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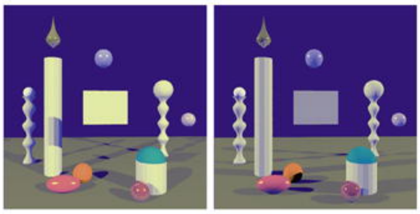

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A spatio-temporal interaction on the apparent motion trace

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Abstract

During the perception of apparent motion, activity along the apparent motion trace has been found in the primary visual cortex. It has been hypothesized that this activity interferes with stimuli presented on the apparent motion trace ("motion masking"). We investigated whether this perceptual interference varies with regard to the trajectory of a moving object token in a detection task. We found a general decrease of detectability of targets presented on the trace. Surprisingly, targets presented in time with the trajectory were detected significantly more often than targets which appeared out of time. We relate this finding to a spatio-temporally specific prediction of visual events along the apparent motion trace.

Keywords: Perceptual masking; Motion; Vision illusion; Feedback; Prediction

1. Introduction

When two spatially separated stimuli are presented in rapid succession, an illusionary percept of motion between the two stimuli emerges, called "apparent" or "stroboscopic" motion. Under certain conditions, a vivid motion trace is perceived and this illusionary percept is hardly distinguishable from real motion (Korte, 1915; Shepard & Zare, 1983). The motion trace can also be investigated for conditions of long-range apparent motion that induce less vivid illusions and are clearly distinguishable from real motion. Recently, several functional magnetic resonance imaging (fMRI) studies in humans have demonstrated that this subtle perceptual filling-in is accompanied by a neuronal filling-in in the primary visual cortex (V1): apparent motion induces a blood-oxygenation-level-dependent (BOLD) response in the primary V1 along the apparent motion trace that is related to the conscious perception of movement (Larsen, Madsen, Lund, & Bundesen, 2006; Muckli, Kohler, Kriegeskorte, & Singer, 2005; Seghier et al., 2000; Sterzer, Haynes, & Rees, 2006; but see Liu, Slotnick, & Yantis, 2004). This activity is thought to be mediated either by lateral interactions within V1 (Series, Georges, Lorenceau, & Fregnac, 2002) or via feedback to V1 from higher visual motion areas such as hMT+/V5, that are activated by real, imagined, and apparent motion (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998). The functional role of the activity along the apparent motion trace in V1 is still unknown. Neurons could, for instance, be involved in representing the motion percept, or neuronal activity could be altered by a prediction of visual events along the trace.

"Motion masking" refers to the finding that the perception of an object on the apparent motion trace is impaired, as shown in psychophysical experiments by Yantis and Nakama (1998). In these experiments, observers had to identify a target on the apparent motion trace. A comparison of the performance for targets on and off the trace showed that the perception of targets on the motion trace was selectively impaired, irrespective of the fact that the physical stimulation was identical in both conditions.

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These findings were interpreted in terms of an explicit representation of a motion token on the trace of apparent motion, mediated via feedback from hMT+/V5 onto V1, which interferes with the representation of the target stimuli (but see Liu et al., 2004). In fact, it has been shown that the apparent location of an apparently moving stimulus advances smoothly, linearly and with almost constant velocity between the two actually presented locations in apparent motion displays (Shioiri, Cavanagh, Miyamoto, & Yaguchi, 2000; but see Caelli & Finlay, 1979; Finlay & Caelli, 1979). Hence, it might be expected that the masking effect varies dynamically in accordance with the dynamics of the representation (Freyd, 1987) of an object moving in space. Such an interference pattern could be taken as an indication of spatio-temporally *specific* feedback from higher order areas onto V1. In this sense, the observed retinotopic activity on the apparent motion trace could constitute the neuronal substrate of a dynamic representation.

Our aim for this study was to clarify whether the interference along the apparent motion trace is temporally uniform or dependent upon the assumed time course of the apparent motion. Underlying was our interest in the functional role of the feedback activity found in V1 which is likely to be involved in motion masking. We varied the time at which we presented low contrast targets on different positions along the apparent motion trace. The appearance of the targets could match or not match the presumed location of the apparent motion illusion. Detection rates for targets presented in time with the illusionary movement were expected to differ from detection rates of targets that did not match in time: matching targets could be masked more strongly than non-matching targets, as it has been shown for real motion (Kolers, 1963a; Kolers, 1963b). This would argue in favor of a dynamic, analog representation interfering with the representation of a stationary stimulus. However, as the stimuli inducing an apparent motion percept are presented with a constant inter-stimulus-interval (ISI) and fixed origin and terminus positions, they are usually also highly predictable. Consequently, matching targets might as well be detected more easily than non-matching targets. This could be related to a time specific prediction (Mumford, 1992) about the trajectory of the apparent motion, or to an attentive mechanism involved in motion detection (Cavanagh, 1991, 1992; Hikosaka, Miyauchi, & Shimojo, 1993; Lu & Sperling, 1995). One or both mechanisms could then counteract the effects of motion masking along the apparent motion trace in V1.

An explanation of the motion masking effects in terms of para- and/or metacontrast masking was sought to be ruled out by comparing the apparent motion condition with control conditions. Additionally, we chose a spatial separation of more than 4° between the targets and the origin and terminus of the apparent motion stimulus. With such a large spatial distance between the targets and the possible masks, forward and backward masking effects break down, whereas the quality of apparent motion remains relatively stable (Breitmeyer, 1984; Efron & Yund, 1999; Weisstein & Growney, 1969).

2. Methods

2.1. Subjects

Eight healthy volunteers (five female), including one of the authors (CMS), all with normal or corrected-to-normal vision, participated in the experiment.

