ORIGINAL ARTICLE

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Long lasting effects of unmasking in a feature fusion paradigm

Abstract In spite of more than 100 years of research, the mechanisms underlying visual masking are still unknown. In recent publications, we introduced an unmasking paradigm involving the fusion of features that revealed interesting spatial characteristics. Here, we investigate the temporal aspects of this paradigm showing very long lasting effects that impose serious restrictions on models of masking. We used a simple feed-forward neural network model to explain these results.

Introduction

In Herzog, Parish, Koch and Fahle (2003b), we introduced a feature fusion paradigm in which a vernier was followed immediately by another vernier with the same spatial parameters but opposite offset direction (Fig. 1; see also Brand, Kopmann, & Herzog, 2004; Brand, Kopmann, Marbach, & Herzog, 2005). Because of its opposite offset direction, the second vernier is called an anti-vernier. Since presentation times are short, the verniers are perceived as one single vernier, i.e., the two verniers cannot be perceived individually. We called this phenomenon feature fusion (see also Efron, 1967, 1973; Ma, Hamker, & Koch, 2006; Yund, Morgan, & Efron, 1983). The perceived offset of the fused vernier is a combination of the offset of both the vernier and the anti-vernier. If such a sequence of vernier and anti-vernier is presented, the anti-vernier dominates performance, i.e., the discrimination between offsets to the left and to the right of the fused vernier is more strongly influenced by the anti-vernier than by the vernier.

When the vernier and the anti-vernier are followed by a grating, the vernier determines performance more strongly (Fig. 1). Dominance has reversed in comparison to the no-grating condition, in which only the vernier and anti-vernier are presented. This dominance reversal is an instantiation of "unmasking" (Herzog et al., 2003b). It cannot be explained by spatially local effects only, such as the masking of the vernier and the anti-vernier by the central grating element, since if this element is omitted, unmasking still occurs (Herzog, Leseman, & Eurich, 2006). Even more surprisingly, if vernier and anti-vernier are followed by this central element only, no clear dominance of either the vernier or the anti-vernier is found. Hence, feature fusion seems to depend on complex spatial aspects of the masking grating.

Here, we expand these results by varying the temporal parameters of the masking grating to determine its influence on feature fusion. We will show that masking gratings can interfere with feature fusion up to 150 ms if the interstimulus interval (ISI) between anti-vernier disappearance and grating onset is varied. Both the dominance reversal and the long lasting effects of the grating can be explained by a feed-forward model with a decay. We will discuss the relevance of these findings related to current models of backward masking.

General materials and methods

General set up

Stimuli were displayed on a point-plotting device (HP 1334 A) controlled by a Power Macintosh computer via fast 16 bit D/A converters (1 MHz pixel rate). Refresh time was 5 or 10 ms. Subjects observed the stimuli from a distance of 1.5 or 2 m in a room illuminated dimly by a background light (0.51x). Luminance of stimuli was around 80 cd/m2. Before stimulus presentation proper, a fixation dot in the middle of the screen and four markers at the corners of the monitor appeared.

