Journal of Experimental Psychology:
Human Perception and Performance
2009, Vol. 35, No. 3, 611–626

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0096-1523/09/$12.00 DOI: 10.1037/a0012317

Going, Going, Gone: Localizing Abrupt Offsets of Moving Objects

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When a moving object abruptly disappears, this profoundly influences its localization by the visual system. In Experiment 1, 2 aligned objects moved across the screen, and 1 of them abruptly disappeared. Observers reported seeing the objects misaligned at the time of the offset, with the continuing object leading. Experiment 2 showed that the perceived forward displacement of the moving object depended on speed and that offsets were localized accurately. Two competing representations of position for moving objects are proposed: 1 based on a spatially extrapolated internal model, and the other based on transient signals elicited by sudden changes in the object trajectory that can correct the forward-shifted position. Experiment 3 measured forward displacements for moving objects that disappeared only for a short time or abruptly reduced contrast by various amounts. Manipulating the relative strength of the 2 position representations in this way resulted in intermediate positions being perceived, with weaker motion signals or stronger transients leading to less forward displacement. This 2-process mechanism is advantageous because it uses available information about object position to maximally reduce spatio-temporal localization errors.

Keywords: flash-lag effect, backward masking, visual transients, motion extrapolation, moving objects

Supplemental materials: http://dx.doi.org/10.1037/a0012317.supp

In the flash-lag effect, a moving object appears to be ahead of a spatially aligned flashed object. This finding has sparked a debate about how the nervous system processes moving objects and determines their perceived position. This is an important problem as neural delays in the retina and the central vision pathway are liable to lead to spatial localization errors. One hypothesis, termed *motion extrapolation*, states that moving objects are spatially shifted forward to counteract the influence of neural delays in the visual pathways on the perceived position of moving objects (Nijhawan, 1994). If one assumes that perceptual awareness of the position of an object requires cortical activity, then a delay in the pathway from the photoreceptors to the primary visual cortex of about 80 ms (Schmolesky et al, 1998) would imply that moving objects are always perceived to lag their "true" position by the distance they moved in that time. However, by analyzing the speed and direction of a moving object, the visual system could extrapolate its position forward by an appropriate amount and so compensate for these processing delays. In the flash-lag effect, this forward shift is apparent, because the flash does not undergo an equivalent spatial shift, thereby resulting in a perceived gap between the moving object and the flash, although they are physically aligned.

Several alternative accounts have been brought forward to explain the findings of the flash-lag effect, amongst them differential attentional deployment (Baldo & Klein, 1995), differential latencies (Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Cavanagh, 2000; Whitney & Murakami, 1998), and temporal integration (Brenner & Smeets, 2000; Brenner, van Beers, Rotman, & Smeets, 2006; Eagleman & Sejnowski, 2000; Krekelberg & Lappe, 2000; Roulston, Self, & Zeki, 2006). There has been considerable debate about which framework is able to explain the experimental data best (for reviews, see Krekelberg & Lappe, 2001; Nijhawan, 2002). One key argument against motion extrapolation has been made from stimulus displays in which the object's motion following the flash is terminated (Eagleman & Sejnowski, 2000) or changes its direction (Whitney & Murakami, 1998). If the moving object is stopped or disappears at the time of the flash, the forward displacement of the moving object is abolished and the flashed object and moving object are perceived to be aligned. When motion is reversed at the time of the flash, the moving object appears shifted in the direction of motion after the flash.

It has previously been argued that these findings do not necessarily contradict the extrapolation account for moving objects (Maus & Nijhawan, 2006; Nijhawan, 2002). Clearly if a moving object undergoes an abrupt change in its trajectory (such as an abrupt offset or a reversal of direction), the extrapolated output would not represent the object's true spatial position. Thus, a second mechanism would be required to correct the extrapolated output if things in the world changed suddenly. Precisely such a mechanism has been known for a long time. In backward masking the presentation of a visual mask can suppress the perception of a previously presented target (Alpern, 1953; Breitmeyer, 1984).

In this article, we directly test the two-mechanism model. Let us assume that the position of a continuously moving object is maintained by an internal model in the visual system, which is spatially

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We would like to thank Beena Khurana, Jim Parkinson, Ruth Habibi, and George Mather for numerous discussions, as well as Glyn Humphreys and Ryota Kanai for helpful comments on a draft of the article.

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shifted forward (e.g., Erlhagen, 2003). When the moving object suddenly disappears, a transient neural off-signal is elicited from the retina. This transient is accurately localized with fixed retinotopic coordinates—like a "stamp" on the retina. It is known that stimulus offset can act as a mask in backward masking paradigms (Breitmeyer & Kersey, 1981) and exhibit strong lateral inhibitory effects (Macknik, Martinez-Conde, & Haglund, 2000). At the level of the internal model, the best hypothesis of the system is that the moving object is still in its spatially forward-shifted position on the motion trajectory. The transient, however, provides new evidence that the moving object disappeared in its offset position, which is given unambiguously. The disappearance position information is unambiguous in the sense that no new input contradicts the offset position information. This offset position information will be integrated with the extrapolated position representation to yield a percept. The visual system is faced with contradictory information and—as the object cannot be perceived as disappearing in one position and continuously moving in another—needs to resolve this conflict, in order to come up with an unambiguous percept of the visual scene. Neural competition has been suggested as a mechanism that deals with conflict resolution in the context of visual attention, visual masking, and rapid serial visual presentation (Desimone, 1998; Keysers & Perrett, 2002). Applied to the present case of an abrupt offset, the two distinct and incommensurate representations of the internal model and the retinal transient will compete. The accurately localized off-transient wins the competition because of its strength and recency, leading to a perceptual suppression of the extrapolated position.

A hallmark of competition models is that when the weightings of the competing representations are changed the perceptual outcome is changed. As noted above, moving objects that disappear abruptly do not usually appear to overshoot their final positions. Although representational momentum (Freyd & Finke, 1984; Hubbard & Bharucha, 1988) states that moving objects are remembered to disappear beyond their final position, these findings can be explained by cognitive processes or eye movements and visual persistence (Kerzel, 2000; Kerzel, Jordan, & Müsseler, 2001). In the flash-terminated flash-lag display, no overshoot of the moving object is perceived. However, some stimulus conditions, for example when stimuli are presented peripherally or are blurred, do lead to perceptual overshoots for abruptly stopping objects (Fu, Shen, & Dan, 2001; Kanai, Sheth, & Shimojo, 2004). The crucial feature that enables the correct localization of the disappearance position of a moving object may be a strong, accurately localized retinal off-transient that wins the neural competition and therefore masks any extrapolated position representation that would otherwise be perceived (Maus & Nijhawan, 2006). On this "correction for extrapolation" view, neural competition acts as a correction mechanism to reduce spatio-temporal localization errors for moving objects disappearing from view. The present study directly investigates the above correction for extrapolation hypothesis.

A Novel Visual Localization Illusion: Offset-Lag

The above hypothesis predicts a new visual illusion of offset-lag: If a part of a moving object disappears abruptly while the rest of the object continues to move, the object should "break apart" at the time of the offset, with the continuing part being perceived further ahead in the direction of motion, in a position distinct from the disappearing part. This is indeed what we observed. In initial displays, we presented a vertical bar, moving horizontally across the screen while observers maintained steady fixation. When the bar had moved halfway across the screen, either its upper or lower half abruptly disappeared (for a demonstration of the stimulus, see the Web supplement). Observers reported seeing the bar break apart into two separate half bars located in different positions prior to the disappearance of one of them. The continuing half bar was always described to lead the offset half bar. Some observers described the disappearing half bar as "jumping back" before disappearing. Additionally, the stimulus used here gave rise to the well-known line-motion illusion (Hikosaka, Miyauchi, & Shimojo, 1993; Jancke, Chavane, Naaman, & Grinvald, 2004; Wertheimer, 1912). The offset half bar seemed to disappear gradually from one end to the other. Some observers also reported the existence of an invisible object that occluded half of the bar. A similar illusion has previously been described by Palmer and Kellman (2001, 2002, 2003). However, in these previous displays an actual occluder was always clearly visible to the observers. For a detailed discussion of the similarities and differences between these displays and those used in our experiments see the General Discussion.

