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Long-lasting visual integration of form, motion, and color as revealed by visual masking

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When two similar visual stimuli are presented in rapid succession at the same location, they fuse. For example, a red and a green disk are perceived as one single yellow disk. Likewise, verniers with opposite offset directions are perceived as one vernier with an almost aligned vernier offset. In fusion, observers have no conscious access to the individual stimuli. Using transcranial magnetic stimulation (TMS), it has been shown that feature fusion for verniers can be modulated for about 400 ms in that either the first or the second vernier dominates the percept, depending on TMS onset. Here, we use light masks to modulate feature fusion for verniers, motion, and color. Our results are similar to the TMS experiment and show that individual visual features are stored for a substantial amount of time before they are integrated.

Introduction

Two visual stimuli that are presented in rapid succession fuse. Only one stimulus with the combined features of the two individual stimuli is perceived. For example, when a red disk is followed by a green disk, only one yellow disk is perceived (Efron, 1967, 1973; Yund, Morgan, & Efron, 1983). Likewise, a left offset vernier followed immediately by a right offset vernier is perceived as one almost aligned vernier. The features of the second stimulus slightly dominate the percept. In the above examples, the disk appears yellow with a greenish tone and the vernier appears slightly offset to the right. However, in both paradigms, observers only perceive one stimulus. For example, Scharnowski et al. (2009) presented two verniers with opposite offset directions and explicitly told observers about the presence of two verniers. Observers had to indicate whether the first or the second vernier was offset to the right. Performance for all observers was around chance level, which shows that observers had no conscious access to the individual stimuli.

To probe feature fusion, Scharnowski et al. (2009) presented two verniers with opposite offset directions and asked observers to indicate the fused vernier offset rather than whether the first or second vernier was offset to the right or to the left. As mentioned above, in this case observers have no conscious access to the individual stimuli. At various SOAs, transcranial magnetic stimulation (TMS) was applied over visual cortex. Because in fusion paradigms the second stimulus slightly dominates the percept, the offset size of the second vernier was changed for each observer individually, so that performance, on average, was balanced at 50%. Paradigm and results are shown in Figure 1B. Early onset TMS (45–95 ms) led to dominance of the second vernier. Later TMS onsets from 95 ms to 420 ms led to dominance of the first vernier. For two reasons these results show that the individual verniers were not fully integrated before 420 ms. First, if the verniers had integrated immediately after presentation, by design of the experiment, performance would have been at 50%, which is both the point of equal dominance and chance level, given that vernier offsets were balanced. Second, if TMS had not affected vernier

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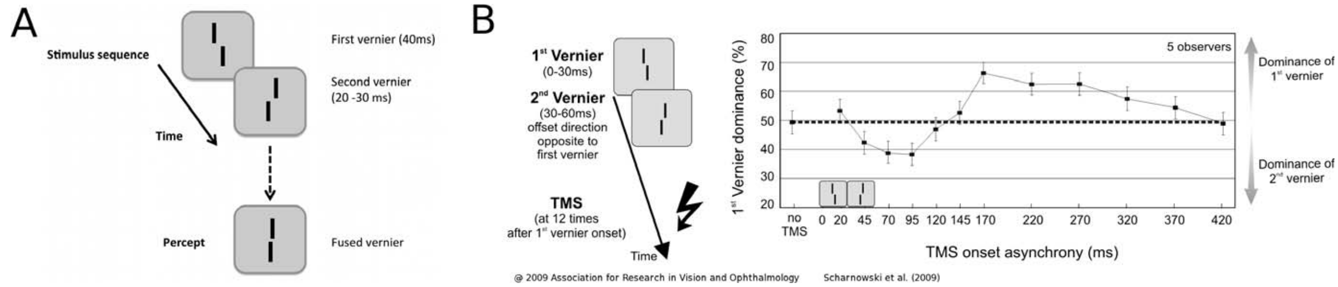

Figure 1. Feature fusion for verniers. (A) A vernier, which is a pair of vertical bars that are spatially offset in the horizontal direction, is followed by a second vernier with an opposite offset direction. Because of the short presentation times, only one fused vernier is perceived. The perceived offset is a combination of the offsets of the two verniers. (B) Effects of TMS on vernier fusion (Scharnowski et al., 2009). First, the offset size of the first vernier was adjusted such that performance was at 50%, which means that on average both verniers contributed equally to performance (no TMS; indicated by the dashed line). Next, TMS was applied at different times after the onset of the first vernier (TMS onset asynchrony). Values above 50% indicate dominance of the first vernier and values below 50% indicate dominance of the second vernier. For onset asynchronies ranging from 45 to 95 ms, the second vernier dominated performance. For TMS onset asynchronies of more than 145 ms, the first vernier dominated. TMS has differential effects for up to 370 ms after the onset of the first vernier. This is about six times longer than the presentation of the verniers.

fusion, dominance would have been at 50% for all TMS onsets, as was the case when TMS was applied over the frontal lobe (Scharnowski et al., 2009). There are two possibilities of how TMS might interfere with the verniers before the integration is complete (Figure 2). Either, the two verniers are stored independently and TMS interferes with the independent memory traces (Figure 2A), or the representations of the two verniers interact and TMS interferes with the fusion process before feature fusion is completed (Figure 2B). In an additional experiment, Scharnowski et al. (2009) presented only a single vernier and applied TMS. In this case, there was no TMS interference, which suggests that TMS does not interfere with vernier encoding. Finally, we like to mention that short interstimulus intervals between the two successively presented verniers lead to the perception of the individual verniers. In this case, TMS over visual cortex does not modulate performance, which again indicates that TMS interferes with vernier fusion (Rüter, Sprekeler, Gerstner, & Herzog, 2013).