2.2. Stimuli

Stimuli were generated using Presentation software (Version 9.90, www.neurobs.com) and were comparable to those used in a previous study (Muckli et al., 2005). Subjects viewed the screen (LG Flatron L1720B, resolution 800 × 600, refresh rate 75 Hz) from 47 cm distance. All stimuli were presented on a gray background (51.8 cd/m^2). A white fixation cross (212 cd/m^2, 0.77° × 0.82°) was always displayed at the center of the screen. We used white rectangles (212 cd/m^2) as stimuli and presented them on the right side of the fixation cross (eccentricity of 7.72°) at two fixed positions with a vertical separation of 16.47°. There were three experimental conditions: in the apparent motion condition, stimuli were flashed in succession at these two positions (see Fig. 1). Each apparent motion cycle started with a lower rectangle. Stimulus duration was 80 ms, with an ISI of 93 ms, and an inter-cycle-interval of 93 ms. This resulted in a presentation frequency of 2.88 Hz, which is known to lie in the range optimal for apparent motion (Finlay & von Grünau, 1987). Two static control conditions were introduced to separate masking effects elicited by the stimuli inducing an apparent motion percept from motion masking caused by the apparent motion itself: in the first control condition (control lower), the same stimulus parameters as in the apparent motion condition were used, except that only the lower rectangle (apparent motion origin) was flashed. In the second control condition (control upper), only the upper rectangle (apparent motion terminus) was flashed. Presentation frequency at each location was the same as in the apparent motion condition.

The targets had the same shape and size as the other stimuli, but a different luminance (72.9 cd/m^2). In pilot experiments, this luminance level was found to yield an appropriate level of task difficulty. Targets were presented randomly at three different locations between the two apparent motion stimuli, (lower position: 4.11°, middle position: 8.23°, upper position: 12.35°; from the apparent motion origin; center-to-center distance). Target timing was calculated by splitting the ISI between the two apparent motion stimuli into seven frames, each lasting 13.3 ms (according to the refresh rate at 75 Hz). The second and the sixth frame (relative to the first apparent motion stimulus) were used for the presentation of targets, yielding an ISI of 13.3 ms for a delay of one frame (delay 1) and an ISI of 66.5 ms for a delay of five frames (delay 5). Following the results of Shioiri et al. (2000), we approximated a linear movement of the motion token with a constant velocity, in our case of about 2° per frame; therefore, the motion token was expected to coincide with the target presentation at the lower position at delay 1 and at the upper position at delay 5. The same timing and position of the targets was used throughout all conditions.

2.3. Procedure

Subjects were seated in front of the screen in a darkened room. Constant head position was assured by the use of a chinrest with forehead support. Subjects were asked to maintain fixation on the center of the screen throughout the experiment. There was one block per condition, each lasting 20 min with a break of variable length after 10 min as well as between every successive block. Condition-specific instructions were given verbally before each trial started: subjects were instructed to press with their right hand a specified key on a keyboard as fast as possible in response to every

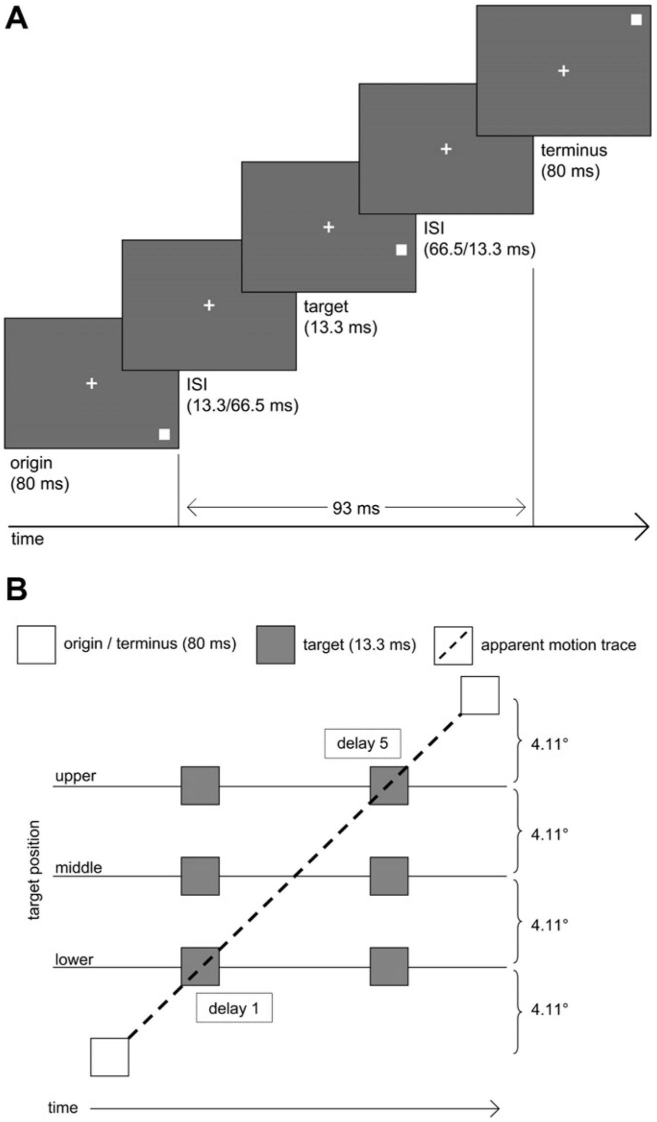

Fig. 1. Stimulus setup. (A) The apparent motion origin and terminus were presented for 80 ms, respectively. The ISI between origin and terminus was 93 ms in case of empty apparent motion cycles. In target trials, target stimuli were presented either with an ISI of 13.3 ms (delay 1), or with an ISI of 66.5 ms (delay 5) with respect to the apparent motion origin. All stimuli were presented at an eccentricity of 7.72° on the right side of the screen. (B) Targets (gray rectangles) were presented at three locations along the apparent motion trace with an ISI of 13.3 ms for delay 1 and an ISI of 66.5 ms for delay 5. The dashed line indicates the presumed linear movement of the apparent motion token in time. The motion token was expected to coincide with the target presentation at the lower position at delay 1 and at the upper position at delay 5. In the control conditions, only the upper or the lower white rectangle was flashed, respectively. Target timing and position stayed the same throughout conditions.

