks detection                     | 0.71  | 0.67  | 0.68  | 0.69    |
| Phase discrimination                 | 1.35  | 1.22  | 1.39  | 1.32    |
| Estimated visual correlation ( $r$ ) | -1.18 | -1.11 | -2.40 | -1.56   |



These estimated correlations are comparable to values obtained by Lappin et al. (2001) with different stimulus conditions and a less direct method of estimation.<sup>5</sup>

In contrast, the relatively high thresholds for stationary phase discrimination yielded a negative correlation between the visibilities of the Center and Flanker oscillations. In fact, the thresholds for stationary phase discrimination were even higher than if the amplitudes of the visual signals for Center and Flanker oscillations were perfectly negatively correlated, if  $r = -1.0$ . Evidently, the stationary oscillation signals from these two sets of features could not be simultaneously attended without a significant loss of sensitivity.

## 7. General discussion

The principal finding was that moving and stationary contrast oscillations have different effects on visual mechanisms. Differences in the visibility of these two forms of image change were found in detecting oscillations of larger individual features (with  $\sigma$  greater than about  $20'$ ) and especially in discriminating phase relations among multiple features. Generally speaking, the image changes produced by motion were visually coherent—correlated—yielding spontaneous organization of the spatially distributed changes within and between features. Stationary contrast changes, however, were visually less organized.

### 7.1. Motions are more detectable than stationary contrast oscillations

The better detectability of moving as compared to stationary oscillations of a single feature was not anticipated and had not been observed in earlier experiments with smaller features ( $\sigma = 7'$ ). The finding that increases in feature size had less effect on detecting motion than on detecting stationary oscillation suggests that vision is more efficient in maintaining information about spatial positions and motions than about contrast as such. Indeed, the visual efficiency in detecting motions of these blurred features seems impressive: the motion detection thresholds for the largest features ( $\sigma = 60'$ ) averaged less than 1% of their  $2\sigma$  width, and

the contrast change thresholds averaged about 0.1% of their total luminance.

The spatial positions of these blurred features were poorly defined relative to their spatial displacements. These Gaussian blobs, especially the larger ones, did not have sharp edges with well-specified positions. Increasing the size of these features reduced their luminance gradients and positional specificity, but this had only a small effect on the visual resolution of their motions. Indeed, if motion sensitivity is measured in relation to either the diameter or total contrast of the feature, then increases in size did not reduce and sometimes even improved motion sensitivity. The hyperacuity for motion that we found with these stimuli is impressive and might be surprising from some perspectives.

The linear relations between feature size and thresholds for detecting both moving and stationary image changes resemble effects found by Toet and colleagues (Toet et al., 1987; Toet & Koenderink, 1987) in static spatial discriminations. Using Gaussian blobs with sizes varied over more than two decades, spatial displacement thresholds in vernier alignment and bisection tasks (Toet et al., 1987) and in two-point discriminations (Toet & Koenderink, 1987) were approximately proportional to the size of the feature. The present study extends this result to acuities for motion. The present motion detection thresholds were on the order of 1% of the spatial scale,  $\sigma$ , of the blobs, whereas Toet and colleagues found alignment and bisection thresholds about 10% and two-point discrimination thresholds near 100% of  $\sigma$ . The approximate scale-invariance of these three quantitatively different spatial discriminations is striking. As Toet and colleagues concluded, scale-invariant mechanisms seem to underly several different spatial discriminations.

A complementary description of the moving stimuli may be given by the contrast change, which was a dynamic *dipole*—a simultaneous decrease in contrast at one location and an increase at another. The moving and stationary contrast changes differed from each other in two ways: (1) Motion produced asymmetrical contrast changes but stationary oscillations produced symmetrical changes. (2) The zero-crossings of these contrast-change dipoles shifted (by half the amplitude of the motion) in the moving but not in the stationary oscillations. The present experiments do not distinguish the roles of these two factors, but the recent results of Hock et al. (2002) strongly implicate the role of dipole contrast changes in motion perception. Hock et al. demonstrated that “counter-changing luminance”—essentially the same property as the dipole contrast change described in the present report—is necessary and sufficient for perceiving apparent motion of a single feature appearing at two spatially and temporally separate locations. The present experiments show the relevance of this property for detecting both motion of

<sup>5</sup> The phase discrimination thresholds were slightly lower here than in Exp. 2 because the phase difference was  $180^\circ$  whereas it was  $60^\circ$  in Exp. 2. Thus, the maximum difference between the two component features was twice as large in this experiment, and this serves to lower the discrimination threshold and to increase the correlation. If the phase discrimination thresholds were twice the values given in Table 2, then the average correlation coefficients would be 0.52 and  $-4.02$  for the moving and stationary conditions, respectively.

single features and relative motion of spatially separate features.

