Spatial interactions determine temporal feature integration as revealed by unmasking

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ABSTRACT

Feature integration is one of the most fundamental problems in neuroscience. In a recent contribution, we showed that a trailing grating can diminish the masking effects one vernier exerts on another, preceding vernier. Here, we show that this temporal unmasking depends on neural spatial interactions related to the trailing grating. Hence, our paradigm allows us to study the spatio-temporal interactions underlying feature integration.

INTRODUCTION

There exists a vast psychophysical literature on how features are integrated in the spatial domain and on the dynamics of visual processing in general. However, only a few investigations studied the dynamics of feature integration (for example, Efron, 1967). Investigating such temporal feature integration, we discovered the following unmasking phenomenon.

We presented a vernier followed by a second vernier. The second vernier had the same spatial parameters as the preceding vernier but an opposite offset direction (Fig. 1a). Hence, if the first vernier was offset to the left, the second vernier was offset to the right and vice versa. For this reason, the second vernier will be called an anti-vernier in the following. For short presentation times (5 ms–60 ms per vernier) and reasonable small vernier offsets (10″–60″), the verniers are fused appearing as one single vernier (Herzog et al., 2003b). Its perceived offset is a combination of the offset of the vernier and the anti-vernier. In this condition, the anti-vernier dominates performance, that is, observer's responses are more in accordance with the anti-vernier than with the vernier. Please note, that in each stimulus presentation, a left and a right offset were presented either as the vernier or the anti-vernier offset.

In the next condition, the vernier and the anti--vernier were followed by a grating mask comprising aligned verniers (Fig. 1d). With this manipulation, the vernier offset determines performance more strongly than the anti-vernier: dominance has reversed from anti-vernier dominance in the no-mask condition to vernier dominance if a mask follows the vernier and the anti-vernier. It seems that dominance does not depend on the temporal order of vernier and anti-vernier per se since in both, the no-masked (no grating presented) and the masked (trailing grating presented) case, the vernier precedes the anti-vernier.

In Herzog et al. (2003b), the vernier and the anti-vernier were followed by a grating of which the central element covered the location of the verniers (except for the displacement of the vernier and anti-vernier, Fig. 1d). Hence, the reversal of dominance may be explained by local interactions only, that is, by a three element sequence: vernier, anti-vernier, central ele-

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ment of mask. In this contribution, we show that this is not the case. Quite to the contrary, strong effects of dominance reversal occur even for metacontrast masks not overlapping with the verniers whereas no change of dominance is found for a mask comprised of one single, aligned vernier spatially overlapping with the verniers. Hence, the temporal integration of features at one spatial location depends on the spatial arrangements of elements at nearby locations. Therefore, our feature fusion paradigm allows us to study the interacting temporal and spatial mechanisms of feature integration.

GENERAL MATERIALS AND METHODS

General setup and stimuli

Stimuli were displayed on an X-Y-display (Tektronix 608 or HP 1334 A) controlled by a Power Macintosh computer via fast 16 bit D/A converters (1 MHz pixel rate). The refresh rate was 100 Hz. Subjects observed the stimuli from a distance of 2 meters in a room dimly illuminated by a background light (about 0.5 lx). Luminance of stimuli was around 80 cd/m^2. Before stimulus presentation, a fixation dot was presented at the center of the screen and four markers were shown at the corners of the monitor.

In most experiments, two sequentially presented verniers preceded a trailing mask. The two preceding verniers had the same spatial parameters except for that offset directions were opposite to each other. The verniers are referred to as vernier and anti-vernier. For example, if the preceding vernier is offset to the left, the following anti-vernier is offset to the right (see Fig. 1a).

The segments of both verniers were 10′ long and separated by a vertical gap of 1′. Hence, the length of the verniers was 21′ altogether. The offset size of the vernier and anti-vernier was identical (only the offset directions differed). The duration of the verniers was always identical. Verniers were shown one after the other, that is, the interval-stimulus-interval (ISI) between the verniers was 0 ms. This condition will be called also the "no-mask" condition (see below).