target flashed between the two apparent motion stimuli, or—in the control conditions—to targets flashed over (control lower) or beneath (control upper) the respective rectangle. The apparent motion stimulus (or flashing control stimuli) started and proceeded continuously at the stimulation frequency of 2.88 Hz. Six to 12 cycles of apparent motion (or flashing control stimuli) without any target stimuli were presented before the first target appeared. During each block, a total of 360 targets (120 targets at each of the three positions, 60 targets for each of the two delays) were presented, with 6 to 12 cycles (nine cycles on average) of apparent motion or flashed control stimuli between target presentations. Targets were only presented during upward apparent motion. Responses within a time window of 1000 ms after each target were recorded; responses with reaction times shorter than 150 ms were later considered as misses (less than 1% of the data). After every 15 targets, there was a break lasting 30 s. This was introduced to reduce adaptation effects that are expected to occur after prolonged viewing of apparent motion and result in a breakdown of apparent motion perception (Finlay & von Grünau, 1987). Breaks were indicated by a black screen (0.43 cd/m^2), which turned gray 2 s before the stimulation would start again. The order of the three conditions (apparent motion, control lower, control upper) was counterbalanced across subjects. All sessions were conducted by the same experimenter.

3. Results

Hit rates were calculated as percent of maximal hits at each position for each delay (60 targets = 100%). Subjects responded with a mean hit rate of 80.32% (*SD* 17.82%). The mean hit rate in the apparent motion condition was 62.18% (*SD* 12.81%). In the control conditions, the mean hit rate was 88.75% (*SD* 7.76%) for control upper and 90.03% (*SD* 8.37%) for control lower. Mean false alarm rates (responses outside a window of 150–1000 ms after target presentation divided by the total number of responses) were 14.12% (*SD* 34.73%) for the lower control condition, 2.02% (*SD* 1.87%) for the upper control condition and 11.85% (*SD* 15.86%) for the apparent motion condition. A repeated measures analysis of variance showed no significant differences between the false alarm rates across conditions ($F(1,196) = 0.667$, $p = 0.464$ Greenhouse–Geisser).

Because masking causes the subjects to miss the targets, we chose the miss rates (100%-hit rate) at each position for further analysis of masking effects. We also conducted the same analyses for the reactions times, but found no consistent effects.

In this study, we focused on the interference of a presumed representation of a motion token during apparent motion with the detection of targets presented along its path. More precisely, we were interested in whether this interference covaries with the time course of the illusory motion percept. This hypothesis can be tested statistically by looking for an interaction between the position of a target and its timing (delay). Additionally, we wanted to establish this interaction as being specific to motion masking; therefore, we compared masking during apparent motion to conditions in which we expected spatial masking effects that vary in time in a different manner.

Both these questions were addressed simultaneously in a repeated measures multivariate analysis of variance (MANOVA) with factors condition (control lower, control upper, apparent motion), position (lower, middle, upper), and delay (1, 5). This yielded significant main effects of condition ($F(2,6) = 17.390$, $p = 0.003$, $\eta^2 = 0.853$), position ($F(2,6) = 24.461$, $p = 0.001$, $\eta^2 = 0.891$), and delay ($F(1,7) = 8.295$, $p = 0.024$, $\eta^2 = 0.542$), as well as significant two-way interactions of condition and position ($F(4,4) = 11.216$, $p = 0.019$, $\eta^2 = 0.918$), and position and delay ($F(2,6) = 12.158$, $p = 0.008$, $\eta^2 = 0.802$), and, critically, a significant three-way interaction of condition, position, and delay ($F(4,4) = 19.713$, $p = 0.007$, $\eta^2 = 0.952$). We concluded from this that there are indeed significant differences between the conditions and that there is an interaction between the position of the target stimuli and their timing in at least one of the conditions.

To further elucidate this finding, we ran a separate MANOVA for each condition. Again, we used the miss rate as the dependent variable, comparing the effects of target position and timing in the different conditions. The results of the three separate MANOVA are shown in Fig. 2: for the lower control condition, we found a trend for position ($F(2,6) = 4.061$, $p = 0.077$, $\eta^2 = 0.575$), but no significant main effect or interaction. For the upper control condition, we found significant main effects of position ($F(2,6) = 21.837$, $p = 0.002$, $\eta^2 = 0.879$), and delay ($F(1,7) = 9.572$, $p = 0.017$, $\eta^2 = 0.578$), and a significant interaction of position and delay ($F(2,6) = 9.118$, $p = 0.015$, $\eta^2 = 0.752$). These results can be seen as an indication of a masking effect at the target positions that are close to the respective mask (lower position for the lower control condition, upper position for the upper control condition). Such spatial masking effects were expected, even though the separation of targets and masks was bigger than in standard masking stimulus configurations. Forward and backward masking effects are known to vary with the stimulus onset asynchrony of target and mask; therefore, an effect of timing on the efficiency of the mask was expected as well.