### 7.2. Relative motions of multiple features are visually coherent, but stationary contrast changes are not

The difference in visual sensitivity to these moving and stationary image changes was particularly pronounced in discriminating phase differences in oscillations of multiple features. Differences in both the overall visibility of these two types of phase relations and in the effects of spatial separation and temporal frequency indicate that these two forms of image change have very different effects on the underlying neural network. The global organization was less visible in the stationary patterns than in the moving patterns. Moving patterns were visually coherent—positively correlated—but stationary contrast oscillations were, in effect, negatively correlated. Perceiving the stationary oscillations of one feature interfered with perceiving the oscillations of another; and contrast relations between features usually were difficult to perceive, even with focused attention.

Why might these two similar forms of image change have such differing effects on the organization of visual responses? A definite answer is not yet available, but at least one hypothesis can be suggested about the excellent visual organization of moving patterns.

Notice that observers exhibited *hyperacutities* for motion phase differences between separate features—detecting positional displacements smaller than the eye's optical point spread function (especially in Exps. 3 and 4). This hyperacuity implies that from retinal input to behavioral output the visual system loses little information about spatiotemporal relations among spatially separate motions. Current electrophysiological research offers little or no evidence of direct physiological interactions among retinal signals elicited by such spatially separate stimuli; but the temporal structure of the spike trains of retinal ganglion cells seems to correlate with the motions of optical features through the receptive fields.<sup>6</sup> Thus, correlated motions of separate features tend to produce correlated spike trains in separate cells.

<sup>6</sup> Relevant physiological evidence about cat retinal ganglion cells was obtained recently by B. Borghuis, M. Lankheet, W. van de Grind, and the first author at Universiteit Utrecht. Acutities and reliabilities of ganglion cell responses were evaluated for spike trains elicited by a variety of moving stimuli, including drifting bars and gratings and small amplitude oscillations of bars at various positions within the receptive fields. Spike trains stimulated by the same stimulus on different trials were highly correlated with one another, with the correlation increasing with luminous contrast. No influence at all could be detected from either in-phase or anti-phase oscillations of flanking bars outside the receptive field. Nevertheless, responses of individual ganglion cells, both ON and OFF responses, were very reliably controlled by the spatiotemporal phase of the stimulation.

Related evidence was reported recently by Buracas, Zador, DeWeese, and Albright (1998), who studied the transmission of information by spike trains of cells in area MT of macaques. The firing rate of these cells often is thought to signal motion in a particular direction (Newsome, Britten, & Movshon, 1989), but Buracas et al. found that much more information is carried by the temporal structure of the spike trains elicited by moving stimuli with a richly varied spatiotemporal structure. The average firing rates elicited by constant motion carried only about 1 bit/s about the direction of motion. Stimuli with a richer temporal structure, however, in which the direction switched randomly between the preferred and anti-preferred directions, yielded transmission rates up to 29 bits/s in controlling the temporal structure of the spike trains, even though the firing rate was lower for these stimuli than for the constant-motion stimuli. The oscillating stimuli in the present experiments may be similarly effective in eliciting time-locked variations in neural responses. In any case, the hyperacuity found here and in other recent studies (Lappin & Craft, 2000; Lappin et al., 2001) suggests that spatially separate motion mechanisms provide correlated spatiotemporal information. The mechanisms that detect such multi-local correlations are not yet known, but evidently they are very efficient.