In most conditions, a mask followed after the verniers without ISI. Masks were a single vernier, gratings comprising 5 or 25 elements, a metacontrast grating mask, a light field, or a grating comprising horizontal lines. Aligned vertical vernier(s) had the same spatial parameters as the target vernier, except for being not offset, if contained in the single vernier, the 5 and 25 element grating, and the metacontrast mask. The spacing between elements in the 5 and 25 element grating was 200″. The metacontrast grating mask was a 25 element grating mask with the center element omitted. The light field was 21′ in height and 1.33° in length; thus, its size was identical to the size of a 25 element grating. The light field was composed of single dots with a spacing of 65″ if not stated otherwise. The dots were arranged in a regular fashion forming a rectangular grid and had the same luminance as the elements in the other masks. With these parameters, the overall luminance of the light field was identical to that of the 25 element grating. The horizontal mask comprised vertical lines of a length of 1.33°. The verniers were presented at the center of the screen where the mask was centered, too. Gratings were displayed for 300 ms.

As a baseline, we determined performance for a sequence of vernier and its anti-vernier only in each experiment. We will call this condition often the "no-mask condition" even though the anti-vernier masks the preceding target vernier, that is, one masking element is present in all experimental conditions of this contribution. However, these two verniers are perceptually fused and we were interested how masks of various types interact with this fusion process. Conditions in which the vernier and its anti-vernier are followed by an additional mask will also be called "masked conditions".

Observers

Most data were obtained from paid students of the University of Bremen and from the authors. All observers had normal or corrected-to-normal visual acuity. The age of observers was between 21 and 50 years. After observers had signed a consent form, acuity was determined by means of the Freiburg acuity test (Bach, 1996). To participate in the experiments observers had to reach a value of 1.0 (corresponding to a visual acuity of 20/20) in this test for at least one eye. Only highly experienced observers participated in the experiments.

In most conditions, the verniers were followed by a mask. Since masking affects performance of observers differently, we determined for each observer an individual presentation time for the vernier and anti-vernier to yield reasonable performance in the no-mask condition (vernier, anti-vernier only). The same duration was used for the anti-vernier and for the vernier.

Task

In a binary task, observers had to determine the direction of the offset of the fused vernier, that is, left vs. right. Performance is determined as the percentage of responses consistent with the first vernier offset. Thus, if performance is below 50%, performance is dominated by the anti-vernier. A performance above

50% indicates dominance of the vernier. No feedback was provided.

Each condition was measured twice for each observer. Conditions were randomized across observers. The order of measurements in the second run was in opposite order to that of the first run to compensate at least partially for learning effects. Experiments were run in blocks of 80 presentations. To prevent tiring of the observers, sessions neither lasted longer than 20 blocks nor exceeded 2 hours.

EXPERIMENTS

Mask types

Dominance of the anti-vernier reverses when vernier and anti-vernier are followed by a masking grating (Fig. 1d; Herzog et al., 2003b). Since the central element of the grating spatially overlapped with the verniers, the reversal of dominance may be explained by spatial local interactions between the vernier, the anti-vernier, and the central grating element only. In this experiment, we varied systematically the spatial layout of a mask, presented after the vernier and anti-vernier, to determine the role of local versus global spatial interactions in feature fusion.

Methods

Stimulus sequences are shown in Figure 1. After the presentation of the vernier and the anti-vernier either no mask (a) or one of five different mask types (b–f) was presented. In the first masked condition (b), the mask comprised an aligned vernier. In the conditions (c) and (d), the mask comprised a grating of 5 or 25 aligned verniers, respectively. In the next condition (e), the mask consisted of 24 verniers (metacontrast grating). This mask is identical with the 25 element grating except for that the central element is omitted. Hence, the gap size between the two inner elements of the two gratings is 400″. In the last condition (f), a rectangular light field composed of dots was used.

Four observers participated in this experiment. The presentation time of the vernier and the anti-vernier was 15 ms for one observer and 20 ms for the other three observers. The vernier and the anti-vernier were each offset by 100″.

In the second part of the experiment, we varied quantitatively the offset size of the vernier and the anti-vernier in the above six conditions. In each particular condition, vernier and anti-vernier had the same offset size. Three observers participated. The presentation time of the vernier and the anti-vernier was 15 ms for one observer and 20 ms for the other two observers.