Here, we investigated whether feature fusion also occurs for other visual features than verniers, namely apparent motion and color. Instead of TMS, we used light masks to modulate the time course of feature fusion.

Experiment 1—Verniers

Materials and methods

Observers

Five observers (two female, mean age = 24 years) participated in this experiment. All observers had normal or corrected to normal visual acuity with a value of 0.8 or above as determined with the Freiburg Visual Acuity Test (Bach, 1996). Observers were either paid students of the University of Bremen or the University of Osnabrück. The study was performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Apparatus

White verniers were displayed monocularly on an analogue x/y monitor (Tektronix 608, equipped with a P11 phosphor, dot pitch of 200 Am at a dot rate of 1 MHz; 200 Hz refresh rate, Tektronix, Inc., Beaverton, OR), controlled by a Macintosh Power Mac via fast 16 bit D/A converters (Apple, Inc., Cupertino, CA). Stimuli were displayed on a dark background at 80 cd/m^2. Observers were seated 2 m away from the monitor. The room was dimly illuminated by a background light (~0.5 lx).

Procedure

Verniers were composed of two vertical bars. Each bar had a length of 10′ (arcminutes) and was separated by a vertical gap of 1′. Therefore, the total length of one vernier was 21′. The width of the bars was about 30″ (arcseconds). The offset between the two bars in the horizontal direction was 50″. A sequence of two verniers was presented foveally in rapid succession. The offset direction of the second vernier was opposite to the offset direction of the first vernier: When the first vernier was offset to the right, the second vernier was offset to the left and vice versa.

All stimuli were presented monocularly. The first vernier was presented for 40 ms. With equal stimulus duration of the two verniers, the second vernier dominated the percept. In the first step of the

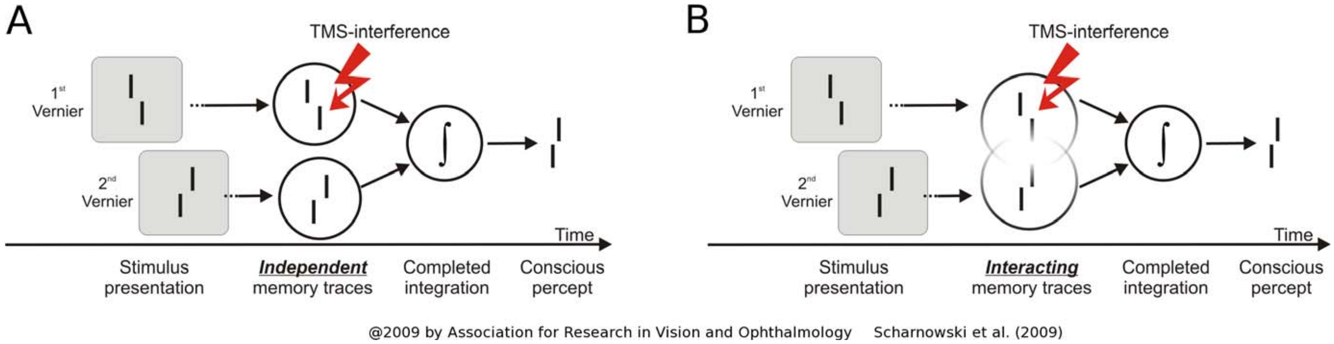

Figure 2. Possible stages of TMS Interference. (A) The consecutively presented verniers are stored independently before they are integrated into a conscious percept. TMS interferes with the processing of the independent vernier memory traces. (B) The vernier offset representations interact before feature integration is completed and a conscious percept is elicited. Given that TMS does not interfere with single verniers, we suggest that TMS exerts its effects during this interaction stage (Scharnowski et al., 2009).

experiment, we determined the duration of the second vernier for each observer to find the presentation time at which performance was at 50% so that neither the first nor the second vernier dominated the percept. In the first block of trials, the duration of the second vernier was set to 30 ms. Depending on whether the first or second vernier dominated the percept we increased or decreased the duration of the second vernier for an amount of 10 ms and ran another block of trials. This procedure was continued until performance was at about 50% (Figure 1A). The optimal presentation time for the second vernier was 30 ms for two observers and 20 ms for the other three observers. For four observers stimuli were presented to the right eye, for one observer stimuli were presented to the left eye.

In the second step of the experiment, we introduced a light mask. The light mask had a size of 21″ × 21″ with a point distance of 65″. Point distance refers to the spatial separation between light points within the mask, with one light point being one pixel. Each light point had a luminance of 80 cd/m^2. The light mask was presented for 30 ms at onsets of −100 ms, −50 ms, 0 ms, 40 ms, 60 ms, 80 ms, 120 ms, and 200 ms relative to the onset of the first vernier (0 ms). Mask onset asynchronies were presented in separate blocks. Each block consisted of 80 trials and took about 3 minutes to complete. No feedback was provided and observers were asked to respond as fast and accurately as possible.

Statistical analysis (Experiments 1–3)

For the statistical analysis, we fitted the data using the following function:

$$f(x) = 50 + a \times (x - t_{50})/d \times exp(-abs(x - t_{50})/d)$$

with a the amplitude difference between the maximum and the minimum of the function, t_{50} the point at which $f(x)$ crosses 50%, and d the decay rate, restricted to values between 5 and 100. t_{50} was estimated for the mean data first and that value was then taken to model the data of each observer. Therefore, only a and d were fitted for each observer individually.