Here, by using psychophysical experiments, we investigate the hypothesis, described above, that the perceived position of a moving object's final position is the outcome of a neural competition process between an internal model and transient retinal signals. The stimuli we used were similar to those described above involving comparisons of the perceived positions of continuously moving and abruptly disappearing objects. In Experiments 1 and 2, we quantify the magnitude of the new illusion and show that the effect scales as a function of the speed of the moving object.

If the perceived position of a moving object is the outcome of a competition between two representations, it should be possible to influence this outcome by manipulating the relative strength of those representations. In a recent study (Maus & Nijhawan, 2006), off-transients were weakened by gradually decreasing a moving object's luminance until it became invisible. An object disappearing without a strong transient was indeed perceived to vanish in an extrapolated position. In Experiment 3 we took the opposite approach and introduced new transients into an otherwise undisturbed motion trajectory. We interrupted the motion of the object for brief varying durations or introduced transients of varying strength into a continuous motion trajectory to investigate how this influenced perceived positions.

Experiment 1: Matching Task

In the first experiment we aimed to quantify the offset-lag effect and to see if it depends on the speed of the moving object. To suppress the perception of the line-motion illusion that some of our observers reported in initial observations (see above), we introduced a spatial gap between the two half bars. To measure the size of the misalignment between the offset bar and the continuing bar, we used a simple matching task: Observers viewed a motion sequence of two bars moving across the screen, one of which disappeared abruptly. Afterwards they were asked to indicate their perception of the relative positions of the two bars at the time of disappearance by adjusting the positions of two stationary bars.

Method

Participants. Four observers, including Gerrit W. Maus (of the other observers, there were three women and three naïve to the purpose and hypothesis of the study), took part in the experiment. All had normal or corrected to normal visual acuity.

Apparatus and stimuli. Stimuli were presented on a 21-in. CRT monitor (Formac Elektronik GmbH, Blankenfeld, Germany) at 100-Hz vertical refresh rate using MATLAB and the Psychophysics toolbox extensions (Brainard, 1997; Pelli, 1997). Observers kept a constant distance of 80 cm from the screen with their heads partially immobilized by means of a chin rest.

The stimuli consisted of two white vertical bars (0.14° × 2.7°, 71.3 cdm^{-2}) on a mid-grey background (10.6 cdm^{-2}). The bars (aligned above each other and separated by a spatial gap of 1.0°) moved horizontally across the screen from left to right at one of three possible speeds (8.1 $°s^{-1}$, 15.9 $°s^{-1}$, 23.1 $°s^{-1}$). After traversing about halfway across the screen (randomly jittered by ±0.27°) one of the two bars (the offset bar) disappeared abruptly, while the other bar continued moving to the right edge of the screen (see Figure 1A). Depending on the speed, the entire motion sequence lasted 3,410 ms, 1,700 ms, or 1,130 ms. Throughout the experiment observers fixated a black fixation cross (0.27° × 0.27°) in the right half of the screen, 6.9° to the right of the midpoint.

Observers were asked to recreate their percept of the positions of the two bars at the time of the abrupt offset. To do so a comparison stimulus consisting of two stationary bars was shown after each motion sequence (see Figure 1B). One bar was presented in the position where the offset bar disappeared in the motion sequence. The other bar, representing the continuing bar of the motion sequence, appeared in a random position between 0.68° to the left and the right of the offset position. The latter bar could be moved horizontally with the arrow keys on the keyboard. Observers were instructed to move this bar so that it matched the perceived relative positions of the bars at the time of disappearance.

Procedure. Trials were structured as follows: The two bars appeared moving and either the upper or the lower bar disappeared near the midline. The other bar continued moving until it reached the right edge of the screen. Immediately afterward the comparison stimulus appeared. Observers adjusted the bars to match their percept of positions in the motion sequence and pressed another key when they were finished. Following this, the next trial started.

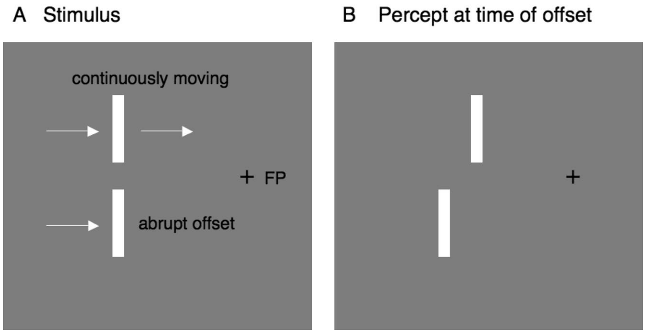

Figure 1. Panel A: The stimulus used in Experiment 1. Observers were instructed to fixate the fixation point (FP) at all times. Two perfectly aligned vertical bars (0.14° × 2.7°; not to scale), separated by 1.0°, moved across the screen, until one of them abruptly disappeared. The other bar continued to move. Panel B: Observers perceived the continuing bar to be further ahead in the direction of motion when the other bar abruptly disappeared. In Experiment 1, two static bars representing the previously shown moving bars were presented after each trial. One appeared in the offset position, while observers could horizontally adjust the other to match their percept at the time of the offset.

In an initial training period, observers familiarized themselves with the stimuli and the task. In the experiment there were three speeds of movement and two possibilities as to which bar disappeared, either the bar in the upper visual hemifield or in the lower visual hemifield. Observers performed 20 trials in each condition for a total of 120 trials (3 speeds × 2 offset hemifields × 20 trials). Trials of all conditions were randomly intermixed. During the experiment there were two short breaks.

Results

All observers adjusted the position of the continuously moving bar to be ahead of the disappearance position of the offset bar. The mean perceived misalignments of the bars are shown in Figure 2. A two-way independent measures analysis of variance (ANOVA) on observers' mean adjustments revealed significant effects for both speed and visual hemifield of the offset: speed, $F(2, 474) = 31.68$, $p < .001$, $\eta^2 = .118$; offset hemifield: $F(1, 474) = 5.58$, $p = .019$, $\eta^2 = .012$, however, the differences for bars disappearing in the upper or the lower visual field are rather small. Collapsed over the two hemifields, the mean misalignment was 0.45° (*SEM* = 0.04°) for the slow speed of 8.1 $°s^{-1}$, 0.65° (*SEM* = 0.03°) for the medium speed of 15.9 $°s^{-1}$, and 0.82° (*SEM* = 0.03°) for the fast speed of 23.1 $°s^{-1}$. These misalignments amount to a temporal forward shift of 55.6 ms (*SEM* = 4.9 ms), 40.9 ms (*SEM* = 1.9 ms), and 35.5 ms (*SEM* = 1.3 ms), respectively.

Discussion

The sudden offset of a moving object can influence its perceived position in a more complex way than one would assume. Differing from previous experiments measuring perceived offset positions (Kerzel, 2000; Kerzel et al, 2001), we did not use static probes for comparison of positions but instead used a continuously moving object. For the first time, we directly compared the perceived positions of moving objects with those of abruptly disappearing objects. The results show that the mechanisms underlying the perception of the offset position of moving objects differ crucially from those underlying the perception of the instantaneous position of moving objects. Assuming that the offset position is perceived veridically (see Experiment 2B), our results show a forward displacement of the perceived position of the moving object. The forward displacement scales with the speed of motion.