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Fig. 1 A vernier was followed by its anti-vernier and a 25 element grating lasting for 300 ms. The onset of the grating was varied. The abscissa shows the ISI, i.e., the blank period between anti-vernier disappearance and grating onset. A 0 ms ISI indicates that the grating followed immediately after the anti-vernier. For this ISI, the vernier dominates performance, as is illustrated (*percept*). Dominance of the anti-vernier increases with increasing ISI. The *lower horizontal line* shows performance in the no-grating condition, i.e., when only vernier and anti-vernier were presented
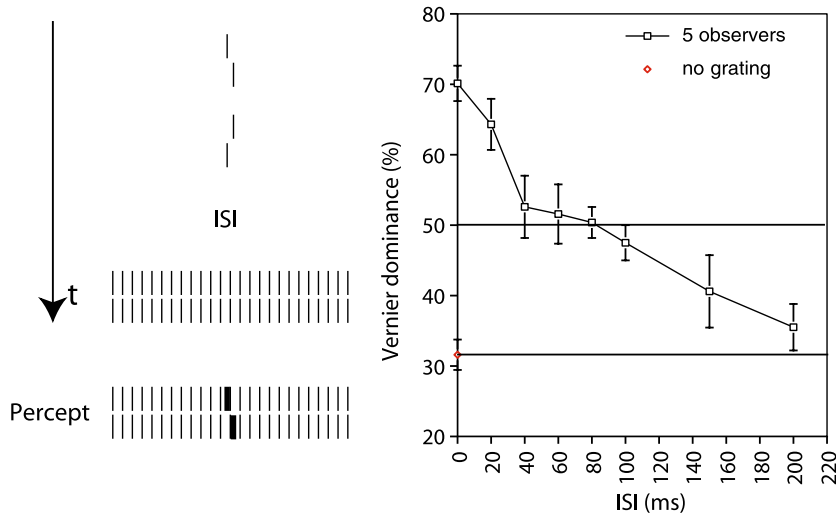
On each trial, two vertical verniers were presented in sequence. The offset direction of the first vernier was chosen randomly from trial to trial. The offset direction of the second vernier was opposite to the offset direction of the first vernier. As mentioned above, we therefore call the second vernier an anti-vernier. Vernier and anti-vernier had the same offset size. The other spatial parameters were also identical. The duration of vernier and anti-vernier was chosen for each observer independently.

Verniers could be followed by gratings comprising either 1, 5, or 25 aligned verniers (see Fig. 3). We will also call a single aligned vernier a grating when convenient. Except for the offset, all spatial parameters of grating elements and verniers were identical. Segments of verniers or grating elements were 600″ long and separated by a small vertical gap of 60″. The spacing between grating elements was 200″. The vernier, the anti-vernier, and the central element of the gratings appeared in the middle of the screen where a fixation dot was displayed before.

We presented the vernier followed by the anti-vernier only, or followed by the anti-vernier and one of the gratings. The condition, in which the vernier and the anti-vernier were presented without the grating, is called the "no-grating" condition. A block of presentations comprised 80 trials.

All subjects were informed about the general purpose of the experiment. Observers did not realize that two verniers were presented in rapid succession. Participants were asked to discriminate the offset direction of the fused vernier based on whatever cue. In the 25 element and in the 1 element condition, subjects looked at the center of the grating. In some conditions with the 5 element grating, some subjects focused on one of the outer elements of the grating where they perceived a very weak offset (feature inheritance, Herzog & Koch, 2001). Other observers reported having attended to the center element. We measured the percentage of correct responses according to the first vernier. Performance above 50% indicates dominance of the first vernier and performance below 50% dominance of the anti-vernier. Performance of 50% indicates the point of subjective equality, i.e., vernier and anti-vernier offsets cancel each other out. No error feedback was provided.

Observers

The first author and graduate students of the University of Bremen participated. They all signed an informed consent. Subjects were told that they could quit the experiment at any time they wished. All observers had normal or corrected to normal acuity as determined by the Freiburg Visus test (Bach, 1996). To participate in the experiments, subjects had to reach a value of 1.0 in this test at least for one eye. The experiments were approved by the local ethics committee.

Experiments

Grating onset

In a previous publication, we showed complex spatial processing characteristics to be involved in feature fusion (Herzog et al., 2006). However, temporal aspects were not investigated. Here, we study the time course of the transition from vernier to anti-vernier dominance by changing the ISI between anti-vernier disappearance and grating onset (Figs. 1, 2). The rationale is as follows. In the masked condition, the preceding vernier dominates whereas the anti-vernier dominates in the no-grating condition. Anti-vernier dominance is also expected for long ISIs since the fusion of the vernier and the anti-vernier has terminated before the grating is displayed. We will determine the critical ISI for which performance reaches the no-grating value.