For apparent motion, we found a significant main effect of position ($F(2,6) = 22.371$, $p = 0.002$, $\eta^2 = 0.882$), a trend for a main effect of delay ($F(1,7) = 4.365$, $p = 0.075$, $\eta^2 = 0.384$), and a significant interaction of position and delay ($F(2,6) = 13.326$, $p = 0.006$, $\eta^2 = 0.816$). As in the control conditions, we found masking effects for both the lower and the upper position; furthermore, these masking effects were stronger for the lower position at delay 5 and for the upper position at delay 1 as compared to the lower position at delay 1, and the upper position at delay 5, respectively. This interaction shows that the perceptual interference is not distributed uniformly over the apparent motion trace, but varies with time and space in accordance with the apparent motion percept. At the same time, the interaction is absent or at least less pronounced in the control conditions.

As we found a significant F for the overall analysis of variance, we now conducted several Fisher-protected post hoc paired t-tests (two-sided) of interest. Kolmogorov–Smirnov tests showed that data of all conditions were normally distributed.

We first examined differences between the conditions for respective positions and delays to validate our control conditions and to establish motion masking as an effect that is different from basic forward and backward masking. As can be seen from Table 1, all comparisons yielded significant differences ($p \leqslant 0.0424$), except for the comparisons between the two control conditions at the middle position, and at the lower position at delay 5.

The results of these paired t-tests indicate that the masking effects in all three conditions stem from different masking phenomena: as expected, the two control conditions yield spatially specific increments of the miss rates for target stimuli closest to the respective control stimuli. In the lower control condition, the targets appear after the mask,

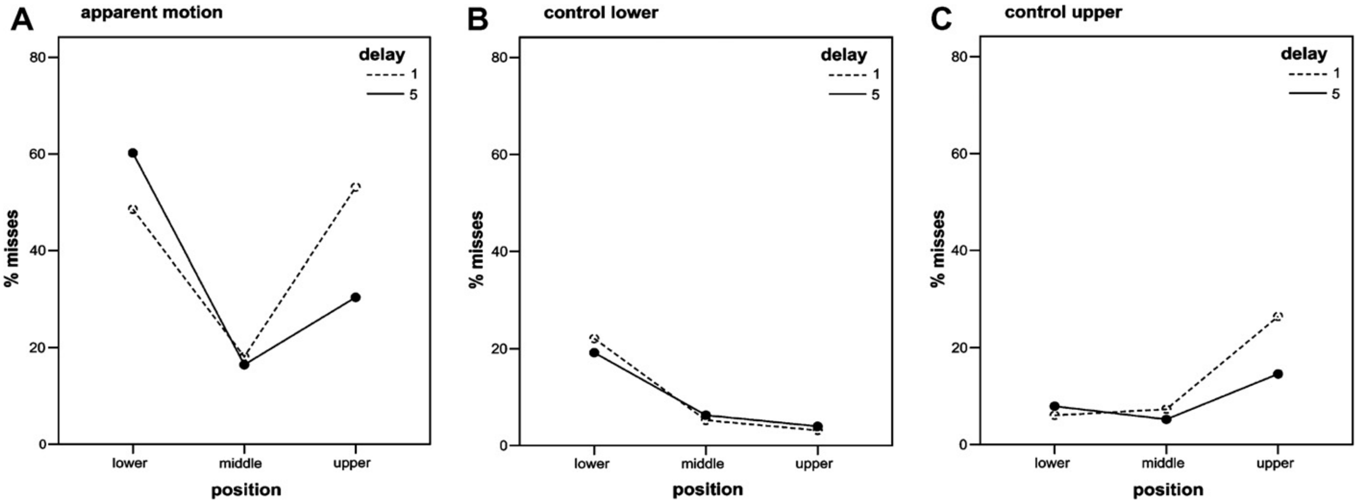

Fig. 2. Results of repeated measures MANOVA for apparent motion and control conditions with miss rates (100%-hit rate) as the dependent variable. (A) For apparent motion, we find a significant interaction of position and delay ($F(2,6) = 13.326$, $p = 0.006$, $\eta^2 = 0.816$). Masking effects were stronger for the lower position at delay 5 and for the upper position at delay 1 as compared to the lower position at delay 1, and the upper position at delay 5, respectively. (B) For the lower control condition, we found a trend for position ($F(2,6) = 4.061$, $p = 0.077$, $\eta^2 = 0.575$). This can be taken as evidence of spatially specific forward masking effects at the target positions close to the masking stimulus. (C) For the upper control condition, we found significant main effects of position ($F(2,6) = 21.837$, $p = 0.002$, $\eta^2 = 0.879$), and delay ($F(1,7) = 9.572$, $p = 0.017$, $\eta^2 = 0.578$), and a significant interaction of position and delay ($F(2,6) = 9.118$, $p = 0.015$, $\eta^2 = 0.752$). The pattern observed in this condition nevertheless argues in favor of spatially specific backward masking effects at the target positions close to the masking stimulus.

Table 1
Results of paired Fisher-protected *t*-tests comparing miss rates (%) across conditions