Although not explicitly tested, it is reasonable to assume that observers perceived the two bars as aligned in the first half of each trial, when both bars were presented moving. Given this, it is remarkable that observers adjusted the two bars as being not aligned at the time of disappearance of one of the bars, because this was contradictory to their prior experience with the relative positions of the two bars. They were always physically and perceptually aligned until the offset bar disappeared. However, anecdotally some observers reported the matching task to be illogical, because the bars were clearly aligned before one of them disappeared. Asking if there was any misalignment could therefore be mislead-

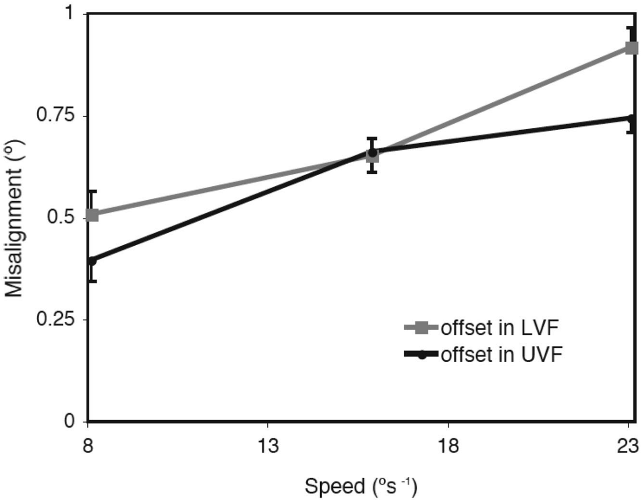

Figure 2. Mean misalignments between the offset bar and the continuing bar in Experiment 1, plotted as a function of speed, separately for offsets in the upper visual field (UVF) and lower visual field (LVF). Error bars show standard error of the mean between observers.

ing for observers. Having a priori knowledge about the relative positions of the bars might also bias observers to cognitively correct for any perceived misalignments of the bars, which may actually explain the nonlinearity of the temporal forward shift.

To eliminate these limitations we conducted Experiment 2 in which the two bars moved in opposite directions. Thus, observers did not have any a priori information about the relative positions of the two bars. We changed the design to a more controlled two-alternative forced-choice method that depended less on perceptual memory.

Experiment 2A: Forced-Choice Task

The purpose of this experiment was to verify the illusory misalignment of disappearing and continuing moving bars of Experiment 1 with a more controlled psychophysical method. In this experiment, two bars moved in opposite directions, so observers did not have any a priori knowledge about the relative positions of the two bars. By varying the relative positions of the bars at the time one of them disappeared, we were able to ask observers a two-alternative forced-choice question. This stimulus display lacked the counterintuitive, illusionary character of the stimulus in Experiment 1, but using motion in opposite directions generalizes the effect to a wider range of stimuli.

Method

Participants. Six observers (three women, three men) volunteered to take part in this experiment, including Gerrit W. Maus. Five of the observers were naïve as to the purpose of the experiment. All had normal or corrected to normal visual acuity.

Apparatus and stimuli. The same setup as in Experiment 1 was used. Observers fixated a black fixation cross in the center of the screen. Two vertical bars (same dimensions as in Experiment 1) moved horizontally across the screen in opposite directions, starting at opposite edges of the screen and passing each other near the midline. One of the two bars abruptly disappeared at the midline (randomly jittered by ±0.27°).

The alignment of the continuing bar with the offset position of the other bar was systematically manipulated. By starting the movement of one bar slightly earlier than the other bar, the continuing bar could either already have passed the offset position, be perfectly aligned with it, or still be slightly short of it. Observers had to indicate in a two-alternative forced-choice task if the continuing bar was visible to the left or to the right of the offset position at the time of the offset.

On every trial both bars moved at the same speed (8.1 $°s^{-1}$, 15.9 $°s^{-1}$, or 23.1 $°s^{-1}$). As either the upper or the lower bar continued to move, there were four possible conditions: The continuing bar performed either (a) leftward motion in the upper visual field (LU), (b) rightward motion in the upper visual field (RU), (c) leftward motion in the lower visual field (LL), or (d) rightward motion in the lower visual field (RL).

Procedure. On every trial observers watched the motion sequence and responded with a key press. Trials of the four motion conditions (LU, RU, LL, RL) were blocked. Before each block, observers were informed about which bar would disappear and which would continue to move. The three bar speeds were randomly intermixed within the blocks, and block order was balanced between observers.

After an initial training block, observers performed one block of 120 trials for each of the four conditions. There were 40 trials for each speed in all conditions for a total of 480 trials (3 speeds × 4 conditions × 40 trials).

For efficient measurement of psychometric functions, we used an adaptive method: For each trial the horizontal distance between the position of the continuing bar and the offset position of the offset bar was determined online by the experimental software. Trial misalignments were centered around the observer's current point of subjective alignment (PSA), as calculated from the QUEST threshold estimation algorithm (Watson & Pelli, 1983). QUEST estimates the current most likely PSA from the performance on all previous trials. In each block there were three independent QUEST estimators, one for each speed of motion. A random jitter taken from a Gaussian distribution with a standard deviation of $\sigma = 20 \text{ ms} \times v$, where v is the speed of the bars in this trial, was added to the current estimated PSA and rounded to the nearest multiple of $0.8 \times \sigma$, so that a coarser distribution of misalignments was used in trials with faster speeds. This method ensured that most trials were placed at the most useful values close to the observer's PSA, but there were also a few trials with greater distance between the two bars' positions that were easier to judge for observers. Independently of this method, after the experiment psychometric functions were fitted with the probit procedure to estimate PSAs and compute bootstrap confidence intervals for each condition and speed (Finney, 1971; Wichmann & Hill, 2001a, 2001b).

Results

The group mean PSAs were analyzed in a 2 × 2 × 3 repeated measures ANOVA (Hemifield of Continuing Bar × Motion Direction of Continuing Bar × Speed). There was a significant main effect for speed, $F(2, 4) = 14.05$, $p = .016$, $\eta^2 = .875$, but not for visual hemifield or motion direction and no significant interactions.

Because the ANOVA did not show any systematic differences between visual hemifields and motion directions, all conditions were collapsed, and new psychometric functions (based on 160 trials) were fit for each speed. Psychometric functions for one naïve observer are shown in Figure 3A. For all observers the continuing bar was required to be short of the offset position to be perceived as aligned at the time of the offset. For the individual data none of the confidence intervals for thresholds included 0 (with the exception of one observer, whose overall mislocalization effects were small; this observer showed a very shallow psychometric function for the fastest speed, including 0 in the confidence interval for the threshold). Figure 3B shows the group mean PSAs for each speed. The mean perceived overshoots of the continuing bar from the disappearance point were 0.62° (*SEM* = 0.14°) for the slowest speed of 8.1 °s^{-1}, 1.05° (*SEM* = 0.21°) for the medium speed of 15.9 °s^{-1}, and 1.54° (*SEM* = 0.30°) for the fastest speed of 23.1 °s^{-1}. These misalignments amount to a temporal forward shift of 76.5 ms (*SEM* = 1.7 ms), 66.0 ms (*SEM* = 1.3 ms), and 66.7 ms (*SEM* = 1.3 ms), respectively, which reveals a roughly linear relationship between speed and amount of forward displacement.

Discussion

All observers perceived the continuously moving bar as further ahead in the direction of motion than the bar that disappeared abruptly. The size of the misalignment of the two bars depended linearly on the speed of motion. The moving bar was shifted forward by a constant amount of time, roughly between 60 ms and 80 ms. The slopes for psychometric functions decreased for increasing speeds, indicating that observers were more confident in judging positions of bars moving at slower speeds.

Contrary to Experiment 1, in this experiment observers did not report any impression of invisible occluders. The use of movement in opposite directions excluded the possibility that the offset-lag effect depends on observers inferring the existence of invisible occluders. The size of the effect is in the same range of what is usually observed in the flash-lag effect (Eagleman & Sejnowski, 2000; Nijhawan, 1994).

Assuming that the offset position was perceived veridically, the measured forward shift is consistent with our hypothesis that the perceived instantaneous position of the continuously moving bar is based on an internal model representing the predicted position of moving objects. The disappearing bar's offset position, however, is perceived correctly due to a correction mechanism, based on transient signals, that inhibits the perception of the predicted position.

An alternative view to that presented above is that the disappearance position is perceived as shifted in the direction opposite to the motion direction. There are reports of abruptly disappearing moving objects appearing to vanish slightly short of their actual offset position (Müsseler, Stork, & Kerzel, 2002; Roulston et al., 2006). If this were the case in the present experiments, then in Experiment 2A the instantaneous position of the moving object is not extrapolated forward and, instead, the disappearance position is perceptually mislocalized in the direction opposite to motion direction. This possibility was explored in Experiment 2B, which directly measured the perceived final position of the abruptly disappearing moving bars.