For each experiment, we performed two t-tests. One t-test evaluated whether the amplitude a significantly differed from 0.0, an indication that the mask affected the fusion process for both stimuli, because the amplitudes would be at 50% for all mask onsets if the mask had not affected fusion. The second t-test evaluated whether the decay rate significantly differed from the lower limit of 5. The decay rate is the amount of time required for the amplitude to fall to half its value as measured at its highest point. Therefore, one can assume that the higher the decay rate, the longer the effect of the mask on the fusion process.

Results

When the light mask was presented before and up to 40 ms after the onset of the first vernier, the second vernier dominated performance (Figure 3). For mask onsets of 40 ms to 200 ms, the first vernier dominated performance. Vernier dominance was strongest for light masks presented 120 ms after the onset of the first vernier.

The mean model fit for verniers was $a = 47$, $t_{50} = 27$ and $d = 60$ and explained 69% of variance (r^2 of 0.69) (Figure 3). Single subject fits explained 36%, 96%, −106%, 70%, and 66% of the variance, which indicates that the function fitted the data of four of the five single subjects well. T-tests confirmed that a was significantly different from 0.0, $t(4) = 8.67$, $p < 0.001$, and d was significantly different from 5, $t(4) = 3.6$, $p < 0.05$.

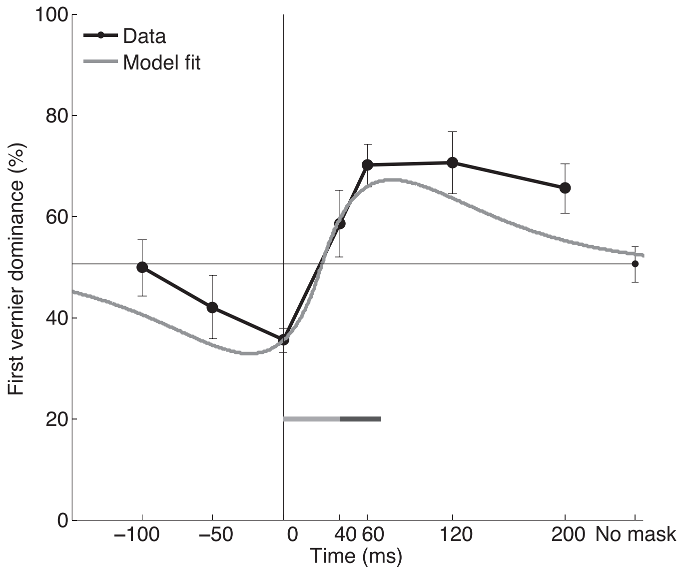

Figure 3. Effects of a light mask on vernier fusion (black). Data was fitted with a linear function multiplied with an exponential decay (gray). For light masks from −100 to 40 ms, the second vernier dominates the percept and from 40 ms to 200 ms the first vernier dominates the percept. The modulation of vernier fusion lasts about four times longer than the duration of the stimuli. Gray bars at the bottom of the Figure indicate the duration of the first vernier (light gray) and the second vernier (dark gray). The horizontal line indicates performance without masks. Error bars represent standard error of the mean.

Experiment 2—Apparent motion

Materials and methods

Observers

Six observers took part in this experiment (two female, mean age = 20.4 years). All observers had normal or corrected to normal visual acuity with a value above 1.0 at the Freiburg Visual Acuity Test in at least one eye (Bach, 1996). All observers were students at the École Polytechnique Fédérale de Lausanne and were paid 20 CHF/hour.

Apparatus

Each observer was seated in a dark room at a viewing distance of 60 cm. A desk lamp provided dim illumination in the room during the experiment (~0.5 lx). Experiments were conducted on a 2.8 GHz Intel Pentium 4 processor PC running Windows XP (Intel, Santa Clara, CA). A Philips 201B4 monitor (Philips, Eindhoven, Netherlands), running at a screen resolution of 1024 × 768 pixels and a refresh rate of 100 Hz was used for stimulus display. Experiments were scripted in Matlab R 7.11 (The Mathworks, Inc., Natick, MA) using custom software and extensions from the PsychToolbox for Windows XP (Brainard, 1997; Kleiner, 2010). A standard QWERTZ keyboard was used to collect observers' responses.

Stimuli and procedure

Stimuli consisted of 400 white dots randomly positioned inside a black 8° square region centered in the middle of the screen. Average dot density was 6.2 dots/$°^2$. Dot luminance was about 80 cd/m^2 and the background luminance was $<$ 1 cd/m^2.

In the first part of the experiment, two dot patterns were displayed sequentially in the center of the screen. The second pattern was identical to the first pattern, except that 80% of the dots were displaced coherently towards the upper left or the upper right corner of the frame. The other 20% of the dots were randomly placed within the rectangular region. The two patterns were displayed successively for 20 ms each. Observers perceived motion in the direction of dot displacement from pattern one to pattern two. The amount of dot displacement to the left and right from vertical from pattern one to pattern two was adjusted individually so that each observer was able to determine the motion direction at a level above 75% in a block of 25 trials. Dot speed was set to 20°/s. Dots that moved out of the square stimulus region were wrapped around and appeared again on the other side of the stimulus region. The angular deviation towards the upper right and upper left from midline for the apparent motion was 10° for three observers, 20° for two observers and 15° for one observer ($M = 14.17°$, $SD = 2.1°$).

In the second part of the experiment, three patterns were presented sequentially. The first two patterns were the same as described above, the third pattern was identical to the second pattern but the dots were horizontally displaced in the opposite direction as from pattern one to pattern two (Figure 4A). We determined the number of dots that moved coherently in one direction from pattern two to pattern three so that observers were not able to discriminate between left and right motion, which means that neither the motion induced by the first and second pattern nor the motion induced by the second and third pattern dominated the percept. When observers reached a level of performance of 50%, which means that observers were not able to discriminate between rightward or leftward motion, they reported to see upward motion. Observers performed 50 trials per tested coherence level. The level of coherent motion from pattern two to pattern three required to reach 50% performance was 70% coherence for three observers, 80% coherence for two observers and 90% coherence for one observer ($M = 0.77\%$, $SD = 3.7\%$).