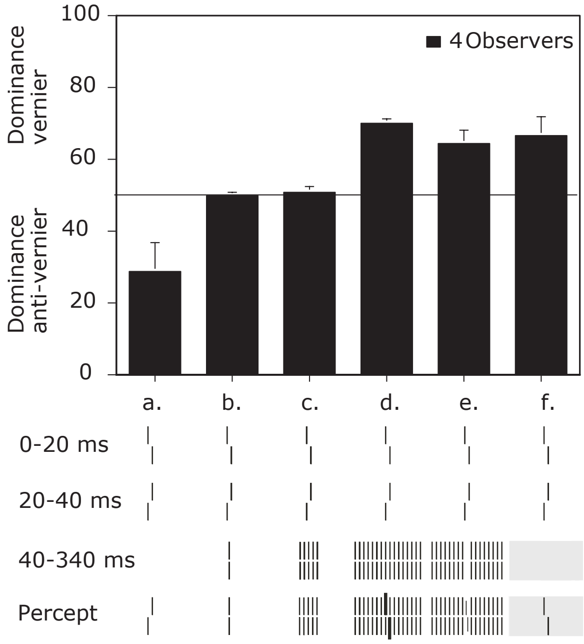

Figure 1.

An offset vernier was followed by its anti-vernier followed by one of six masks. a) No mask. b) Aligned, single vernier. c) A grating comprising five elements. d) A grating comprising 25 elements (only 16 of which are drawn because of space considerations). e) Metacontrast mask: a 24 element grating with a gap in the center. f) A light mask with its luminance being equal to the 25 element mask (d). Presentation times are typical examples. At the bottom, the percept in each experimental condition is shown. Only in the conditions d-f, the fused vernier is clearly visible with the vernier rather than the anti-vernier dominating performance in the averaged data. For values above 50%, performance is dominated by the vernier whereas for values below 50%, performance is dominated by the anti-vernier. ***Results****. If only the vernier and the anti-vernier are presented, the anti-vernier dominates performance (a). For a mask comprising only one single or 5 aligned verniers, no clear dominance is found (b,c). For the 25 element grating, the metacontrast grating, and the light field, the vernier dominates performance (d-f). Mean performance for four observers and respective standard errors.*

Results and Discussion

Figure 1 shows the mean performance for the six conditions. If no mask is presented, performance is dominated by the anti-vernier (Fig. 1a). For the mask comprised of an aligned vernier, performance is neither dominated by the vernier nor by the anti-vernier (Fig. 1b). The same result is found for the 5 element mask (Fig. 1c). In the other three conditions (d–f), that is, for extended masks, performance is dominated by the vernier.

Subjectively, if a single, aligned vernier follows the verniers, observers perceive only one single fused vernier (b) as in the no-mask condition (a). If a grating comprising 5 elements follows the verniers (c), observers may

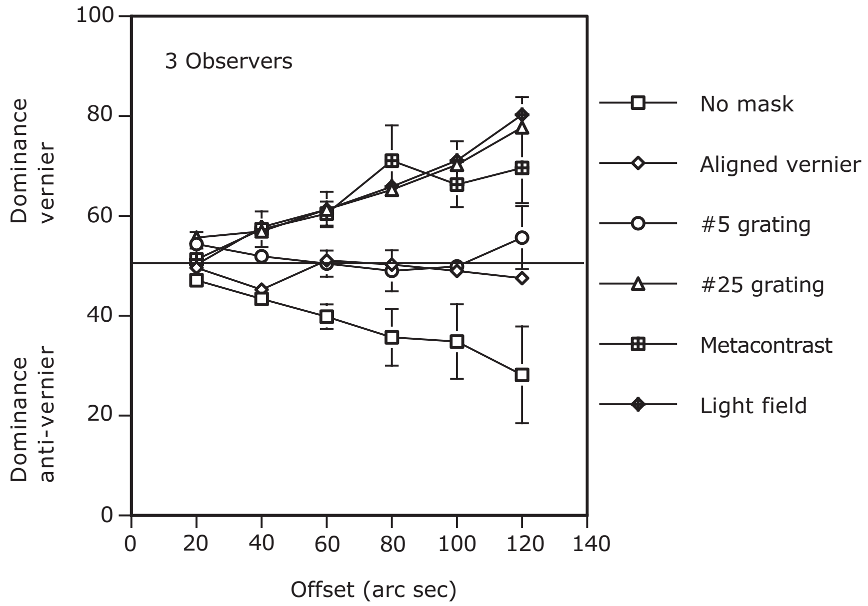

Figure 2.