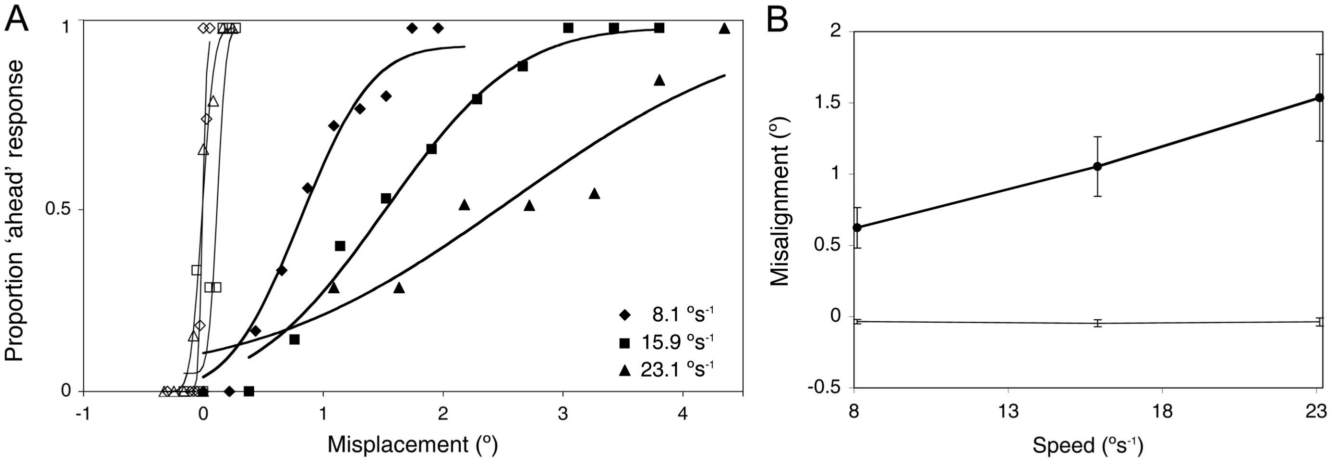

Figure 3. Panel A: Raw data and fitted psychometric functions from Experiment 2A (filled symbols, thick lines) and Experiment 2B (open symbols, thin lines) for one naïve observer. In Experiment 2A, two bars moved in opposite directions and one of them disappeared abruptly. Observers judged the relative positions at the time of the offset. Points of subjective alignment (PSAs) are the points where the psychometric functions cross 0.5 proportion "ahead" responses. All PSAs are significantly different from 0 and increase linearly with speed. The slopes of psychometric functions decrease with speed, indicating more uncertainty in observers' responses. PSAs in Experiment 2B, where both bars disappeared, are all close to 0 with no apparent speed dependency; slopes were much steeper than in Experiment 2A. Panel B: Mean PSAs for six observers in Experiment 2A (thick line) and four observers in Experiment 2B (thin line). Error bars show standard errors of the mean between observers.

Experiment 2B: Control Experiment With Two Offsets

This experiment served as a control for Experiment 2A to investigate the accuracy with which the offset positions of the disappearing bars were perceived. Two bars moved across the screen in opposite directions and both of them disappeared abruptly. In a two-alternative forced-choice task, observers judged their relative offset positions.

Method

Participants. Four observers (two women, two men), who previously participated in Experiment 2A, including Gerrit W. Maus, took part in this control experiment in a separate session.

Apparatus and stimuli. Stimuli were identical to Experiment 2A. The only difference was that both bars disappeared simultaneously close to the midline. The experimental manipulation was the time of the offset, which could be slightly before or after the two bars crossed each other.

Procedure. Observers were instructed to base their judgment on either the upper bar or the lower bar and to indicate whether it disappeared to the left or to the right of the other bar. Again there were four possible conditions: The "judgment bar" could be moving leftward or rightward and could be presented in the upper or the lower visual hemifield (LU, RU, LL, RL; see *Method* of Experiment 2A). This way of posing the question reduced the possibility of a judgment bias. If observers were asked whether the two bars did or did not cross before disappearing, a perceived perfect alignment could be assigned to either of the two categories. In our way of posing the question, a bias to subsume perceived perfect alignments to either the "left" or "right" response category would become apparent in the analysis of responses in the separate conditions.

For the placement of trial values, the same adaptive method as described in Experiment 2A was used. After an initial training block, observers performed one block of 39 trials in each condition (13 trials for each speed) for a total of 156 trials (3 speeds × 4 conditions × 13 trials). The order of blocks was balanced between observers.

Results

Observers gave very consistent responses, and although there were only 13 trials for one speed in each condition, psychometric functions were exceptionally steep. The PSAs were analyzed in a 2 × 2 × 3 repeated measures ANOVA (Hemifield of Judgment Bar × Motion Direction of Judgment Bar × Speed) that revealed no significant main effects or interactions.

The data from all four conditions were then collapsed to fit new psychometric functions for each speed (based on 52 trials). The thin lines in Figures 3A and 3B show one naïve observer's psychometric functions and the group's mean PSAs. For all observers, the two bars had to cross each other to be perceived as aligned at the time of disappearance (with the exception of one observer, who showed a small effect in the opposite direction). Thus observers actually perceived the bars to disappear before they reached their physical offset position. None of the individual psychometric functions' confidence intervals included 0. However, the effect was at least an order of magnitude smaller than the misalignment measured in Experiment 2A. The mean absolute misalignments (distances from the actual disappearance point of the bars) were −0.07° (*SEM* = 0.01°), −0.09° (*SEM* = 0.02°), and −0.07° (*SEM* = 0.03°) for the slow, medium, and fast speeds, respectively. These values result in temporal shifts of −8.6 ms (*SEM* = 1.2 ms), –5.7 ms (*SEM* = 1.3 ms), and –3.0 ms (*SEM* = 1.3 ms), less than the time for a full refresh cycle of the monitor (10 ms).

Discussion

Experiment 2B showed that the abrupt offset of a moving object is perceived accurately. Indeed, in line with earlier studies (Müsseler et al, 2002; Roulston et al, 2006), we found a small but significant perceptual undershoot of the offset position of the moving bar. A speed dependency of this effect, however, as reported by Roulston et al. (2006), could not be confirmed in this experiment. Furthermore, this small mislocalization of abruptly disappearing objects cannot explain the effect we found in the previous experiment. The undershoots measured here were at least an order of magnitude smaller than the overshoot of continuously moving objects reported in Experiment 2A. This leads us to conclude that the misalignment measured in Experiment 2A is indeed a forward displacement of the instantaneous position of the continuously moving object.

Experiment 3A: Interruption of Motion for Different Durations

In the previous two experiments, we presented empirical evidence that demonstrates the substantial role that retinal off-transients play in the visual system's ability to localize moving objects. Together with an earlier study that showed how objects disappearing without such transients are mislocalized (Maus & Nijhawan, 2006), this lends support to our central hypothesis that the perceived position of a moving object is the outcome of a neural competition between two distinct position representations. One representation is maintained by an internal model that is spatially shifted forward to compensate for neural processing delays, while the other is mediated by the bottom-up retinal transients and is localized accurately.

This hypothesis also predicts that it should be possible to influence the perceptual outcome of this competition process by manipulating the relative strength of these two representations. In the studies presented above, one bar was moving continuously, so the perceived position was fully determined by the internal model. In contrast, the offset bar disappeared with a strong retinal transient. Additional evidence supporting the internal motion model for the offset bar was not available after the offset, so the transient won the neural competition and observers perceived the bar vanishing in its "real" offset position.