Pairs		Paired differences					*T*	*df*	Significance (two-sided)
		Mean	*SD*	*SE*	95% CI				
					Lower	Upper			
con low, pos1, del1	con up, pos1, del5	16.04	18.32	6.48	0.72	31.36	2.48	7	0.0424*
con low, pos1, del5	con up, pos1, del5	11.25	16.13	5.70	−2.23	24.73	1.97	7	0.0891
con low, pos2, del1	con up, pos2, del1	−2.08	5.55	1.96	−6.72	2.55	−1.06	7	0.3233
con low, pos2, del5	con up, pos2, del5	1.04	2.35	0.83	−0.92	3.00	1.26	7	0.2495
con low, pos3, del1	con up, pos3, del1	−23.33	11.48	4.06	−32.93	−13.74	−5.75	7	0.0007*
con low, pos3, del5	con up, pos3, del5	−10.62	8.99	3.18	−18.14	−3.11	−3.34	7	0.0124*
con low, pos1, del1	app mot, pos1, del1	−26.46	19.77	6.99	−42.99	−9.93	−3.79	7	0.0068*
con low, pos1, del5	app mot, pos1, del5	−41.04	20.83	7.37	−58.46	−23.62	−5.57	7	0.0008*
con low, pos2, del1	app mot, pos2, del1	−12.92	8.20	2.90	−19.77	−6.06	−4.45	7	0.0030*
con low, pos2, del5	app mot, pos2, del5	−10.21	10.02	3.54	−18.58	−1.83	−2.88	7	0.0236*
con low, pos3, del1	app mot, pos3, del1	−50.00	19.68	6.96	−66.45	−33.55	−7.19	7	0.0002*
con low, pos3, del5	app mot, pos3, del5	−26.46	16.34	5.78	−40.12	−12.80	−4.58	7	0.0025*
con up, pos1, del5	app mot, pos1, del1	−42.50	26.17	9.25	−64.38	−20.62	−4.59	7	0.0025*
con up, pos1, del5	app mot, pos1, del5	−52.29	28.17	9.96	−75.84	−28.74	−5.25	7	0.0012*
con up, pos2, del1	app mot, pos2, del1	−10.83	7.35	2.60	−16.98	−4.69	−4.17	7	0.0042*
con up, pos2, del5	app mot, pos2, del5	−11.25	9.16	3.24	−18.91	−3.59	−3.47	7	0.0104*
con up, pos3, del1	app mot, pos3, del1	−26.67	11.41	4.03	−36.20	−17.13	−6.61	7	0.0003*
con up, pos3, del5	app mot, pos3, del5	−15.83	13.27	4.69	−26.93	−4.74	−3.37	7	0.0119*

con low, lower control condition; con up, upper control condition; app mot, apparent motion condition; pos1, lower position; pos2, middle position; pos3, upper position; del, delay; SD, standard deviation; SE, standard error; CI, confidence interval.

* Significant ($p < 0.05$).

so these miss rates can be related to forward or paracontrast masking. In the upper control condition, the target appears before the mask, so the effects can be related to backward or metacontrast masking. Because of the spatial specificity, the miss rates at the different positions differ. Where they do not differ, it is likely that no masking has taken place because the spatial separation is too big.

Additionally, the masking effects in the apparent motion condition are stronger than in the control conditions for all positions and timings, as can be seen from the negative sign of the mean difference. The masking effects in the control conditions differ from the masking effects in the apparent motion condition, even though the spatial proximity is preserved. Hence, motion masking can probably not be accounted for by a summing of the two control conditions.

In the initial MANOVA, we found significant interaction effects not only for the apparent motion condition but also for the upper control condition. In order to further differentiate the two conditions and to investigate the main effect of delay, we examined differences between the delays within experimental conditions. We found differences between delay 1 and delay 5 at the lower ($T(7) = -4.249$, $p = 0.004$) and the upper position ($T(7) = 4.664$, $p = 0.002$) for apparent motion and a significant difference between delay 1 and delay 5 only at the upper position ($T(7)=4.204$, $p = 0.004$) for the upper control condition. There were no significant differences between delays in the control lower condition. These tests suggest that the interaction between position and delay found in the control upper condition stems from the more pronounced backward masking effect on targets with a short delay at the upper position only. The interaction found under apparent motion conditions stems, however, from a dissociation of the delays 1 and 5 at both the lower and upper positions.

To further support this claim, we tried to isolate the effect of timing by calculating the differences between the two delays (1 − 5) at the respective positions within conditions. A comparison of all difference scores to 0 yielded significant results for apparent motion at the lower ($T(7) = -4.249$, $p = 0.004$) and the upper position ($T(7) = 4.664$, $p = 0.002$) and for the upper control condition at the upper position ($T(7) = 4.204$, $p = 0.004$) only. From this it can again be concluded that the timing of the targets had a differential effect in apparent motion and for a specific position in the upper control condition, but that there was no difference for the two timings in the lower control condition.

We then compared this measure of timing differences across conditions (results of the paired *t*-test are in Table 2). As can be seen from Fig. 3, performance under apparent motion conditions is best at the short delay at the lower position and at the long delay at the upper position, consistent with the notion that it coincides with an illusion that starts at the lower position and moves upwards. This relationship is apparent as a sign shift in Fig. 3 from the lower position to the upper position, which shows that targets which appeared in time (delay 1 at the lower position, delay 5 at the upper position) were subject to weaker masking than targets which appeared out of time. We do not find this sign change for any of the control conditions; therefore, the interaction between position and delay is specific to motion masking.

As the most conservative measure of difference between motion masking and forward and backward masking, we suggest the timing discrepancy of control lower and apparent motion at the lower position and of control upper and apparent motion at the upper position because of the spatial specificity of the masking effects. As can again be seen from Table 1, both comparisons yield significant differences, which is indicative of an influence of timing in motion masking which is different from the one expected in combined forward and backward masking.