In the main part of the experiment, we used the angular deviation as determined in step one and the level of coherence as determined in step two and

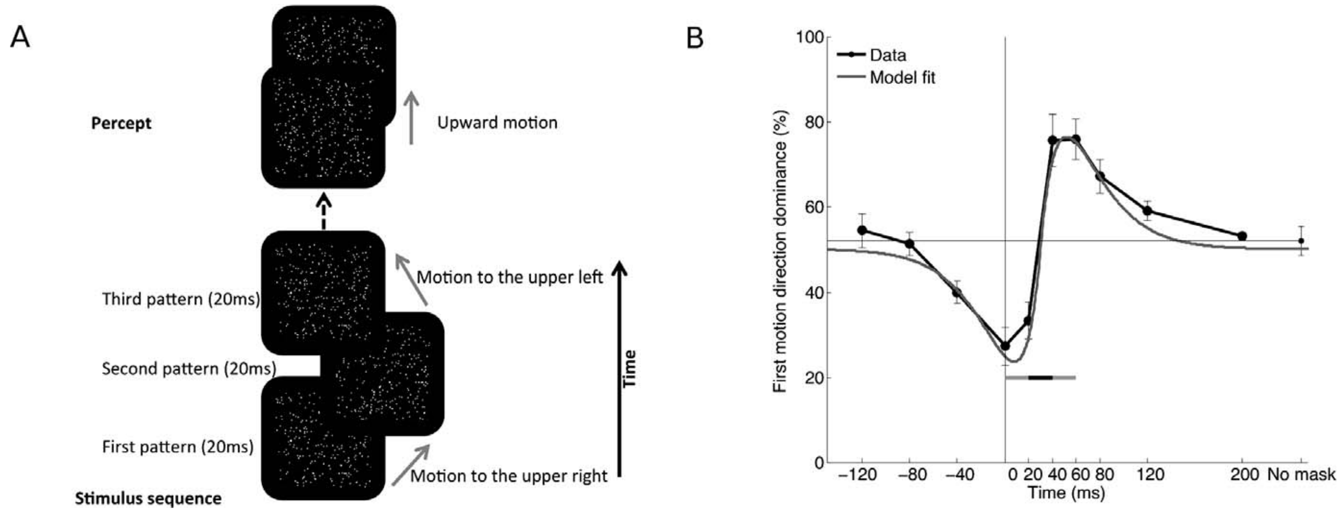

Figure 4. A) Motion fusion: We presented a pattern with random dots, followed by a second pattern, in which the dots were displaced towards the upper right or upper left from midline. The second pattern was followed by a third pattern in which the dots were displaced towards the other direction. When the dots were displaced towards the upper left from pattern one to pattern two, they were displaced towards the upper right from pattern two to pattern three. When all three patterns were presented sequentially in rapid succession, upward motion was perceived, which is the combined motion direction of the first two and the last two patterns. B) Effects of a light mask on apparent motion (black). Data was fitted with a linear function multiplied with an exponential decay (gray). For light masks from −80 to 40 ms the second motion direction dominates the percept and from 40 ms to 200 ms the first motion direction dominates the percept. The modulation of apparent motion fusion lasts about three to four times longer than the duration of the stimuli. Gray bars at the bottom of the Figure indicate the duration of the first and third pattern (light gray) and the second pattern (dark gray). Error bars represent the standard error of the mean.

presented the three frames sequentially. Observers had to indicate the direction of perceived motion, which was upwards motion towards the left or towards the right of the vertical midline. In addition to the three dot patterns, we introduced a light mask which was presented for 20 ms with onset asynchronies at −120 ms, −80 ms, −40 ms, 0 ms, 20 ms, 40 ms, 60 ms, 80 ms, 120 ms, and 200 ms relative to the onset of the first dot pattern. The mask had the same size as the patterns and a luminance of 17 cd/m^2. Given the high luminance of the stimulus dots and the low luminance of the mask, the stimulus pattern was still visible when both mask and stimulus pattern were presented at the same time. However, stimulus dots appeared at lower contrast. There were 80 trials per mask onset asynchrony resulting in 800 trials in total. Conditions were randomly intermixed throughout the experiment and observers were allowed to take a short break after every 200 trials. No feedback was provided and observers were asked to respond as fast and accurately as possible. The whole experiment took about 1 hour to complete.

Results

When the light mask was presented before or up to 20 ms after the onset of the first random dot pattern, performance was dominated by the motion induced by the last two patterns (Figure 4B). At mask times from 40 ms to 200 ms after the onset of the first pattern, the percept was dominated by the motion induced by the first two patterns. The modulation of the light mask on feature fusion for apparent motion stimuli is comparably strong and ranges from 20% up to 80%.

The mean model fit for apparent motion was $a = 70$, $t_{50} = 30$, and $d = 22$ and explained 95% of variance (r^2 of 0.95) (Figure 4B). Single subject fits explained 88%, 82%, 70%, 95%, 37%, and 94% of the variance, which indicates that the model fitted the data of all single subjects well. T-tests confirmed that a was significantly different from 0.0, $t(5) = 6.3$, $p < 0.01$ and the d was significantly different from 5, $t(3) = 31.1$, $p < 0.001$.