In a further experiment, we used stimuli ranging between those two extremes. We introduced a brief blank of varying durations into an otherwise undisturbed motion trajectory. The moving object was simply turned off for a variable period ranging from 20 ms to 120 ms and turned back on in the position it would have occupied had it continued to move at constant speed (see Figures 4A and 4B). Equivalently one might say the object passed behind an invisible occluder, although one crucial difference is that an occluded object will move out of view gradually, with its leading

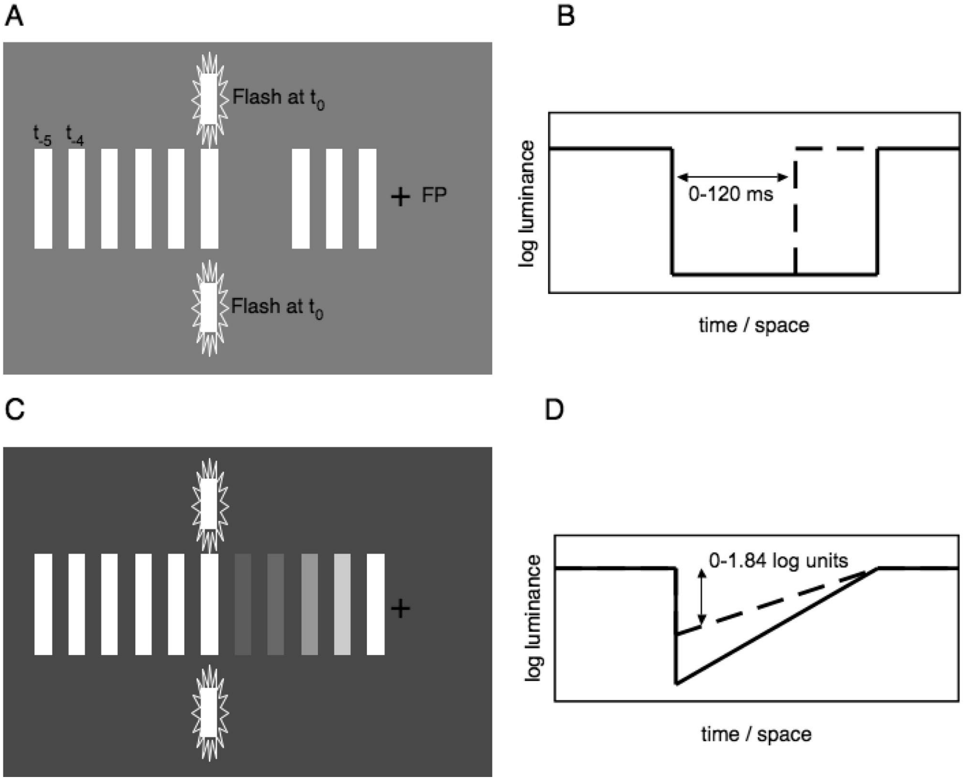

Figure 4. Panel A: Snapshots of discrete time points of the stimulus used in Experiment 3A. The white bar moved smoothly from left to right, indicated by the shift in position from time t_{-5} to t_{-4} and so on. At t_0 two bars were flashed above and below the moving bar's trajectory. In the illustration, the flashes are physically aligned with the moving bar. In the experiment, observers had to adjust the position of these flashes to appear perceptually aligned with the moving bar. Following the flash, the moving bar was turned off for a variable duration, after which it came back on and continued moving. Panel B: The luminance profile of the moving bar. Following the flash, the luminance of the bar was abruptly decreased to the level of the background and then turned back up to the original intensity up to 120 ms later. Panels C & D: Snapshots and luminance profile of the stimulus in Experiment 3B. Here the luminance was decreased abruptly to various intensity levels at the time of the flash. During the subsequent 200 ms, it was logarithmically increased to its original intensity.

edge disappearing first and its trailing edge disappearing later. In our stimulus the entire object disappeared and re-appeared all at once. The abrupt offset resulted in a transient off-signal; the fact that the object reappeared shortly afterwards, however, resulted in additional evidence for the internal motion model and therefore changed the relative strengths of the two position representations.

To measure the effect of blanks in the motion trajectory on the perceived position we used a flash-lag nulling method (e.g., Baldo & Klein, 1995). Observers were presented with two brief flashes above and below the trajectory of a moving bar. The task was to adjust the position of these flashes, such that they would appear to be aligned with the bar. At the same time as the flashes, the bar could be blanked for a short period of up to 120 ms. For a trajectory without a blank, we expected to find a typical flash-lag effect, that is, observers would adjust the flashes to be physically ahead of the moving bar's position. We predicted that for long blanks the transient would win the competition, as it did in Experiments 1 and 2, and as reported in the flash-terminated flash-lag condition, where usually no flash-lag effect is found. For shorter blanks between the two extremes, however, we expected the moving object to be perceived in intermediate positions. Although there is an off-transient, it would not be able to exhibit its full effect on the perceived position due to the short interval before new evidence for the internal motion model is accumulated.

Method

Participants. Six observers (three women, three men) including Gerrit W. Maus took part in this study. All had normal or corrected to normal visual acuity.

Apparatus and stimuli. Observers fixated a black fixation cross in the right half of the screen, 6.8° from the midline. A white vertical bar (0.14° × 2.7°) moved horizontally from the left of the screen to the right at a constant speed of 15.9 $°s^{-1}$. When the bar reached the midline (randomly jittered by ±0.14°), two bars (0.14° × 1.4°) were flashed for one refresh frame (10 ms), 1.0° above and below the moving bar's trajectory. In the next refresh frame, the moving bar either continued moving (0-blank condition) or was turned off for 20, 40, 60, 80, 100, or 120 ms. The bar then re-appeared in a position consistent with its constant speed (Figures 4A and 4B).

The two flashed bars were initially placed in a random position between 1.7° and 2.3° to the left or the right of the moving bar's position. The observers' task was to align the flashes with the moving bar. To do so, after the motion sequence the two flashed bars were presented again, this time continuously visible, and observers could move them horizontally in either direction by using the arrow keys. To see the motion sequence with their adjusted flash positions again, observers pressed the space bar. They could repeat this cycle of stimulus presentation and adjustment as often as necessary, until they felt the flashes were aligned with the moving bar. When observers pressed the return key, the experimental software registered their adjusted flash position, and the next trial started.

Procedure. Trials of all six blank durations and the 0-blank condition were randomly interleaved. In each condition, the initial flash position was equally often to the right and to the left of the moving bar, so that the direction of observers' adjustments was counterbalanced.

Observers first performed 24 trials of training to familiarize themselves with the task. In the actual experiment there were 12 trials for each of the six blank durations and for the 0-blank condition for a total of 84 trials. Note that each trial consisted of repetitive viewings of the same motion sequence, so the actual number of stimulus presentations was higher. Trials, in which observers viewed the motion sequence only once, were excluded from further analysis, as it could not be assumed that observers performed the task properly on these trials. Furthermore trials in which the observers' adjustment deviated more than two standard deviations from their mean adjustment in this condition were also excluded. A total of 2.6% of trials were excluded in accordance with these criteria.

Results

Figure 5A shows the means of observers' adjustments in all conditions. In the 0-blank condition observers showed a baseline flash-lag effect of 45.1 ms (*SEM* = 4.8 ms). A one-way repeated measures ANOVA on observer's mean adjustments revealed a significant effect of blank duration on the size of the flash-lag effect, $F(6, 30) = 11.75$, $p < .001$, $\eta^2 = .701$. Linear regressions for each individual observer showed negative slopes ($M = -0.26$, $SEM = 0.04$), one-sample $t(5) = -6.34$, $p = .001$, indicating that for all observers the introduction of blanks led to a reduction in the size of the forward displacement. However, even for the longest blank of 120 ms there was still a small but significant flash-lag effect ($M = 13.80$ ms, $SEM = 3.03$), one-sample $t(5) = 4.56$, $p = .006$.