Mean performance for three observers for all six conditions (a-f) from Fig. 1 as a function of vernier and anti-vernier offset size. With increasing offset, the respective dominance increases whereas for the single aligned vernier and the 5 element grating (# 5 grating) no obvious changes occur.

focus attention on one edge of the grating where they perceive a weak illusory offset (Herzog & Koch, 2001). The foregoing verniers remain largely invisible, that is, observers are not aware of the generation of the illusory offset (Herzog et al., 2003b). In the condition in which a grating comprising 25 elements is presented, observers perceive a single shine-through element looking wider, brighter, sometimes even longer than the vernier (d). Attention is focused on this element, which appears to be superimposed at the center of the grating. The bottom line in Fig. 1 shows the subjective perception of the respective experimental conditions.

Fig. 2 shows the quantitative results for various offset sizes. For an offset of 20″, performance is close to 50% in all conditions. As the offset increases, the differences in dominance become prominent. If no mask is presented, anti-vernier dominance increases with increasing offset size. If the mask comprises a vernier with no offset, performance remains at about 50%. For the 5 element mask, performance is slightly above 50% (c). In the other masked conditions (d–f), performance is dominated by the vernier. In these cases, the dominance effect of the vernier increases with increasing offset size (d–f).

The single, aligned vernier mask yields no clear dominance whereas the 25 element grating shows a dominance of the vernier. Hence, local interactions at the vernier position exclusively cannot explain our results since the single vernier mask is contained in the 25 element grating. Moreover, omitting the central element of the 25 element grating yields a reversal of dominance.

Metacontrast mask

The last experiment has shown that the spatial layout of the mask is an important factor to explain the reversal of dominance. In the following experiments, we will investigate the effects of the spatial layout of the mask on feature fusion quantitatively.

The metacontrast mask yielded a clear reversal of dominance even though the vernier and the anti-vernier were not covered by this mask. However, the gap between the central, inner elements of the metacontrast mask was rather small, that is, 400″ only. To investigate the extent to which vernier rather than anti-vernier dominance prevails, we vary the size of the central gap of the metacontrast grating. The rationale of the experiment is that for large gap sizes, the inner contours of the metacontrast grating do not influence the two verniers, resulting in a dominance of the anti-vernier. This condition is comparable to the no-mask condition. With decreasing gap size, vernier dominance should increase.

Methods

The metacontrast grating was composed of two gratings comprising 12 aligned verniers each. Within the two gratings, the distance between elements was 200″.

One grating was presented to the left of the center, one to the right. Thus, a grating comprising 24 elements with a central gap was presented. We used

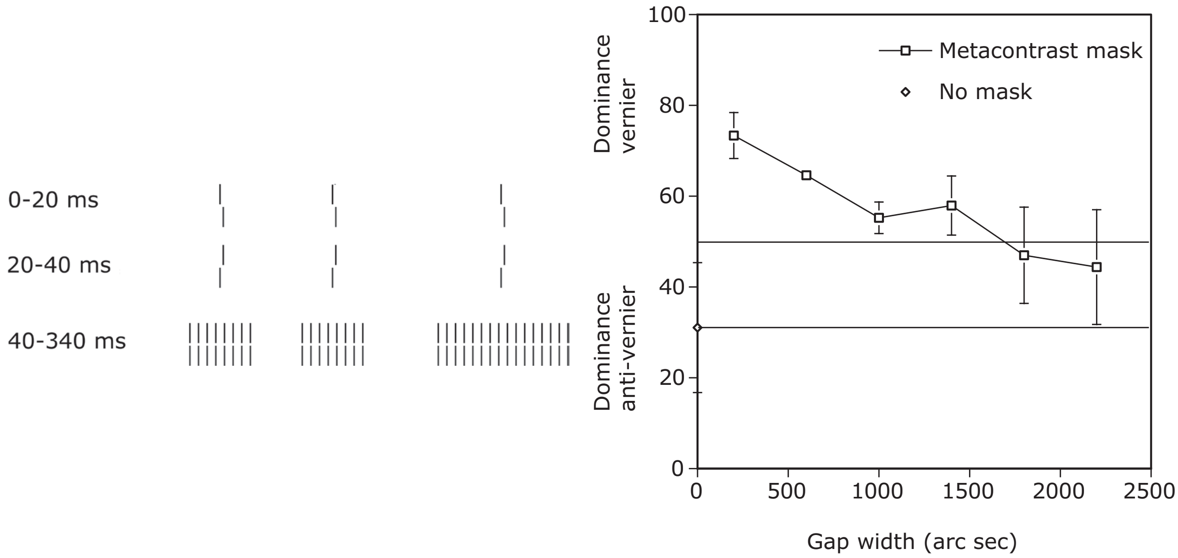

Figure 3.
Vernier and anti-vernier were followed by a metacontrast grating comprised of two gratings. We varied the gap between the gratings. On the left hand side, the no-mask control condition and two masked conditions are shown as examples (presentation times are typical values; only 16 elements are drawn for each metacontrast grating). For the smallest gap distance of 200″, a regular grating of 24 aligned verniers is presented (right most stimulus example); the vernier and anti-vernier fit in the spacing of the two center elements (the vernier and anti-vernier offset are drawn unproportionately larger than the grating's spacing). ***Results****. With an increase in gap size, performance approaches performance in the no-mask condition (lower horizontal line). Mean performance of three observers with the respective standard errors.*