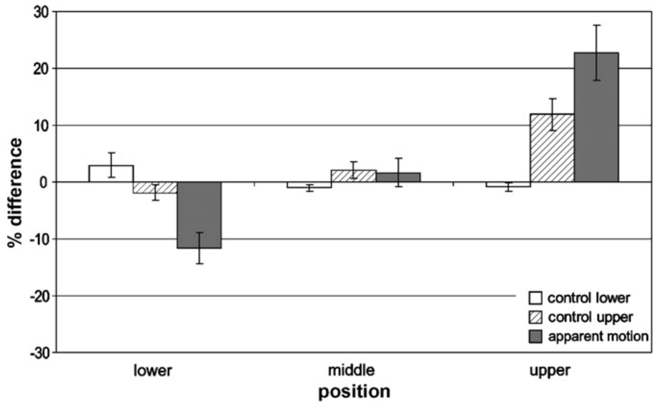

Fig. 3. Differences between the two delays (1 – 5) at the respective positions within conditions. Differences scores are significantly different from 0 for apparent motion at the lower ($T(7) = -4.249$, $p = 0.004$) and the upper position ($T(7) = 4.664$, $p = 0.002$) and for the upper control condition at the upper position ($T(7) = 4.204$, $p = 0.004$) only. As can be seen from Table 2, the difference in timing observed for apparent motion differs from the difference obtained in the control conditions at the upper and the lower target position. Critically, a sign shift is evident only in the case of apparent motion. This sign shift can be taken as evidence for a spatio-temporal pattern of motion masking which is consistent with the assumed time course of the apparent motion: targets which appear in time with the presumed linear movement of an apparent motion token are detected significantly more often than those that appear too early or too late, respectively (delay 5 > delay 1 at the lower position, delay 1 > delay 5 at the upper position).

4. Discussion

4.1. Dynamic representation?

The results of this experiment show that apparent motion has a diminishing effect on the detectability of targets on the apparent motion trace, thereby replicating the results of Yantis and Nakama (1998) with a different criterion content. In our control conditions, we also show that the masking observed in the apparent motion condition is different from the masking found under paracontrast (forward-) and metacontrast (backward-) masking conditions: by presenting only one part of the apparent motion stimulus configuration at a time, namely the upper or the lower blinking stimulus, we dissociate the para- and metacontrast masking effects form the motion masking; a comparison of these with the apparent motion condition leaves us with the effect of motion masking. Critically, we extend the notion of motion masking by the identification of a spatio-temporal pattern that is consistent with the assumed time course of the apparent motion: while the overall level of detectability during apparent motion is significantly lower than in the control conditions, targets that appear in time with the apparent motion percept are detected more often than those that appear at an unexpected position or point in time.

We can show a facilitating effect of the matching for a short delay close to the starting point of the apparent motion illusion, as well as for a long delay close to the endpoint of the illusion. The miss rates for these combinations of target locations and timings are significantly lower than for those targets which appear too late or too early at the same locations. This specific pattern of detectability argues further against the case of masking effects unrelated to motion, as the detectability is higher at short intervals between target and masks, whereas the opposite could be expected for para- and metacontrast.

In an experiment comparing real and apparent motion, Kolers (1963a, 1963b) only found a U-shaped function of detectability for targets that appeared on the path of real motion. The minimum in this function was identified at the point where the motion stimulus and the target over-

Table 2
Results of paired Fisher-protected *t*-tests comparing timing differences across conditions

Pairs		Paired differences					*T*	*df*	Significance (two-sided)
		Mean	*SD*	*SE*	95% CI				
					Lower	Upper			
con low, pos1	con up, pos1	4.79	4.49	1.59	1.04	8.55	3.02	7	0.0195*
con low, pos2	con up, pos2	−3.13	4.83	1.71	−7.17	.92	−1.83	7	0.1102
con low, pos3	con up, pos3	−12.71	7.23	2.56	−18.76	−6.66	−4.97	7	0.0016*
con low, pos1	app mot, pos1	14.58	9.20	3.25	6.89	22.28	4.48	7	0.0029*
con low, pos2	app mot, pos2	−2.71	6.04	2.13	−7.76	2.34	−1.27	7	0.2451
con low, pos3	app mot, pos3	−23.54	13.90	4.91	−35.16	−11.92	−4.79	7	0.0020*
con up, pos1	app mot, pos1	9.79	6.81	2.41	4.10	15.49	4.07	7	0.0048*
con up, pos2	app mot, pos2	.42	8.90	3.15	−7.02	7.86	.13	7	0.8984
con up, pos3	app mot, pos3	−10.83	12.12	4.28	−20.96	−0.70	−2.53	7	0.0393*

con low, lower control condition; con up, upper control condition; app mot, apparent motion condition; pos1, lower position; pos2, middle position; pos3, upper position; SD, standard deviation; SE, standard error; CI, confidence interval.

* Significant ($p < 0.05$).

lapped perfectly. This finding is somehow intuitive, as one would certainly expect two overlapping stimuli to somehow interfere with each other. Using only a single target position, Kolers (1963a, 1963b) found no such U-shaped function in the case of apparent motion. The detectability of targets was generally low, but it increased for incidents where apparent motion and targets appeared together in time.

Collapsing the results of our two extreme target positions, we actually find a function of detectability with a maximum at 'in time' as compared to targets that appear too early or too late. If the motion token was represented dynamically and analogous to real motion, a further decrement of detectability could be expected for targets which fit the apparent motion percept spatially as well as temporally, resembling the finding by Kolers (1963a, 1963b) for targets that spatio-temporally fitted real motion. This prediction is not met by our data. Still, the general decrease of detectability can be interpreted as a consequence of the conflicting representations of a moving stimulus and of a stationary target stimulus, as in object substitution masking (Di Lollo, Enns, & Rensink, 2000; Enns & Di Lollo, 1997).