Methods

The vernier was followed immediately by the anti-vernier. After the anti-vernier, a grating with either 5 or 25
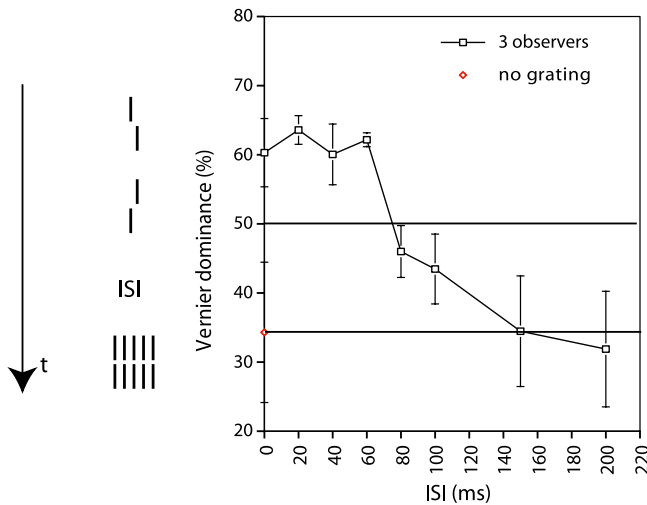
Fig. 2 We presented a vernier, its anti-vernier, and a 5 element grating in sequence. The onset of the grating was varied. The abscissa shows the ISI between anti-vernier disappearance and grating onset. As for a grating with 25 elements, dominance of the anti-vernier increases with increasing ISI. The *lower horizontal line* shows performance in the no-grating condition

elements was presented with various ISIs between anti-vernier disappearance and grating onset. This ISI was varied from 0 to 200 ms. For each observer, we determined the offset size and the shortest presentation time of the preceding verniers for which performance was clearly above 50% in the condition with a 25 element grating, presented at ISI = 0 ms, and lasting for 300 ms. Offset sizes ranged from 60″ to 110″ and presentation times ranged from 10 to 40 ms. We determined performance for the 25 and 5 element grating in different sessions. Different ISIs were tested in blocks of 80 trials in one session. Afterwards, the order of conditions was reversed for a second run of each condition. These two runs were collapsed, yielding a total of 160 trials for every ISI. Five observers participated in the conditions with a 25 element grating and three observers in the conditions with a 5 element grating.

As a baseline, we determined performance also in the no-grating condition (lower horizontal line in Figs. 1, 2). Performance was quantified as the percentage of trials in which the offset of the fused vernier corresponded to the offset direction of the vernier (in the plots denoted as 'vernier dominance').

Results and discussion

For both gratings, dominance of the vernier decays with increasing ISI (Figs. 1, 2). For long ISIs, apparent motion or flickering could not be avoided for most observers. Cancellation of vernier and anti-vernier offset is reached at ISIs between 40 and 80 ms, depending on the observer (50% line in Figs. 1, 2). The grating has a long lasting impact on the dominance. In the 25 element grating condition, the anti-vernier dominance level of the no-grating condition (lower horizontal line) is not

reached until an ISI of 200 ms. In the 5 element grating condition, this level is not reached before 150 ms. Subjectively, for long ISIs, observers perceive the fused vernier, followed by a blank period, followed by the grating. Still, the grating can influence the perceived offset of the fused vernier by affecting vernier and anti-vernier of which it consists differently.

Grating duration

Clearly, feature fusion with verniers can be influenced by the masking grating for a considerable period of time. This holds for both the 5 and the 25 element grating. Particularly for longer ISIs, the unmasking effects seem to be approximately comparable and, hence, mask unspecific. This is surprising since feature fusion depends strongly on the spatial layout of the masks for a condition with an ISI of 0 ms (Herzog et al., 2006). To study both temporal and spatial aspects of the mask layout, we varied the duration of three gratings. The rationale is analogous to that in the previous experiment. A 0 ms duration is identical to the no-grating condition, in which the anti-vernier dominates. With increasing grating duration, the impact of the grating increases and the dominance of the vernier increases. By varying the number of grating elements, we can determine when mask specific effects occur.

Methods

Vernier and anti-vernier were presented one after the other, immediately followed by a grating with 1, 5, or 25 elements without ISI. We varied the duration of the gratings from 0 ms (no-grating condition) to 300 ms. In the first set of measurements, a grating comprising 25 elements followed the verniers, in the second set a grating containing 5, and in the last set only 1 aligned vernier was presented after the verniers. In one set, all durations for one grating were tested in blocks of 80 trials. The order of durations in one set was pseudo-randomized for each observer individually. In the 0 ms duration condition, no grating was displayed. In the third, fourth, and fifth sets, the order of presentations was reversed. Hence, each condition, i.e., each combination of duration and grating type, was measured twice: once in the first three sets, once in the last three sets. These two measurements were collapsed, yielding a total of 160 trials for every condition.