Apparently, however, such coherent responses are not stimulated by stationary contrast oscillations. The stationary patterns differed both locally and globally from the moving patterns. Locally, the stationary contrast oscillations changed both the total luminance and its spatial distribution but not the positions of features; whereas the moving patterns altered positions but not total luminances. Globally, motion phase differences altered spatial relations between features, but the spatial structure of stationary patterns was unaffected by phase differences. If visual mechanisms are responsive to global image structure, then these may be much more sensitive to spatial structure and its changes than to the spatiotemporal distribution of luminance per se. In any case, visual mechanisms are more sensitive to the global organization of moving than stationary contrast oscillations.

The difference in visual sensitivity to these two forms of spatiotemporal organization seems to reflect what vision does best. Vision seems to be directly sensitive to relative motion but less sensitive to the spatiotemporal organization of stationary contrast. Image motion probably is a more important form of visual information than stationary contrast changes.

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**Appendix A. Definition of stationary contrast changes**

For clarity, the computations are restricted to one dimension. This is a valid simplification as all motions/oscillations in the current study are horizontal. The contrast change produced by motion,  $D_s$ , is defined as the difference between a Gaussian shifted by  $s$ ,  $G_s$ , and the initial Gaussian,  $G_0$ ,  $s = 0$ .

$$G_0 = e^{-x^2/2\sigma^2}$$

$$G_s = e^{-(x-s)^2/2\sigma^2}$$

$$D_s = G_s - G_0 = e^{-(x-s)^2/2\sigma^2} - e^{-x^2/2\sigma^2}$$

Next, for the stationary contrast changes, the zero crossing of the contrast change  $D_s$  must be aligned with the center of the initial Gaussian,  $G_0$ . This is accomplished by translating  $D_s$  by  $-s/2$  (see Fig. 5, bottom).

$$D_{s(\text{re-centered})} = e^{-(x-s/2)^2/2\sigma^2} - e^{-(x+s/2)^2/2\sigma^2}$$

The absolute value of  $D_{s(\text{re-centered})}$  is used to compute the stationary contrast oscillation,  $C_s$ .

$$C_s = G_0 + \frac{s}{|s|} |D_{s(\text{re-centered})}|$$

$$C_s = e^{-x^2/2\sigma^2} + \frac{s}{|s|} |e^{-(x-s/2)^2/2\sigma^2} - e^{-(x+s/2)^2/2\sigma^2}|$$

The absolute value ensures that the contrast changes are bilaterally symmetric. Value  $s/|s|$  determines whether the contrast change is added to or subtracted from  $G_0$ . As  $s$  oscillates about 0 with a fixed amplitude, stationary contrast oscillation is produced (Fig. 1). From this computation of  $C_s$ , it follows that for any given amplitude of oscillation, the magnitude of contrast changes produced by motion and by stationary contrast oscillation are identical.

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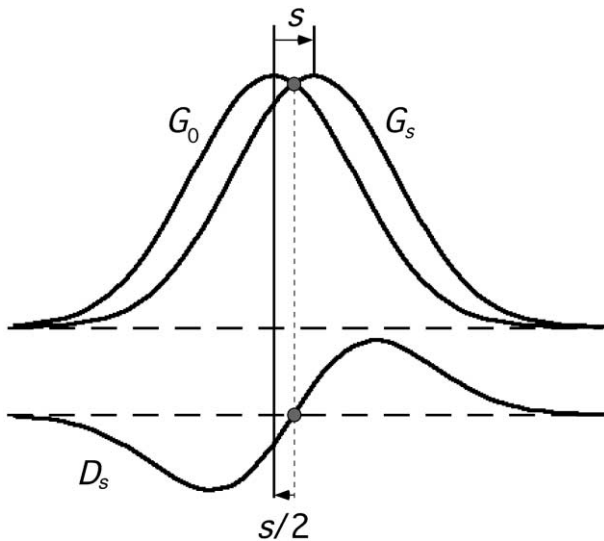


Fig. 5. The difference pattern,  $D_s$ , between two Gaussian distributions,  $G_0$  and  $G_s$ , spatially shifted relative to each other. For stationary oscillations, the zero-crossing of  $D_s$  was centered, and the contrast changes were equal on both sides of the zero-crossing—both positive or both negative. These 1D illustrations are used for simplicity; the actual Gaussian blobs and difference patterns were 2D.

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