central gap sizes of 200″, 600″, 1200″, 1400″, 1800″, and 2200″. Performance was determined for the no-mask condition, that is, vernier and anti-vernier only, too. Vernier and anti-vernier offset was 80″. Three observers participated in this experiment. The presentation time of both the vernier and the anti-vernier was 20 ms for two observers and 15 ms for one observer.

Results and Discussion

As gap distance increases, performance in the masked conditions approaches the performance in the no-mask control condition without completely reaching it for the parameters used in this experiment (Fig. 3). The point of equal dominance is reached for a gap size of about 1600″, that is 20 times the vernier (or anti-vernier) offset size, hence, surprisingly large.

It should be mentioned that, because of the long presentation time of 300 ms, this metacontrast mask does not yield B-type masking if only a single vernier is presented instead of a vernier, anti-vernier sequence (Herzog, Harms, Ernst, Eurich, Mahmud, & Fahle, 2003a).

Light masks

Extended light masks yield a strong vernier dominance comparable to an extended grating mask. Hence, the line structure of the grating masks seems to be relatively less important for the vernier dominance. The light masks offer the opportunity to study the reversal of dominance by changing the luminance of the mask not being affected by pattern effects. Here, we study the transition from vernier to anti-vernier dominance by varying the spacing between the dots and the presentation time of the light field.

Methods

Three observers participated in the first part of this experiment. The presentation time of the vernier and the anti-vernier was 15 ms for one observer and 20 ms for the other two observers. The mask consisted of a light field as used in condition (f) of the first experiment (size: 1.3° × 21′). The density of dots in the field was varied in order to change the luminance of the mask. The distance between light dots was 32″, 65″, 97″, 130″, 195″, and 260″. Performance was determined also in the no-mask condition.

Two observers took part in the second part of the experiment in which the duration of the light field was varied. The presentation time of the vernier and the anti-vernier was 20 ms. As in the first part of the experiment, the mask comprised a light field of 1.3° × 21′. Dot distance was 65″ (as in Fig. f). The presentation time of the mask was varied from 10 to 300 ms which is the "standard" duration used in the experiments concerning this contribution. Performance was determined also in the no-mask condition, that is, in the vernier anti-vernier sequence only.

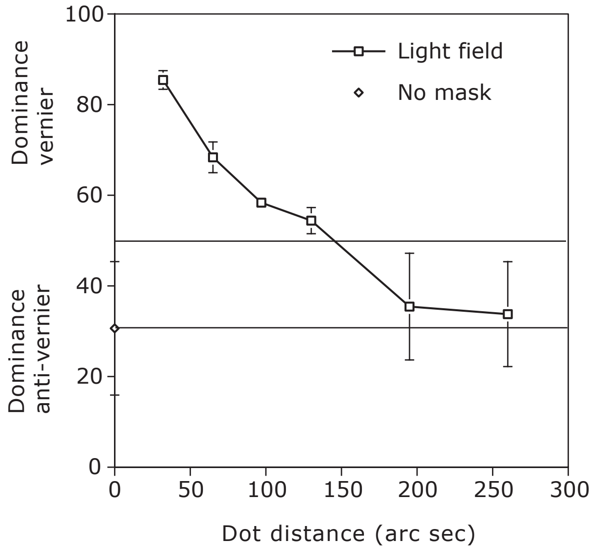

Figure 4.

After the vernier and the anti-vernier, a light mask was presented composed of regularly ordered dots. We varied the spacing between the dots mimicking a change of the overall luminance of the light mask. With increasing dot distance, performance approaches performance in the no-mask condition indicated by the lower horizontal line. Mean performance and standard errors for three observers.