Experiment 3—Color

Materials and methods

Observers

Six observers took part in this experiment (six female, mean age = 24 years). All observers had normal or corrected to normal visual acuity with a value above 1.0 at the Freiburg Visual Acuity Test in at least one eye (Bach, 1996). Except for the experimenter, all observers were students at Ecole Polytechnique Fédérale de Lausanne and were paid 20 CHF/h. All observers passed the Ishihara's Test for Colour Deficiency (Ishihara, 2004). Two observers (two male, mean age = 22.5 years) had to be excluded from further analysis, because they were not able to perform the task.

Apparatus

The same apparatus was used as in Experiment 2 with the following exceptions and additions: Stimuli were presented using custom made software. The white point of the monitor was adjusted to be D65, approximately. D65 or daylight illuminant, corresponds roughly to daylight with a correlated color temperature of 6500K. Color space was computationally linearized by applying individual gamma correction to each color channel. Maximum white luminance was 80 cd/m^2, maximal green luminance was 68 cd/m^2 and maximum red luminance was 24 cd/m^2 as checked with a GretagMaceth EyeOne Display 2 colorimeter (X-Rite, Inc., Grand Rapids, MI).

Stimuli and procedure

A red and a green disk were presented in rapid succession. Disks had a diameter of 3° visual angle and were displayed in the centre of the screen for 10 ms each.

In the first step, we determined the relative luminance of the two disks for which neither of the colors dominated the percept and observers perceived a yellow disk. This was done separately for the condition in which the red disk appeared first and for the condition in which the green disk appeared first. Observers had to indicate whether the disk was perceived as being rather green or red. For each condition, we started at two extreme luminances for the red and green disk so that only one color dominated the percept. We used the adaptive PEST procedure (Creelman & Taylor, 1969) to determine the point at which observers were not able to differentiate between green and red. Each block lasted for 80 trials. Starting values were 30.07 cd/m^2 for the green disk and 7 cd/m^2 for the red disk, when the green disk was presented first and 26.65 cd/m^2 for the green disk and 10.15 cd/m^2 for the red disk when the red disk was presented first (Figure 5).

In the second step, we used the luminances as determined for each observer individually in step one together with a white mask. The mask had a diameter of 4° visual angle and a luminance of 24 cd/m^2. The mask was presented at onsets of −90, −60, −30, 30, 60, 90, 120, 150, 180 ms relative to the onset of the first colored disk. Mask duration was 10 ms. Stimuli were presented in three blocks of 180 trials each, with 20 trials per condition in each block. In total there were 60 trials per condition.

Results

The mask had a stronger effect on the second disk than the first disk (Figure 6, top left). For light masks from −60 to 60 ms relative to stimulus onset, the second color dominated the percept. The first color dominated the percept slightly from 60 to 150 ms relative to stimulus onset for only a few observers. To investigate the effect of masking on the second color further, we separated the data into three blocks (Figure 6).

In all blocks, the early effects of masking were very apparent and the second color dominated the percept for mask presentation times from −60 to 60 ms around stimulus onset. The effect of early masking increased with each block. The opposite was true for the effect of masking on the second color: The first color clearly dominated the percept from 60 to 180 ms after stimulus onset, however, this effect disappeared completely in blocks 2 and 3.

We only fitted data from the first block of trials. The mean model fit for the first block of color was $a = 50$, $t_{50} = 50$ and $d = 36$ and explained 90% of variance (r^2 of 0.90) (Figure 8).

Single subject fits explained 80%, 24%, −0.1%, −0.7%, and −1% of the variance, which indicates that the model fitted the data of only one single subject well. *T*-tests showed that a was significantly different from 0.0, $t(4) = 2.8$, $p < 0.05$, and d was significantly different from 5, $t(4) = 13.9$, $p < 0.001$.

Discussion

We used visual masking as a tool to investigate the time course of feature fusion for verniers, apparent motion, and color. Our results are not about the effects of visual masking on single features such as vernier offsets, apparent motion direction or color per se but on their integration. The rationale of the current experiments is the same as with TMS (see Introduction and Scharnowski et al., 2009): By design of the experiments, performance would be at 50%, if the two successively presented stimuli fused immediately. The light mask would have no effect on performance, because the 50% dominance level is both: equal dominance and chance level. Therefore, performance levels different from 50% indicate that the mask modulated feature fusion. The surprising result of a rather long fusion process is only partly related to long lasting masking effects, but much more to the long lasting memories of the features and the long lasting

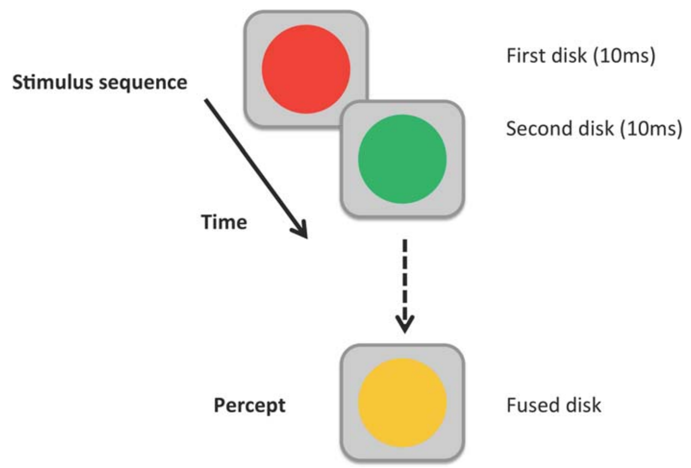

Figure 5. Color fusion: We presented a red or green colored disk followed by a second disk with the alternative color. Because of their short durations, the two disks are perceived as one fused disk that appears yellow.

integration process that was revealed by visual masking. Light masks usually exert much shorter effects on single verniers (Herzog et al., 2003).