How then, can these specific dynamics be explained? The activity in V1 on the apparent motion trace can be interpreted as a prediction (Mumford, 1992) of a token moving over retinotopic space. This prediction is potentially generated by visual motion areas such as hMT+/V5, which feedback the prediction as activity onto V1. Here, the prediction could be compared with the existing or incoming evidence for a moving object. One indication for such a search for evidence is the phenomenon of path-guided apparent motion, where additional evidence presented on the whole path between apparent motion origin and terminus (Shepard & Zare, 1983) can override the usual spatio-temporal conditions for apparent motion. Our results point in a direction that the prediction is not only spatial (as indicated by previous neuroimaging studies), but indeed spatio-temporal. Evidence for the prediction should therefore accord to the spatial as well as temporal aspects of the prediction. A stationary object is not necessarily evidence for a moving token, and thus it might conflict with the predicted token. The result would be "motion masking", in our case the general decrease of detectability of both the in-time and the out of time targets during apparent motion. The closer a target gets to the predicted token in a hypothetical feature space, the less masking should occur. A target that appears in-time with the moving token would fit the prediction better than a target that will appear out of time. Therefore, it should be masked less. A spatio-temporally fitting motion stimulus on the apparent motion trace might not be masked at all (Attneave, 1974).

Moreover, it can be argued that a target stimulus which is very different from the stimuli inducing the apparent motion percept (as in the Yantis and Nakama study) will be masked more than a stimulus that is very similar to the apparent motion origin and terminus (as in our study), because the later stimulus will fit the prediction better than the former. However, the neuronal locus of interference during a letter discrimination task has been suggested not to be in V1, but at the border of hMT+/V5 and the lateral occipital complex (Liu et al., 2004), where the analysis of form and the analysis of motion might interfere with each other (but see Downing, Wiggett, & Peelen, 2007; Spiridon, Fischl, & Kanwisher, 2006).

The model for a prediction has to be established over time: when only a single cycle of apparent motion is presented, the motion percept is postdicted (Beck, Elsner, & Silverstein, 1977), rendering motion masking unlikely (see below). However, after several cycles of apparent motion, the system is thought to be able to compute the motion percept in real time (Kolers, 1972). In fact, the perception of motion persists for a few additional cycles if one of the inducing stimuli is suddenly eliminated (Wertheimer, 1912). A study on perceptual learning complements these results: if an irrelevant motion stimulus is paired with a reinforced task-relevant stimulus, subjects report seeing motion in the direction of the paired motion stimulus in blank displays. This effect is not seen for non-paired motion directions (Seitz, Nanez, Holloway, Koyama, & Watanabe, 2005). Furthermore, strong expectations can indeed override bottom up apparent motion cues (Tse & Cavanagh, 2000), and prior knowledge about the direction and velocity of moving targets enhances their detectability (Ball & Sekuler, 1980; Sekuler & Ball, 1977).

Whether the specific spatio-temporal pattern of motion masking (or any motion masking at all) can be found under unpredictable apparent motion conditions, is an open question. It can be argued that in a case where the direction and velocity of an apparent motion percept are not already established, the sudden presentation of an additional transient stimulus on the apparent motion trace would disrupt or change the formation of a stable perceptual object over the whole intended trajectory. Depending on the spatio-temporal relationship of the stimuli, two-step apparent motion or a series of successive events with little or without any motion between them would then be perceived (Kahneman, 1967). Without the formation of a perceptual object spanning the whole trajectory, motion masking on this trajectory is unlikely to occur. Evidence for this line of argumentation stems from the finding that motion masking occurs only under optimal apparent motion conditions (Yantis & Nakama, 1998).

Another explanation of our results involves attention as a second mechanism which counteracts the effects of motion masking. Attention is a likely candidate, as it has been shown that two mechanisms subserve the perception of motion: one basic mechanism that relies exclusively on the activity of motion-detectors, and an additional attentional mechanism, that actively tracks the moving stimuli (Cavanagh, 1991, 1992; Hikosaka et al., 1993; Lu & Sperling, 1995). Both mechanisms work in parallel, and are confounded in our detection paradigm.

The relative increase in detectability of in-time targets could then be interpreted as a result or byproduct of an attentive tracking that follows the highly predictable trajectory of the apparent motion stimulus. The focus of attention could either jump or shift positions from one stimulus to the other. As attention is alternately attributed to the lower and the upper part of the stimulus configuration (or across the trace), targets in the attentional focus profit from facilitated processing.

The detection of targets appearing not in time with the motion percept remains impaired, as no attention-dependent facilitation can take place at that instant. This is a speculative account, as we did not explicitly control the allocation of attention in our paradigm. Different dynamics of the representation of the moving stimulus might surface in a case where attention is allocated elsewhere and does not counteract the masking. However, it seems difficult to explain the general decrease in detectability of both in-time and out of time stimuli when invoking attention as the sole explanation of the observed spatio-temporal dynamics of motion masking.

4.2. Motion masking is not forward and backward masking

Apparent motion and forward as well as backward masking stimulus configurations are indeed very similar: basically, spatially non-overlapping stimuli are repeated in rapid succession. The separation of para- and metacontrast masking from motion masking is important, because they mimic the effects of motion masking. For example, detailed contour information of the apparent motion origin is suppressed by the apparent motion terminus (Breitmeyer, Battaglia, & Weber, 1976; Breitmeyer, Love, & Wepman, 1974). Nonetheless, it has been shown that (metacontrast) masking and apparent motion differ substantially (Breitmeyer, 1984; Weisstein & Growney, 1969). In addition, metacontrast masking can be observed in situations where no apparent motion is perceived (Stoper & Banffy, 1977). Thus, apparent motion is neither sufficient nor necessary to produce (metacontrast) masking, but this does not necessarily imply that apparent motion and masking do not share some of their basic mechanisms.