For each observer, before the experiment proper, we determined an offset size of the preceding verniers that yielded about 75% dominance of the vernier in the condition when a 25 element grating lasting for 300 ms followed. Offset sizes ranged from 60″ to 100″. The presentation time of the verniers was chosen to be as short as possible, still yielding a reliable performance level. Stimulus durations ranged from 10 to 20 ms. Five observers participated.

Results and discussion

If no grating follows the verniers, performance is below 50% indicating dominance of the anti-vernier. For all gratings that were displayed for 20 ms, performance is around 50% suggesting a cancellation of the vernier and the anti-vernier offset on average. For gratings with 1 and 5 elements, performance only slightly rises above this level for longer mask durations (see Fig. 3). For a grating with 25 elements, the vernier becomes more dominant with increasing duration.

These effects occur for grating durations between 20 and 80 ms. However, results differed between observers. For some observers, saturation was achieved not before 80 ms. One observer asymptoted already with 20 ms.

Subjectively, luminance fusion is perceived for 5 and 25 element gratings displayed shorter than 40–80 ms, depending on the observer. In luminance fusion, an element appears in the center of the grating that is brighter and wider than the other grating elements. For longer durations the verniers become invisible for a 5 element grating. Nevertheless, performance is slightly above 50% because participants could make use of the feature inheritance effect which renders the offset of the previous vernier visible at the edges of the grating (Herzog & Koch, 2001). For a 25 element grating of longer durations, shine-through is perceived. The perceptual difference between shine-through and luminance fusion is that the shine-through element looks superimposed on the grating as an independent entity shortly flashed. The grating appears to be a homogeneous object with identical elements (Herzog & Koch, 2001). In luminance fusion, the brighter center element is part of the grating and not appearing as an independent object which is superimposed on the grating. For a single element following the verniers, perception is independent of mask duration. Just a single line is perceived for all durations.
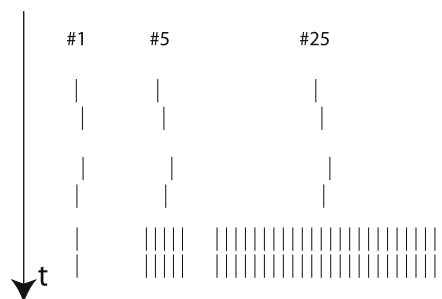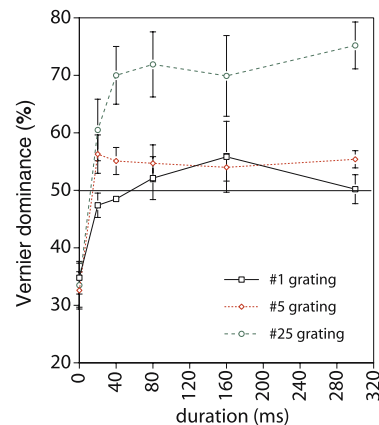
Clearly, the spatial layout of the mask has a strong effect on feature fusion for grating durations of 40 ms and longer. It is important to note that the vernier and the anti-vernier were locally followed by the same element in all three conditions, i.e., the central line in the 5 or 25 element grating or the single aligned vernier. Hence, the "local" vernier, anti-vernier, single-element sequence does not determine feature fusion and unmasking. One caveat is that performance, as a function of mask duration, in the 1 and 5 element grating conditions may indicate a floor effect, rather than the no vernier anti-vernier dominance (i.e., the point of subjective equivalence). Further experiments will have to clarify this issue.

The strongest reversal of dominance is found for the 25 element grating. It might be argued that this grating has the highest energy (luminance × no. of elements × duration) and, hence, yields strongest masking on both verniers. Therefore, strongest backward masking on the anti-vernier should occur since the grating follows the anti-vernier immediately. However, as shown in previous studies (Herzog & Koch, 2001; Herzog, Fahle, & Koch, 2001), the 25 element grating yields weakest masking if only the vernier and no anti-vernier is presented.