For vernier fusion, in Experiment 1, results obtained with light masks were very similar to the TMS results (Scharnowski et al., 2009). First, as with TMS, the light mask affected the fusion process towards dominance of the second vernier for early onsets and towards dominance of the first vernier for later onsets. Second, dominance of the first vernier lasted longer than for the second vernier. Third, the duration of modulation in both cases was long lasting, i.e., lasted far beyond the duration of the stimuli. However, it has to be noted that effects of TMS and light masks cannot be compared directly, because different mask luminances or lower TMS amplitudes may have led to different results.

Interestingly, the modulatory effects of masking were qualitatively very similar for verniers and appar-

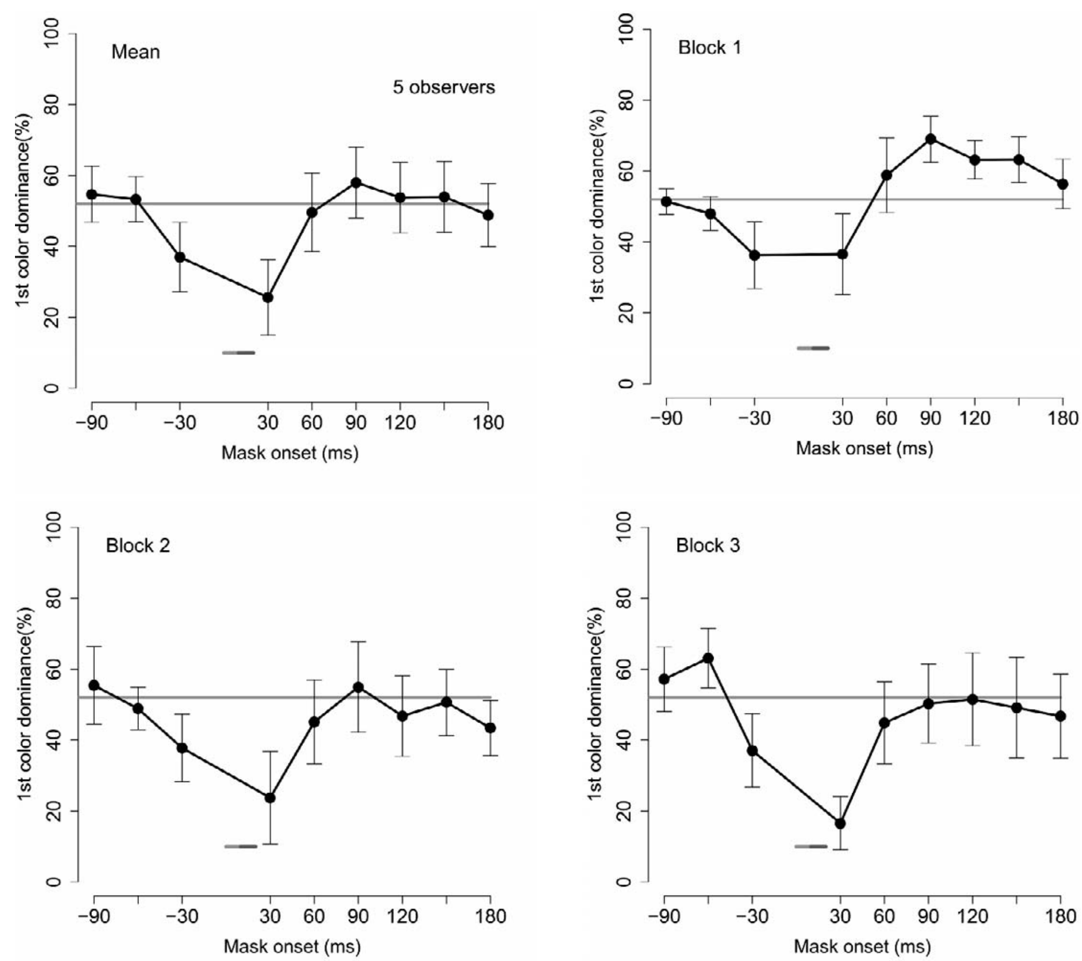

Figure 6. Effects of a light mask on color discrimination. Data are plotted for the mean (top left) block 1 (top right), block 2 (bottom left) and block 3 (bottom right). In all three blocks, the second color dominates the percept for light masks from −80 to 60 ms. Only in block one the first color dominates the percept from 60 ms to 200 ms. This effect disappears in block 2 and 3. Gray bars at the bottom of the Figure indicate the duration of the first disk (light gray) and the second disk (dark gray). Error bars represent standard error of the mean.