We expected only limited masking effects in the non-apparent motion conditions, because the large spatial separation (>4°) of our stimuli is clearly above the maximum separation at which forward (<1°; Efron & Yund, 1999) and backward masking (3°; Weisstein & Growney, 1969) have been observed. But as the precise effects of masking strongly vary with criterion as well as stimulus configuration, we decided to control for these effects. Given that forward and backward masking take place, we tried to isolate the stimuli responsible for possible masking effects unrelated to the apparent motion itself. As can be seen from Fig. 2, the detectability in the presence of apparent motion drops significantly even below the levels reached in the aforementioned masking conditions. Thus, the presence of motion seems to have an effect on the representation of the targets on the motion trace. We claim that the differences from the maximally possible hit rate in the control conditions stem from masking effects, but they might as well be caused by inattention. Still, the pattern observed across positions in the control conditions seems to be indicative of a limited effect of forward and backward masking on the nearest respective stimuli.

A further speculative point has to be made on the question of the generally high detectability of the target at the middle position. As we only used two delays, there was no target that appeared in time at this location. Therefore, we would have expected a generally low hit rate in the apparent motion condition, but in fact, the opposite was found. Basically, we propose that it was easier to detect these targets, because the targets were closer to the fixation cross and because no spatially determined para- and metacontrast masking effects took place.

Another possibility is that the large receptive fields in hMT+/V5 always overlapped at the middle position. If attention jumps or shifts in accordance with the spatial layout of the apparent motion stimulus configuration detected by these receptive fields, it might always be allocated to the middle position as well, even though the focus or center lies on the apparent motion origin or terminus. The same holds true for a spatio-temporal prediction that would always include the middle position.

A mechanism that seems likely to be involved in motion masking is object substitution masking (Di Lollo et al., 2000; Enns & Di Lollo, 1997): this particular form of masking is thought to take place on the level of representations. Specifically, it is hypothesized to be a consequence of perceptual hypothesis testing on the basis of re-entrant feedback loops between higher and lower cortical visual areas. If re-entrant information, initially caused by the target and the mask, is confirmed by the actual stimulus display or a decaying trace of target stimulus activity on the lower level, no masking takes place. If, however, the re-entrant information does not match the actual representation and the target signal has already decayed, a new representation is created, and masking takes place: the visual token "target" is replaced by the visual token "mask". Attention or a precise prediction concerning the target reduce the amount of iterations needed to test the perceptual hypothesis, and therefore facilitate the detection of decaying target activity. Hence, the effects of object substitution masking are diminished when attention is focused or pre-cued on the target location (Di Lollo et al., 2000).

4.3. Connection to neurophysiological results

During apparent motion, neuronal activity between the apparent motion origin and terminus has been shown to exist in V1; this activation is without a physical counterpart and has been related to re-entrant feedback from higher visual motion areas such as hMT+/V5 to V1 (Larsen et al., 2006; Muckli et al., 2005; Sterzer et al., 2006). In line with previous theoretical considerations (Yantis &

Nakama, 1998), we suggest that it is this feedback activity that interferes with the representation of the stationary target stimulus on the level of V1, and thereby hinders its detection. This interpretation seems plausible given the evidence of re-entrant processing between motion-sensitive areas and V1 (Angelucci & Bullier, 2003; Galuske, Schmidt, Goebel, Lomber, & Payne, 2002; Hupe et al., 2001, 1998; Sillito, Cudeiro, & Jones, 2006).

Whereas interference on the level of V1 can account for the general decrease in detectability of the targets on the apparent motion trace, it cannot necessarily account for the improved detection of targets that appear in time with the apparent motion percept. Present models need to be extended with a component that explains temporally variant interference.

We have argued that the reduction of motion masking for the in-time targets is possibly due to an attentional process. Previous evidence from fMRI suggests that motion information is read out by parietal and frontal regions and used to guide the focus of attention during attentive tracking of moving objects (Culham et al., 1998). To account for the present results, it is possible to assume that the feedback information from hMT+/V5 and from parietal and frontal regions converges in V1: targets that would otherwise be masked profit from facilitated processing in the attentional focus that moves with the motion trace.

However, the activity found in V1 is not solely due to attention, as it persists even when attention is drawn away from the motion stimulus (Muckli et al., 2005). Mumford (1992) proposed as a general principle that higher order areas send "templates" (or predictions; Gilbert & Sigman, 2007) via descending pathways to lower order areas where these templates are compared to the incoming information. The templates are thought to be stored in the synaptic weights of deep pyramidal cells (layer 6) of hMT+/V5 and sent to layer 6 of V1. Evidence that fits the templates is thought to be processed preferentially. Residuals are computed by more superficial layers and send back via layer 4B to the higher order areas, where templates will be updated accordingly. After several loops, the system reaches a stable state, and continues working with the established model. When no residuals are to be computed, the superficial layers stop firing, while the deeper layers continue to receive and send incoming feedforward information.

Illusions such as apparent motion can be interpreted as "templates" that affect the lower areas by themselves, even without further input. The lateral geniculate nucleus (LGN) of the thalamus (Mumford, 1991) or areas V1/V2 (Bullier, 2001; Lee, Mumford, Romero, & Lamme, 1998) have been proposed to serve as "active blackboards" that integrate in their neuronal responses these computations carried out in higher order areas.

We suggest that hMT+/V5 generates a spatio-temporally specific motion model that is fed back to V1 (or via V1 to the LGN). This model could be used to search for more evidence for a moving stimulus on the predicted trajectory. The stationary in-time targets we present do not perfectly fit the model, but they might serve as evidence because they are spatio-temporally congruent with the model. Therefore, they might be processed preferentially, resulting in a higher hit rate than for the out of time stimuli.

Our finding of a behavioral spatial-temporal interaction along the motion trace can be taken as an indication that the activity found in V1 is not simply an epiphenomenal byproduct of the computations in hMT+/V5. Activity in V1 could reflect the result of motion information extraction in higher visual areas and play a relevant role in the processing of new upcoming information. We propose that the phenomenon of motion masking might be a valuable tool for investigations of the dynamical interaction between predicted information and the processing of new sensory stimulation.

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