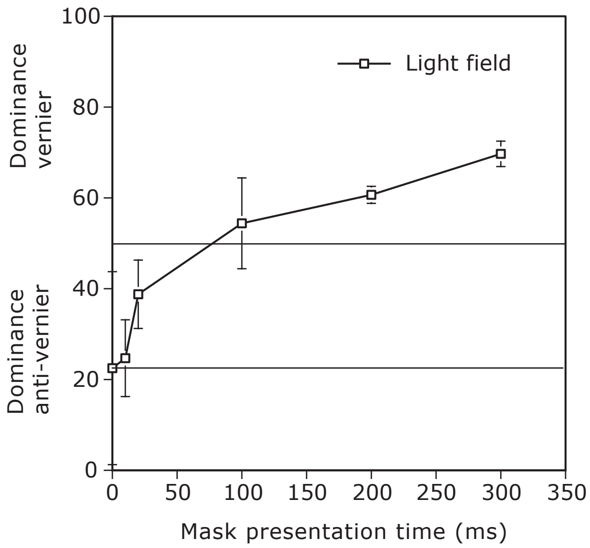

Figure 5.

As in figure 4, after the verniers a light mask was presented. We varied the duration of the light mask. For short presentation times, performance is dominated by the anti-vernier. An increase in presentation time increases the dominance of the vernier. Mean performance and standard errors for two observers.

Results

Dominance of the vernier decreases as the dot density decreases (Fig. 4). For a dot distance of 260”, performance closely resembles the results for the no-mask condition.

Figure 5 shows the mean performance for the various durations of the light field. If no light field is presented, that is the vernier-(anti-vernier) sequence only, performance is dominated by the anti-vernier (0 ms condition). As the presentation time of the mask increases, vernier dominance increases. If the light field is presented for 300 ms, performance is clearly dominated by the vernier. Hence, an increase in the presentation time of the light field yields a reversal from anti-vernier to vernier dominance.

Horizontal line masks

The spatial layout of the mask can have a pronounced effect on feature fusion modifying the degree of vernier or anti-vernier dominance. Here, we ask the question whether the reversal of dominance is orientation-specific by using a grating mask comprising horizontal lines. The number of horizontal lines was varied.

Methods

Four observers participated in this experiment. The presentation time of the vernier and the anti-vernier was 20 ms for all observers. The mask was a grating comprising horizontal lines. The horizontal spacing of elements was 200”. Elements were 1.33° in length. Hence, the size of a grating comprising 7 horizontal elements was comparable in size to a grating comprising 25 vertical elements. The number of grating elements was varied. Performance in the no-mask condition was determined as well. Verniers were offset by 80”.

Results

For gratings comprising 5 or 7 horizontal lines, the vernier dominates (Fig. 6). For a grating composed of 1 or 3 horizontal line(s), performance is close to 50%. Performance in the no-mask condition is clearly below the performance in the above conditions. Hence, also an extended horizontal line mask can yield vernier dominance.

Forward Masking

In the previous experiments, we have shown that extended masks can yield a strong vernier dominance. In these conditions, the anti-vernier was forward (by the vernier) and backward masked (by the various masks) whereas the vernier was only backward masked (by the anti-vernier). To determine the effects of forward masking, we presented an aligned vernier before a sequence of vernier, anti-vernier, and, in some conditions, a trailing grating mask.

Methods

First, we presented a sequence comprised of an aligned vernier, an offset vernier, and its anti-vernier (Fig. 7A). Second, only the vernier and its anti-vernier were presented (Fig. 7B; baseline condition). Third,