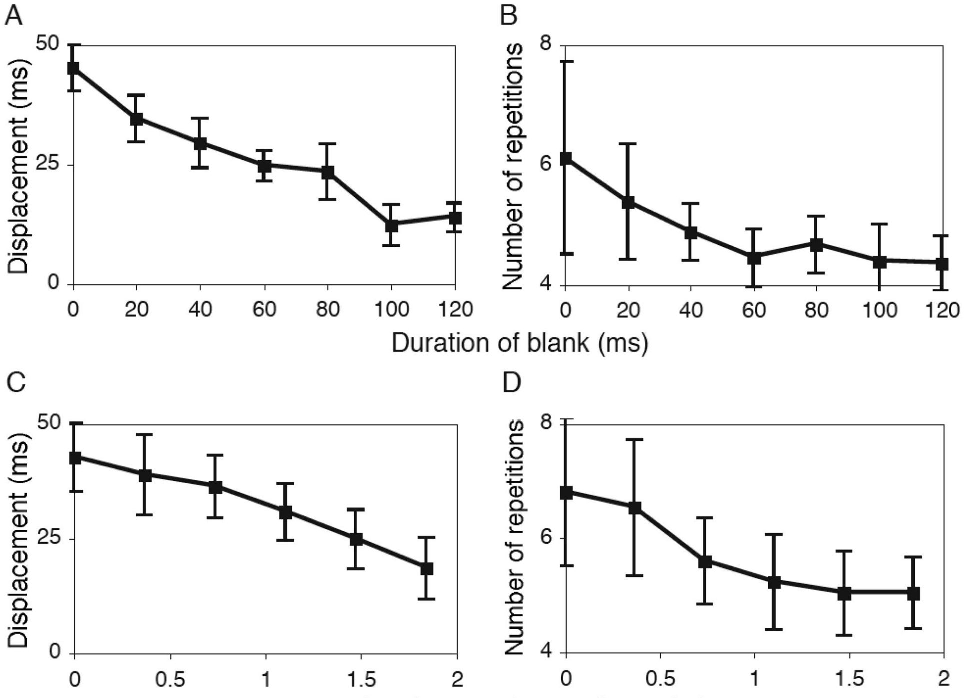

Figure 5. Panel A: Mean flash-lag effects in milliseconds as a function of blank duration in Experiment 3A. The leftmost data point (blank duration 0 ms) shows the baseline flash-lag effect that reduced as motion was interrupted for increasing durations. All error bars are standard errors of the mean. Panel B: The mean number of repetitions observers used in the flash-lag nulling task plotted against blank duration. Panel C: Mean flash-lag effects as a function of the amplitude of luminance change at the time of the flash in Experiment 3B. Panel D: Mean number of repetitions plotted against luminance change.

During the debriefing, none of the five naive observers were able to identify the way in which stimuli were manipulated across different trials. However, all observers reported that in some trials the task seemed far easier than in others. This was also reflected in the number of repetitions observers used in each condition (Figure 5B), 6.1 repetitions (*SEM* = 1.6) in the 0-blank condition, compared with 4.3 repetitions (*SEM* = 0.5) in the 120-ms-blank condition. It seems the longer the blank lasted, the easier the task got and the more confident observers were with their adjustments. However, a one-way repeated measures ANOVA could not confirm this trend, $F(6, 30) = 1.74$, $p = .147$, $\eta^2 = .258$.

Discussion

This experiment showed that the introduction of an abrupt offset into an otherwise undisturbed motion trajectory reduces the forward displacement of a moving object as measured with the flash-lag effect. Blanking the moving object for 100 ms or longer achieved a maximal reduction of the flash-lag effect. Turning the moving object off for a long period is basically equivalent to the often-cited flash-terminated flash-lag condition. However, in this experiment we did not find a total elimination of the flash-lag effect; a small but significant forward displacement for blanks of 120 ms was still measured. This effect is likely due to the fact that observers did not foveate the position of the flash, a finding that is consistent with Kanai et al. (2004), who reported a flash-lag in the flash-terminated condition for peripherally presented stimuli. In previous pilot studies, where stimuli were presented foveally and the separation between the moving object and the flashes was smaller, observers actually achieved close to perfect localization performance, that is, a total elimination of the flash-lag effect (data not presented).

Longer blanks lead to a larger reduction of the flash-lag effect. Although the transient is equally strong in all conditions, the degree to which it influences the perceived position is determined by its relative strength compared with that of the internal motion model. When after a short blank new evidence for the motion model is acquired (i.e., the moving object is registered in the predicted position) the perceived position remains closer to the forward displaced position, as in the baseline flash-lag with no transient. Varying the time until such evidence is accumulated again influences the relative strength of the motion model. In Experiment 3B we directly manipulated the strength of the transient, rather than the strength of the motion representation (see below).

Interestingly, the abrupt offset seems to make perceptual localization not only more accurate but also easier. The longer the blank, the less stimulus repetitions observers needed to be confident with their adjustment (see Figure 5B). This is consistent with the idea that the off-transient is an accurately localized retinal signal that gains influence over the perceived position as the strength of the internal motion model decreases. Kanai and colleagues (2004) attributed mislocalizations in the flash-lag effect to higher perceptual uncertainty (see also Brenner et al, 2006). Our finding here is consistent with this idea. The number of repetitions observers use in the nulling task is a simple measure of perceptual uncertainty and correlates nicely with the size of the spatial mislocalization.

It is worth noting that the abrupt re-appearance of the moving bar after the blank in this experiment does not seem to influence the perceived position at the time of the flash. It is known that the flash-initiated flash-lag condition, in which the moving object abruptly starts at the same time as the flash is shown, leads to an unabated flash-lag effect (Khurana & Nijhawan, 1995). In other words, an abrupt onset does not lead to a reduction in error or a more accurate localization, as we propose the offset does here. In fact, if the onset had played any role in our task, it would be expected that a later onset (i.e., a longer blank) would lead to a larger forward displacement, which is contrary to our results. Our findings also pose a challenge to common temporal integration models for the flash-lag effect (see the General Discussion).

Experiment 3B: Transients of Different Magnitude

Instead of varying the temporal interval for which the internal motion model was not supported by visual input, in this experiment we directly manipulated the strength of the abrupt offset. We varied the amplitude of the decrease in luminance contrast of the moving bar in the frame following the flash. Either the luminance contrast of the bar was reduced to zero in the frame following the flash (as in the previous experiment) or it was reduced to intermediate levels between full and zero contrast. In the 200 ms following the abrupt change, the luminance was quickly ramped back to its full contrast (see Figures 4C and 4D) to avoid possible influences of luminance contrast on the perceived speed of motion (Hess, 1904).

Method

Participants. Six observers (three women, three men) including Gerrit W. Maus, four of whom earlier took part in Experiment 3A, and two new naïve observers participated in this study.

Stimuli and procedure. The stimuli were now shown on a dark grey background (1.5 cdm^{-2}). Again, the white bar (71.3 cdm^{-2}) moved across the screen, and white flashes appeared for one refresh frame when the bar crossed the midline (see description of Experiment 3A). In the next refresh frame the luminance of the moving bar was abruptly reduced to the background level (luminance change of 1.84 log units) or various fractions of the luminance value for the white bar (which corresponded to luminance changes of 1.48, 1.11, 0.74, or 0.37 log units). In the 200 ms following the abrupt change, the moving bar's luminance was logarithmically increased until it matched the preflash contrast (Figures 4C and 4D). To measure the baseline flash-lag effect, we also used a no-change condition, in which the luminance of the white bar remained unchanged throughout the motion sequence.

The task was identical to the task in Experiment 3A. Observers adjusted the flashes to appear aligned with the moving bar (flash-lag nulling method). Again, each trial consisted of repeated presentations of the same stimulus, until observers were satisfied with their alignment of the flashes and the moving bar. Twelve trials of all six conditions were randomly interleaved for a total of 72 trials. A total of 3.5% of trials were excluded due to the same criteria as mentioned in Experiment 3A.

Results

Figure 5C shows the mean adjustments observers made in all conditions. Observers showed a baseline flash-lag effect (in the no-change condition) of 42.6 ms (*SEM* = 7.4 ms). A one-way repeated measures ANOVA on observers' mean adjustments revealed a significant effect of the magnitude of luminance change on perceived forward displacements, $F(5, 25) = 17.64$, $p < .001$, $\eta^2 = .779$. Linear regressions for each individual observer showed negative slopes ($M = -12.9$, $SEM = 2.0$), one-sample $t(5) = -6.41$, $p = .001$, indicating that for all observers stronger transients led to smaller forward displacements. The largest change, when the luminance was abruptly decreased to the background level, led to a reduced flash-lag effect of just 18.5 ms (*SEM* = 6.7 ms), which is significantly different from 0, one-sample $t(5) = 2.77$, $p = .039$, but much less than the baseline flash-lag.

Again, all naïve observers were unable to identify the specific manipulation of the stimuli and reported that on some trials the task was much easier to perform than on others. Figure 5D shows the number of stimulus repetitions observers used for their adjustment in each trial. A one-way repeated measures ANOVA showed a significant effect of transient magnitude on the number of repetitions, $F(5, 25) = 3.73$, $p = .012$, $\eta^2 = .427$. In the no-change condition they used 6.8 (*SEM* = 1.3) repetitions, compared with 5.0 repetitions (*SEM* = 0.6) in the condition with the largest change, indicating that a larger luminance change made the adjustments easier.