To explain the shine-through effect, we previously employed a Wilson–Cowan type neural network (Wilson & Cowan, 1972). Our computer simulations with this model show that shine-through can be explained with lateral interactions dynamically weakening the central elements of the grating displayed for 300 ms, i.e., neural activity corresponding to these elements diminishes with longer grating durations (Herzog, Ernst, Etzold, & Eurich, 2003a). However, in this case vernier dominance should decrease and anti-vernier dominance increase, which is not what we found here.

Mask unspecific effects, influencing feature fusion and unmasking, can last up to 200 ms (Fig. 3). Therefore, it

Fig. 3 Immediately after the vernier and the anti-vernier, a grating with 1, 5, or 25 elements followed for a variable duration. In contrast to the previous experiments performance depends strongly on the number of grating elements. For durations longer than 40 ms, the vernier dominates in all three conditions. For gratings with 1 and 5 elements, performance remains on a level slightly above 50%. For a 25 element grating, dominance of the vernier increases with increasing duration of the grating

seems that there are at least two time constants that are important for the modeling of these effects: one dependent on the spatial layout of the mask and one independent of the layout.

Models and modeling

Feed-forward model

The long lasting effects of the grating are feature fusion specific in the following sense. Effects, such as noise (N), that equally affect the left (L) and the right vernier (R) detection mechanism at a certain point of time, will not be visible in the data since our dominance measure determines only the differential effect between both mechanisms. This is true, for example, for both additive and multiplicative mechanisms combining the offsets: $(L - N) - (R - N) = L - R$ and $(L/N)/(R/N) = L/R$. Hence, performance is not affected by such unspecific effects (N).

Interestingly, unspecific noise, related to the masking grating, can explain the reversal of dominance if taken into account that this noise enters the two different

detection mechanisms at different times of processing. We employed a simple four-neuron feed-forward model with a decay (Fig. 4). Evidence for a left and a right vernier is collected in separate neurons (L and R), respectively, and then merged in an integrator neuron (C). An incoming grating inhibits the activation in the evidence collector neurons (L and R). If the grating comes in early, more evidence has been collected for the vernier than for the anti-vernier, and the vernier dominates. If the grating comes in late, evidence for the vernier has decayed and more evidence has been collected for the anti-vernier, resulting in an anti-vernier dominance. Hence, this model can explain the dominance reversal in feature fusion, i.e., the transition from vernier to anti-vernier dominance or vice versa, depending on the grating presentation.

As the results in Fig. 3 show, the vernier dominates already at very short grating durations. This aspect is well captured by the model (Fig. 4).

Although the model can explain the data fairly well, it has its limitations too. The model predicts, contrary to the experimental findings, that the asymptote of performance will be reached within a fixed time, independently of the level of the asymptote. In addition, the model cannot explain the spatial layout effects of the mask on the
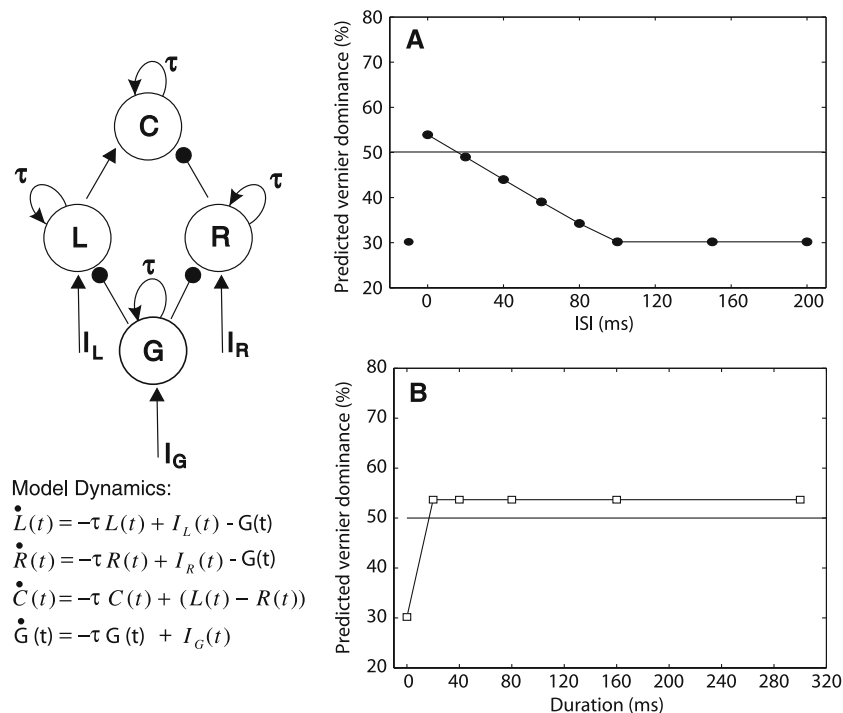