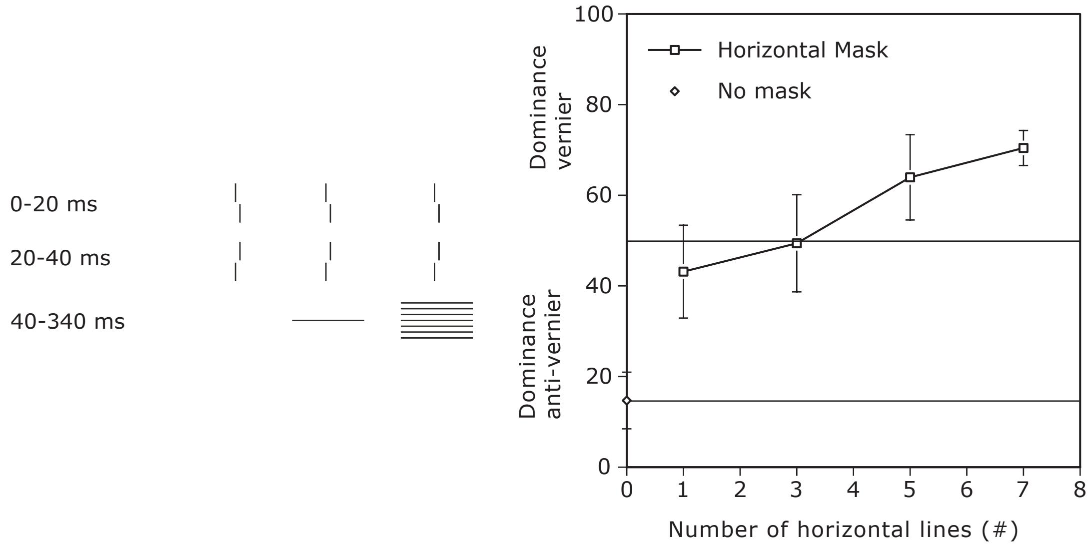

Figure 6.
The mask comprised a grating of horizontal lines with a spacing of 200". Presentation times as indicated are typical examples. As the number of horizontal lines increases, dominance of the vernier increases. The lower horizontal line indicates performance in the no-mask condition, that is, 0 horizontal lines. Mean performance and standard errors for four observers.

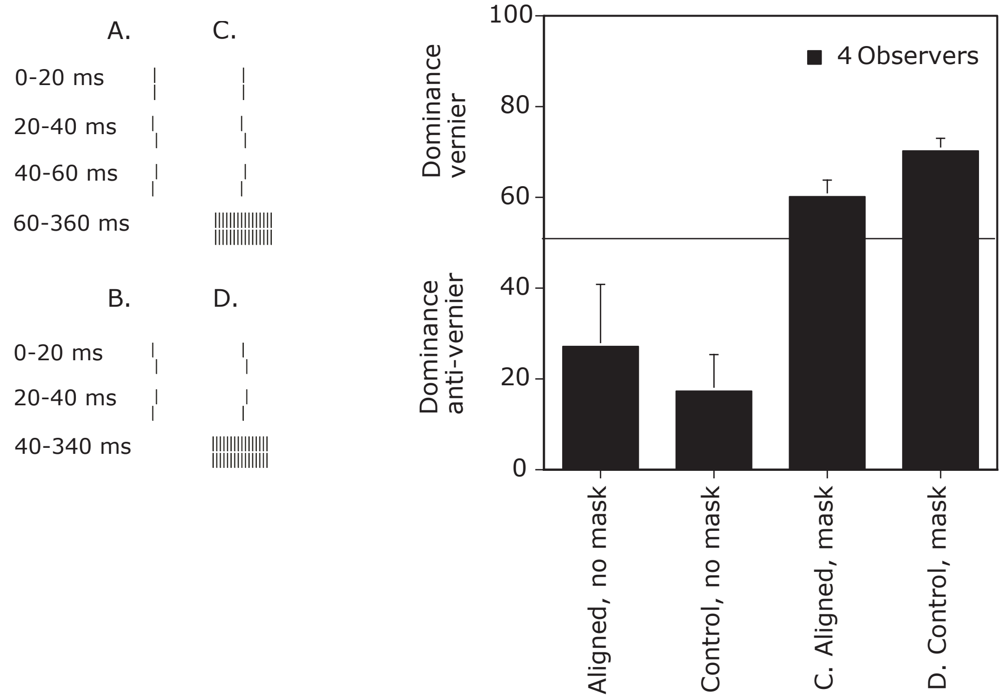

Figure 7.
***A**. Aligned vernier, offset vernier, anti-offset vernier sequence (aligned, no-mask); **B**. No-mask control condition (control, no mask); **C**. Masked condition with a preceding aligned vernier (aligned, mask); **D**. Masked control condition (control, mask). Only 16 elements of the gratings are shown. **Results**. In both conditions without the grating mask (A,B), the anti-vernier dominates whereas in both masked conditions the vernier dominates (C,D). The preceding aligned vernier yields qualitatively the same results as without it. Mean performance and st.err.for 4 observers.*

we presented a sequence comprised of the aligned vernier, the offset vernier, the anti-offset vernier, and a 25 element grating mask (Fig. 7C). Fourth, this sequence was presented without the aligned vernier (Fig. 7D). The presentation time of the aligned vernier, the preceding vernier, and the anti-vernier was 20 ms for all observers. The 25 element grating, if presented, lasted for 300 ms. The vernier and the anti-vernier offset size was 80". (Fig. 7). Four observers participated in this experiment.