Discussion

Introducing an abrupt offset into a motion trajectory reduced the size of the flash-lag effect. Stronger transients, that is, bigger changes in luminance, led to more accurate localization of the moving bar and higher confidence of the observers in their adjustment performance, as indicated by the number of stimulus repetitions.

Contrary to the previous experiment, where we interrupted the continuous motion of the object for varying amounts of time, here the object motion never got completely disrupted. Just one frame after the abrupt decrease in the bar's luminance, it appeared brighter again and continued to ramp back to its full preflash intensity in just 200 ms. Therefore the strength of the internal motion model remained almost undiminished. Indeed, even the strongest transient—when the luminance of the bar was reduced to the background level—still led to a considerable flash-lag effect. Due to the parafoveal viewing and the fact that motion was never stopped, we did not expect a total elimination of the flash-lag effect. Our manipulation produced a similar pattern of reduction of forward displacements as in Experiment 3B. Even weak transients led to a dramatic reduction in the size of the flash-lag effect.

We hypothesized that two processes, an extrapolated internal motion model and transient retinal signals, compete to determine the perceived position of an abruptly disappearing moving object as well as that it is possible to influence the outcome of this competition by manipulating the relative strengths of these two processes. The findings of Experiments 3A and 3B provide empirical support for this idea.

General Discussion

Summary of Present Findings and Proposed Model

The findings presented in this article demonstrate crucial differences between how the visual system processes positions of abruptly disappearing objects and continuously moving objects. Experiment 1 showed that a continuously moving object is seen shifted forward in the direction of motion when compared with the position of an abruptly disappearing moving object, in a way similar to other well-known visual illusions such as the flash-lag effect (Nijhawan, 1994) and the Fröhlich effect (Fröhlich, 1923). Experiments 2A and 2B examined this finding more systematically and found this forward displacement to be robust to different directions of motion, linearly dependent on speed, and a consequence of a true forward displacement of the continuously moving object, rather than a backward displacement of the offset object.

Preliminary findings on a similar illusion have been previously reported by Palmer and Kellman (2001, 2002). In their aperture capture illusion, an occluded moving bar seen through misaligned apertures is perceptually distorted. In another version of their display (Palmer & Kellman, 2003) only one part of a bar became occluded, while the other part remained visible. This resulted in a percept equivalent to the one described in our Experiment 1. They explained the misalignment by perceptual persistence of the occluded part of the bar together with an underestimation of velocity for occluded objects. However, the stimulus used in the present experiments differs in important aspects. First, there is no occluder. The offset bar disappears abruptly, that is, it is fully presented in its last position and completely absent in the next frame. When objects become occluded, as in Palmer and Kellman's (2001, 2002, 2003) displays, their parts disappear sequentially over time, with the leading edge disappearing first and the trailing edge last. Even if observers inferred the existence of an invisible occluder in the display in Experiment 1, an explanation in terms of an underestimation of velocity of occluded parts of the bar can be ruled out. In Experiment 2A, where the two half bars moved in opposite directions, observers never had the impression of one moving bar that gets partially occluded but rather had that of two independently moving objects. Our proposed model might actually explain the findings of Palmer and Kellman (2001, 2002, 2003) at a much lower level of the visual system, without assuming any special role for object occlusion.

We proposed a two-process model to explain the current findings and previous results in the literature on the flash-lag effect and other similar illusions (Maus & Nijhawan, 2006). One process is active whenever an object is moving on a consistent, predictable trajectory. The visual system analyzes the speed and trajectory of the moving object and uses this information to predict positions of the object in the near future. This prediction is advantageous in the control of behavior, because any information about a moving object's position available to the nervous system is subject to processing and conduction delays within the retina and the visual pathway extending to the cortex. The system therefore is able to prevent a spatial lag of the perceived position of moving objects behind their physical position (Erlhagen, 2003; Nijhawan, 1994). However, if the system relied exclusively on a predictive model, abruptly disappearing objects would suffer another localization error: They would overshoot their offset position. Thus, the second process serves as a correction mechanism, similar to the mechanisms underlying backward masking and metacontrast (Breitmeyer, 1984), relying on the accurate spatial information provided by the retinal transient of the abrupt offset of the moving object. This mechanism changes the perceived position and incorporates newly acquired information about the object's disappearance into the percept. The two-process mechanism we propose is advantageous because it minimizes spatio-temporal localization errors for both continuous, easily predictable events and sudden, unpredictable events.

When two processes produce contradicting outcomes, the conflict needs to be resolved to form a coherent percept of the visual scene. In the case of abruptly disappearing objects, as presented here, two separate position representations compete for perceptual awareness: one based on extrapolated information and the other on the retinal off-transient. In most cases investigated previously, for example in the flash-terminated flash-lag display, and in the present Experiments 1 and 2, the off-transient wins this competition for perception. However, in Experiment 3 we actively manipulated the relative strengths of the two competing representations and as a result measured intermediate positions being perceived. In Experiment 3A we introduced an abrupt offset of the moving object and varied the time until it became visible again, in other words the time duration for which the support for the extrapolated model was suspended. In Experiment 3B the strength of the retinal transient was manipulated. Both manipulations led to reductions in the measured size of the flash-lag effect, with stronger transients or longer disruption of motion leading to a smaller forward displacement. Both Experiments 2 and 3 also showed that position judgments based on visual off-transients are less “noisy”—that is, they lead to steeper psychometric functions and more confident judgments from observers.

Implications for Theories of the Flash-Lag Effect and the Localization of Moving Objects

Several theories attempting to explain the flash-lag findings have been proposed; some of them aim to be general accounts of how moving objects are localized by the visual system (for reviews, see Krekelberg & Lappe, 2001; Nijhawan, 2002). Several researchers have stated that the forward displacement of the moving object in the flash-lag effect can be explained by differential latencies for moving and flashed objects (Purushothaman et al., 1998; Whitney & Cavanagh, 2000; Whitney & Murakami, 1998). Others have suggested that the positions of a moving object are sampled over an extended time window and then integrated to yield the perceived position, thereby explaining the mismatch in position between moving and flashed objects (Brenner et al, 2006; Eagleman & Sejnowski, 2000; Krekelberg & Lappe, 2000; Roulston et al, 2006). Finally, some researchers claim that in the flash-lag effect—and in general—the perceived position of moving objects is spatially extrapolated resulting in a forward shift, possibly to overcome neural processing delays in the visual pathway (Berry, Brivanlou, Jordan, & Meister, 1999; Kanai et al, 2004; Nijhawan, 1994; Sheth, Nijhawan, & Shimojo, 2000). The present study has important implications for aforementioned theories.

Differential latencies. The differential latency account assumes that moving objects are processed faster than are flashes. In a flash-lag paradigm, by the time the flash is being processed the moving object has moved on, therefore leading to the spatial misalignment. On this view the flash-lag effect is a purely temporal effect, that is, any spatial misalignment results from a temporal processing advantage for the moving object. When the moving object abruptly disappears, it never overshoots but is perceived in its veridical position, like the flash.[1] In Experiment 1, we employed two aligned objects, moving side by side at the same speed. They should be processed with the same latency. Nevertheless, when one of them abruptly disappeared, it seemed to lag behind the continuously moving object. The differential latency account, at least in its simplest version, does not readily explain this finding.

A special role for an abrupt offset of a moving object, such as proposed in this article, is usually not assumed in the differential latency account. However, the transients of the flash and the transient of an abrupt offset are physiologically similar. If the moving object were perceived to disappear only when the slower transient signal is registered at some cortical level, this would offer an explanation for the present findings in the framework of differential latencies. It remains unclear, however, what is perceived in the time between the motion signal being registered at a particular retinotopic position and the transient signal later being registered at the same position.