Model Dynamics:

$$\dot{L}(t) = -\tau\, L(t) + I_L(t) - G(t)$$

$$\dot{R}(t) = -\tau\, R(t) + I_R(t) - G(t)$$

$$\dot{C}(t) = -\tau\, C(t) + (L(t) - R(t))$$

$$\dot{G}(t) = -\tau\, G(t) + I_G(t)$$

Fig. 4 Predictions of a simple model consisting of four neurons (illustrated on the *left*). For the simulations, we set $I_L(t) = 1$ for $t_0 < t < t_1$, and $I_L(t) = 0$ otherwise. Similarly, $I_R(t) = 1$ for $t_1 < t < t_2$, $I_R(t) = 0$ otherwise, and $I_G(t) = 0.5$ for $t > t_3$, $I_G(t) = 0$ otherwise. In these equations, t_0 denotes the onset of the vernier, t_1 its disappearance or equivalently the anti-vernier onset, t_2 denotes anti-vernier disappearance. At t_3 the grating was presented. Positive input is denoted by an *arrowhead*, negative input as a *filled dot* at the end of the *connecting line*. The value of the decay parame-

ter τ and two additional parameters, related to the read-out time of information and the mapping of neural activation to performance, were fitted on a large data set, not shown here. **a** Simulation results for the experiments varying ISI (Figs. 1, 2). The model correctly predicts a vernier dominance for short ISIs, and an increasing dominance of the anti-vernier as the ISI increases. **b** Simulation results for the experiment in which the duration of the 5 element grating was varied (Fig. 3). The data for the single element grating and the 25 grating could not be fitted with the model

relation between mask duration and vernier dominance, since no spatial layout components (see neuron *C* in Fig. 4) are included in the model. It is important to note that our model contains recurrent but no reentrant connections. However, feed-forward models, without decay, cannot explain the reversal of dominance in general since they consistently predict that either the vernier or the anti-vernier will dominate (see Herzog, et al., 2003a).

Dual channel models

One of the open questions in visual masking research is about how the mask catches up with the target so that backward masking can take place. Dual channel models postulate interference of an unspecific processing with a more specific processing mechanism. For example, a "spatially coarse" transient system interacts with a more fine grained sustained system (Breitmeyer, 1984), or unspecific thalamic projections facilitate specific visual cortical processing (Bachmann, 1994). The latter models can explain why the anti-vernier dominates the vernier, since the late coming anti-vernier is facilitated by subcortical resources elicited by the vernier. However, the reversal of dominance in the masked conditions seems to be hard to explain in these models, since the trailing grating should not influence unspecific responses elicited by either vernier. Moreover, if the reversal of dominance, caused by the gratings, is related to the unspecific processing systems, these systems must be specific to the grating structure (Fig. 3), i.e., they are not completely unspecific.

Object substitution models

Object substitution models (Di Lollo, Enns, & Rensink, 2000; Enns, 2004) can easily explain anti-vernier dominance in the no-grating condition. The anti-vernier overwrites the vernier representation. However, it remains unclear why a trailing grating can reverse dominance when the vernier representation has already been erased. The current results challenge such a model even more. For example, it remains unclear why a late coming grating can still yield a recovery of the vernier after such long ISIs (Figs. 1, 2). Why does object substitution depend on the mask layout, and why does a higher energy mask, such as the 25 element grating, exert stronger effects on the anti-vernier than a weaker energy mask such as a 5 or 1 element grating?

These considerations do not doubt the value of the mentioned models for explaining the enigmatic B-type masking phenomenon. Nevertheless, our feature fusion results reveal interesting unmasking phenomena that can be explained by simple feed-forward models that include self-inhibiting feedback loops allowing for neural persistence. This project was supported by the Swiss national Fund (SNF)

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