Results and Discussion

In the no-mask conditions (Fig. 7A,B), performance is dominated by the anti-vernier, whereas in the masked conditions the vernier dominates (Fig. 7C,D). The presence of the aligned vernier preceding the other stimulus elements may decrease the signal-to-noise ratio since performance is closer to 50%; however, the qualitative pattern is the same as without this aligned forward masking vernier, that is, forward masking does not yield a reversal of dominance.

GENERAL DISCUSSION

The spatio-temporal dynamics of visual information processing are of major interest in the neurosciences. Here, we studied the interactions of temporal and spatial mechanisms using a feature fusion paradigm.

If an offset vernier is followed by its anti-vernier, performance is dominated by the anti-vernier (see also Bachmann & Allik, 1976). If the vernier and anti-vernier are followed by extended pattern masks, the vernier dominates. Hence, dominance has reversed (see also Herzog et al., 2003b). In this contribution, we found that the spatial characteristics of the mask, following the vernier and anti-vernier, have a complex influence on feature fusion. Extended masks, such as the 25 element grating and the metacontrast grating can clearly reverse dominance compared to the no-mask condition whereas an unspecific effect is found for a single, aligned vernier mask even though we tested fairly large offsets (Fig. 2; still it might be that vernier/anti-vernier offset sizes or durations were too small or short in this condition to yield a dominance effect of either the vernier or the anti-vernier; in the case of the 5 element grating, dominance of the vernier is found for longer vernier durations than used in this contribution, see Herzog et al., 2003b).

Since the single, aligned vernier mask is part of the 25 grating mask, spatially local interactions cannot explain feature fusion. This result is corroborated by the fact that dominance reverses also if the metacontrast grating follows the verniers – even though this mask does not even contain a central element overlapping with the verniers. Vernier rather than anti-vernier dominance is found even for very large gap sizes of the metacontrast grating.

Vernier dominance occurs also for masks with the extended horizontal line masks and unstructured light fields. Hence, the reversal of dominance seems to be an unspecific kind of masking occurring with any extended mask of a certain luminance. As our parametric experiments (Figs. 4 and 5) show, this luminance can be relatively low. A light field with a dot distance of about 130″ yields a performance of 50%.

A performance of 50% may indicate a cancellation of offsets or that performance is at chance level. Chance level performance may occur, for example, if the light field is so strong that the verniers themselves were invisi-ble and therefore offset discrimination is impossible. However, this assumption is unlikely since for a dot spacing of 130″, the light field masks rather weakly. Moreover, stronger masks yield performance clearly above 50% (vernier dominance) and masking of light fields increases monotonically with mask luminance manipulated either via duration or dot density (Herzog, et al., 2003a).

If the anti-vernier is forward masked by the vernier and backward masked by an extended mask, the vernier dominates. Our results clearly show that this result cannot be explained by the fact that the vernier is not forward masked itself. In an (aligned vernier)-vernier-(anti--vernier)-grating sequence, still, the vernier dominates (Fig. 7). Hence, the central position of the anti-vernier in the vernier-(anti-vernier)-grating sequence is not the key explanation for unmasking.

Our results can be taken as an instance of unmasking. If two masks sequentially follow a target, performance can be better than if only one mask is presented after the target (Bachmann & Hommuk, 2005; Breitmeyer, Rudd, & Dunn, 1981; Briscoe, Dember, & Ward, 1983; Dember & Purcell, 1967; Dember, Schwartz, & Kocak, 1978; Tenkink, 1983; Tenkink & Werner, 1981; Robinson, 1966). The second mask unmasks the first one. Analogously, in our paradigm, the introduction of the anti-vernier deteriorates the discrimination of the vernier. Then, if the extended mask follows the presentation of the vernier and the anti-vernier, the discrimination of the first vernier improves. However, our results indicate that the anti-vernier is fused with the vernier rather than simply masking it: Offsets of both the vernier and the anti-vernier are taken into account for the decision. In this sense, in our experiments two targets are followed by a mask rather than the first vernier by two masking elements (Herzog et al., 2003b). The vernier dominance reversal indicates a feature specific (un)-masking since we determine the respective "strength" between the vernier offsets.

The results of this study clearly show that spatial interactions related to the mask can have a tremendous impact on the temporal processing of the target(s).

Visual masking cannot be explained by spatially local interactions exclusively.

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