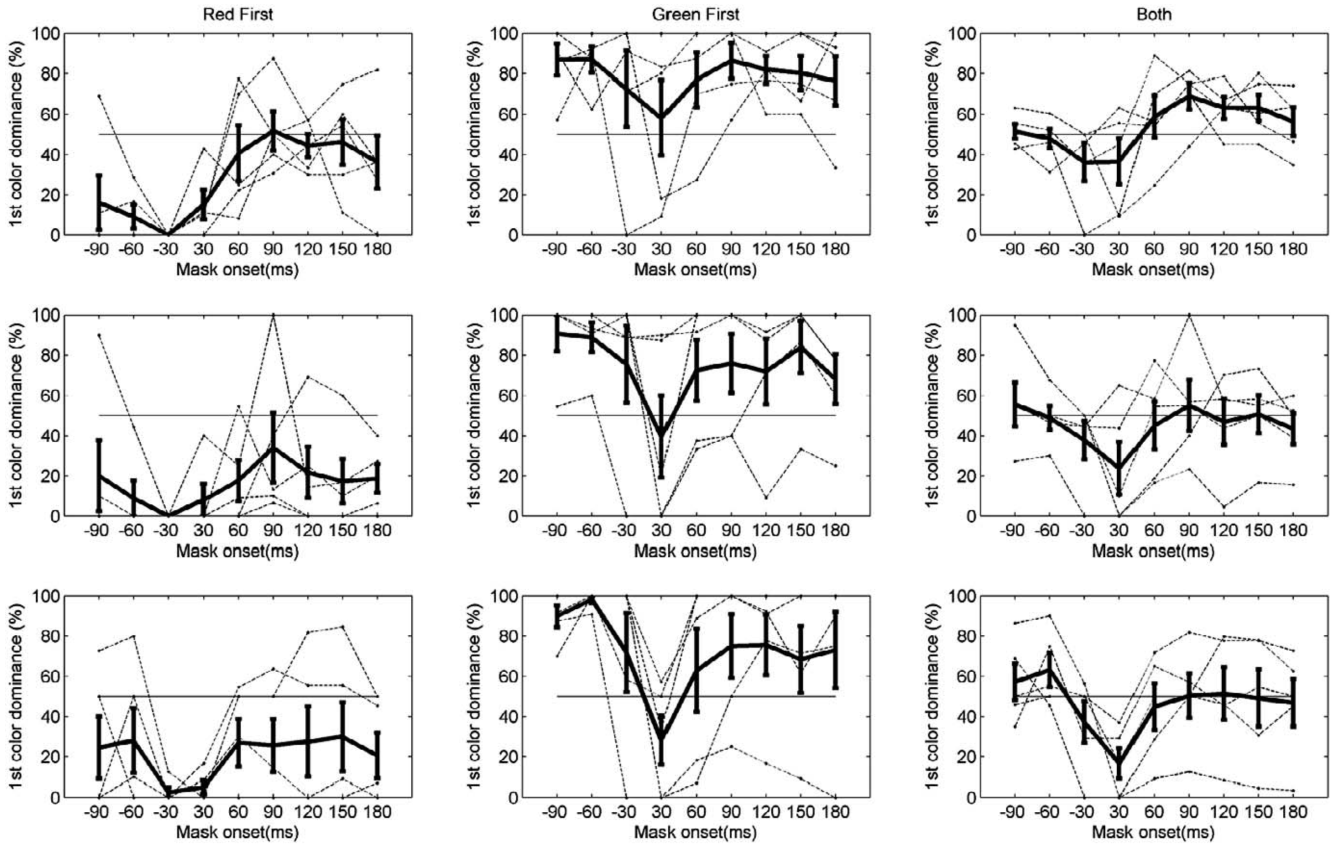

Figure 7. Effects of a light mask on color discrimination. Data are plotted for block 1 (top row), block 2 (middle row), and block 3 (bottom row) and the condition in which the red disk was presented first (left column), when the green disk was presented first (middle column) and both together (right column). Thin dotted lines represent single subject data, thick lines represent the mean. Error bars represent standard error of the mean. Individual response criteria change throughout the blocks.

ent motion, but differed significantly for color. There are several possible reasons for these differences, which might not necessarily be exclusive. First, the luminance values for red and green were adjusted separately for the condition in which the green disk was presented first and the condition in which the red disk was presented first. Therefore, a difference in the perceived luminance of the two conditions is highly likely. This difference in perceived luminance might have interfered with the perceived color when both conditions were presented randomly interleaved during the experiment. Using isoluminant stimuli might be a way to circumvent this issue in future experiments. Second, it has been suggested that forward masking, when the mask precedes the target, is based on peripheral processes, possibly taking place at the level of the retina, whereas backward masking, when the target precedes the mask, is based largely on central or cortical mechanisms (Kim & Blake, 2005; Breitmeyer, 2007). Therefore, the strong effects of early masks, which are most prominent for color fusion in Experiment 3, might be due to light adaptation on the level of the retina. In future experiments the use of monocular and dichoptic stimulation will be helpful to investigate whether light masks affect stimulus processing already at the level of the retina. Using TMS in a previous experiment, we could not modulate color fusion (unpublished results). Therefore, it is possible that color fusion occurs in areas not accessible by TMS such as, for example, the lateral geniculate nucleus (LGN). However, it has to be noted, that Experiment 3 was the only experiment, in which the mask did not temporally overlap with the stimulus presentation. Still, the results are very similar to Experiments 1 and 2, especially in block 1 of stimulus presentation, which indicates that retinal processes are not necessarily involved in the fusion process.

It is difficult to directly compare the time-courses for the three features given the different mask and stimulus durations in the three experiments. These different durations might be a reason for the shifts in dominance for the first and second stimulus. However, we would still like to highlight a few interesting similarities and differences, which might provide some more information towards an understanding of feature fusion. Our results indicate that the dominance of the second stimulus is longer for color stimuli despite the shorter

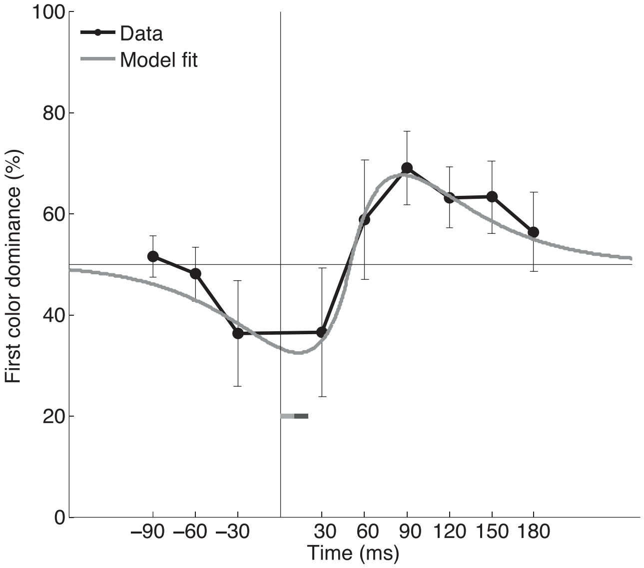

Figure 8. Effects of a light mask on color discrimination for block 1 (black). Data was fitted with a linear function multiplied with an exponential decay (gray). Gray bars at the bottom of the Figure indicate the duration of the first disk (light gray) and the second disk (dark gray). Error bars represent standard error of the mean.

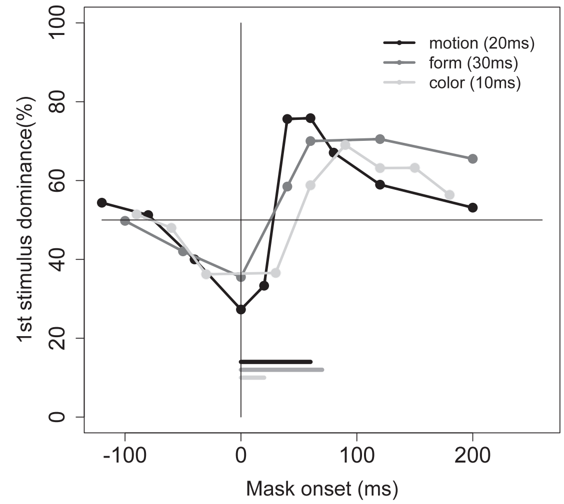

Figure 9. Effects of a light mask on motion (black), verniers (dark gray), and the first block of trials for color discrimination (light gray). Bars at the bottom of the Figure indicate the total stimulus duration for all three conditions. Mask durations are indicated in brackets behind each condition in the legend. Interestingly, masking effects seem to last longest for color, despite the shortest stimulus duration.

stimulus and mask durations, followed by form. Dominance for the second stimulus is shortest for motion stimuli (Figure 9). It has been suggested before that motion is primarily processed via the magnocellular pathway, whereas perception of form and color primarily depends on the parvocellular pathway (Livingstone & Hubel, 1988; Merigan, Byrne, & Maunsell, 1991). Magnocellular signals reach visual cortex significantly faster than parvocellular signals due to faster axon conductivity in magnocellular layers of the LGN (Maunsell & Newsome, 1987). These temporal advantages might be reversed or at least eliminated on the level of the cortex (Maunsell et al., 1999), but could still have an effect on the dominance values shown in the current study. In addition, there is evidence that wavelength properties of stimuli are processed more slowly than form properties of a stimulus, which might explain the shift in dominance of about 30 ms for form compared to color stimuli (Breitmeyer, Ogmen, & Chen, 2004). These findings are supported by our results from the modeling, in which the dominance shift from the second to the first stimulus for form and motion occurs at almost the same time, around 30 ms after stimulus onset, whereas the dominance shift for color stimuli happens much later at around 50 ms.

A more general question that arises from the current experiments is the question about the role of the long-lasting window of integration. It has been suggested that short-term visual memories facilitate the perception of continuous visual input and therefore, play a key role in, for example, detecting visual change and the perception of visual motion (Sperling, 1960; Di Lollo, 1977; Di Lollo & Dixon, 1988; Becker, Pashler, & Anstis, 2000; Nicolic, Haeusler, Singer, & Maass, 2009). Indeed, such a long window of integration might be necessary to perceive continuous motion instead of a series of single snapshots. Nicolic et al. (2009), for example, recently showed that networks in visual cortex are capable of performing online computations utilizing information about temporally sequential stimuli, which suggests that integration over time is already an essential component of early visual processes.

The current study demonstrates that light masks provide an adequate alternative to TMS to study the temporal dynamics of feature fusion. However, there are some differences between the modulation of fusion by TMS and light masks. TMS affected fusion only after stimulus presentation whereas light masks affected the fusion process before and after stimulus presentation. In addition, the effects we obtained with light masks were about 80 ms shorter than with TMS. These temporal differences can have several reasons: First, TMS disrupts visual processing at the level of the cortex. Light masks have been suggested to have an effect on feature fusion already earlier along the visual pathway (e.g., Kim & Blake, 2005; Breitmeyer, 2007; but also see Fahrenfort, Scholte, & Lamme, 2007). Second, it has been suggested that TMS disrupts processing unspecific of the underlying visual pathways, whereas light masks act on much more defined neuronal pathways given, for example, by the luminance and the size of the mask (Breitmeyer, 2007). More specifically, Breitmeyer, Ro, and Ogmen (2004) suggested that the difference between light masks and TMS can be attributed to the retina-cortical transmission time, which delays the effect of a mask on target processing by several tens of milliseconds. Whereas TMS is applied directly to visual cortical areas, visual masks first have to go through a transduction process at the retina and an additional transmission process from the retina to the cortex. Breitmeyer, Ro, and Ogmen (2004) found that stimulus onset asynchrony (SOA) epochs obtained with visual masks and TMS are delayed by around 60 ms, which is very similar to the difference we found between the current studies and Scharnowski et al. (2009).

In summary, our results show that unconscious feature fusion is much longer lasting than the duration of stimulus presentation, which indicates that individual features are stored for a substantial amount of time before they are integrated. This effect holds especially for form and apparent motion. Light masks provide an adequate alternative to TMS to study the temporal dynamics of feature fusion in the visual system and, in addition, can reveal effects that are not testable with TMS, such as color fusion.

Keywords: feature fusion, color, motion, form, light masks

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