In Experiment 3A we measured a baseline flash-lag effect of 45 ms, that is, on the differential latency account the difference in the latencies of the flash and the moving object in this particular stimulus display should be approximately 45 ms. Presumably this would also be the additional delay the offset transient undergoes. When the motion was disrupted briefly for just 20 ms, the flash-lag effect was reduced, although by the time the flash was registered the motion should again be processed normally as in the baseline flash-lag effect. Similarly to the present proposal, the differential latency account would have to resort to interactions between separate representations for the moving object and the transient to explain these findings. In this case differential latency as an explanation for the flash-lag phenomenon loses its appeal of simplicity. However, for the case of continuously moving objects the proposals of faster processing or spatial extrapolation remain indistinguishable and might well share common underlying neural mechanisms (see below).

Temporal integration. Temporal integration theories state that all positions an object occupies over a certain time window (typically about 100 ms) are integrated and averaged to yield the perceived position of the object. To account for the flash-lag effect it has to be additionally assumed that this time window extends into the future, or rather that the outcome of such an averaging process is then “postdicted,” that is, the percept is assigned back in time to an earlier moment (Eagleman & Sejnowski, 2000).

Temporal integration is incompatible with the findings of Experiment 3A. Consider Figure 4A: To explain the baseline flash-lag effect the time window from which positions are sampled to determine the perceived position at t_0 (the time of the flash) has to include mainly positions after the flash (in the figure to the right of the flash). As the duration of the blank is increased, fewer positions in the immediate vicinity of the flash contribute to the average, shifting the output of the integration mechanism to the right. This would predict an increase in the size of the flash-lag effect, which is contrary to what we found. Only for long blanks, when the duration of the blank is longer than the duration of the integration window, does the temporal integration account predict

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[1] The differential latency account predicts that in a flash-terminated flash-lag display the moving object should be seen to disappear before the flash is perceived. However, temporal order judgment tasks have not revealed a generally shorter latency for moving objects (Nijhawan, Watanabe, Khurana, & Shimojo, 2004).

accurate localization. The same reasoning holds true for an integration window that is centered around the time of the flash but weighted toward more recently sampled positions (Roulston et al, 2006).

Temporal integration of some manner is certainly also necessary in our proposed two-process model. Motion is defined as change of position over time; thus, in order to initialize the extrapolation process, positions need to be sampled over some time interval. This interval, however, can be remarkably short (Nijhawan, 2008). Once the system has identified a coherently moving object, it relies on the predicted internal model to provide an estimated position at a certain point in time. Abrupt events, such as sudden offsets, can however override this position estimate.

Motion extrapolation. One feature that distinguishes the extrapolation account of the flash-lag phenomenon from the two previously discussed accounts is that it involves a spatial shift of the moving object's position, rather than an underlying temporal effect. This spatial shift is dependent on the previous motion of the object, which conveys the information necessary to compute the current position of the object, despite the fact that the information is out of date due to delays in earlier visual pathways. Motion extrapolation is, however, prone to errors when sudden events, like the offset of the moving object, contradict the predicted information. These predicted errors are not apparent in most cases (Eagleman & Sejnowski, 2000; Kerzel, 2000). In this article, we show how the visual system uses a correction mechanism to minimize such errors.

Prediction Versus Postdiction

Postdiction originally maintained that the flash resets motion integration (temporal averaging), so that the perceived position of the moving object is determined by the average of positions after the flash. This average position then gets *postdicted*, that is, reassigned, to the time of the flash (Eagleman & Sejnowski, 2000). Apart from experimental findings on the standard flash-lag paradigm, this account assumes that moving objects are perceived to trail their physical position. Thus, this account also predicts a speeding up of the moving object at the time of the flash to get ahead of this position, which has never been observed (Nijhawan, 2002). In a more recent account Eagleman and Sejnowski (2007) claimed that motion signals from after the flash bias the position of the moving object toward the direction of motion, a proposal more similar to the original motion extrapolation account (Nijhawan, 1994). The crucial difference in these two positions now is whether the spatial shift depends on past motion signals, so it is in fact a prediction, or whether it depends on future motion signals, in other words it is a postdictive determination of the perceived position.

It should be noted here that there are no a priori reasons why one or the other possibility should be preferred or why they should be mutually exclusive. Some of the experimental data on the flash-terminated flash-lag seem to favor a purely postdictive account. While it might be tempting to apply Occam's Razor and accept a postdictive account as the simpler model, even the newer account (Eagleman & Sejnowski, 2007) has one major disadvantage: It states that our perceptual awareness of the world always lags temporally behind the physical events giving rise to these perceptions.[2] In a purely postdictive account, the position of a moving object can be perceived as spatially correct but temporally incorrect—at a time when the physical object is actually occupying a different position. This is problematic when we consider that the ultimate goal of perceiving the environment is to enable an organism to interact with its surroundings. For dynamic interactions with moving objects, a temporal localization error is equally disadvantageous as a spatial localization error. An organism will certainly benefit from being able to anticipate changes of position of behaviorally relevant stimuli at the earliest possible processing stage. Further, retrospective computations of position are costly. Visual information of an extended time period would need to be held in some kind of sensory store and subsequently integrated, whereas an on-the-fly extrapolation of incoming data can in principle be implemented by a process as simple as a linear filter (Grush, 2005).

The two-process account outlined here, involving both prediction and retroactive correction, is advantageous because it minimizes computational cost as well as spatial and temporal localization errors in the best way possible, depending on the information available at any given time. If an object is moving continuously and predictably, an organism will benefit from using some kind of prediction. If, however, sudden, unpredictable events make this prediction inaccurate, retroactive mechanisms correct what is now faulty perceptual content (Grush, 2005; Maus & Nijhawan, 2006).

Possible Neural Mechanisms

The model we propose consists of two separate processes: (a) an extrapolation process shifting the position of a coherently moving object forward in the direction of motion and (b) a retroactive correction mechanism that is based on transient retinal signals. There is substantial evidence in the literature that both these processes exist and are at work in several phenomena of visual processing.

Extrapolation mechanism for the forward shift of moving objects. Several studies have shown that lateral interactions between neurons in retinotopic maps can cause an asymmetric spread of neural activity in response to moving visual stimuli, as early as in retinal ganglion cells (Berry et al, 1999), but also in retinotopic cortical maps (Jancke et al, 2004; Sundberg, Fallah, & Reynolds, 2006; Whitney et al, 2003). In effect, these interactions cause the peak of neural activity to be at the leading edge or even ahead of the stimulus in retinotopic neural space. Additionally, it is well known that in the wake of a moving stimulus neurons are inhibited, a process that arguably contributes to the de-blurring of a moving stimulus (Burr, 1980). These local excitatory and inhibitory interactions have been proposed as the underlying mechanisms of the flash-lag effect, either by facilitating shorter processing latencies in the path of moving objects (Whitney & Murakami, 1998) or by biasing localization forward in the direction of motion (Kanai et al, 2004; Kirschfeld & Kammer, 1999). Computational simulations have shown that traveling waves of activity in a map of neurons can be self-sustained to some extent (Erlhagen, 2003), that is they can keep moving even in the absence of continued bottom-up input. Such a self-sustained wave of activity could be the underlying mechanism of an internal model for object motion. Feedback

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[2] This is nicely demonstrated in Figure 2 of Rao, Eagleman, and Sejnowski (2001), in which subjective time is viewed as an entirely different entity to physical time and therefore plotted on a different axis.

connections from an area maintaining such a model can then shift the neural peak activity in another retinotopic map even further in the direction of motion.

The role of cortical feedback in perception has recently received much attention (Lamme & Roelfsema, 2000). For example, several studies using transcranial magnetic stimulation have shown that feedback from motion-sensitive areas to earlier retinotopic maps seems to be pivotal for the perception of motion (Pascual-Leone & Walsh, 2001; Sack, Kohler, Linden, Goebel, & Muckli, 2006; Silvanto, Lavie, & Walsh, 2005). Even thalamic neural activity in response to moving stimuli, supposedly forming the bottom-up input to the visual cortex, is highly shaped by cortical feedback (Sillito, Cudeiro, & Jones, 2006; Sillito & Jones, 2002). It is reasonable to assume that these feedback connections are also active when stimuli involving moving objects (such as those used in the present experiments) are presented. The role of feedback in causing the flash-lag effect and related forward displacement illusions remains to be examined in more detail.

Retroactive correction based on transients. The second ingredient in the present model is a mechanism that corrects the forward shift, when a bottom-up transient signal from the retina indicates that the moving object is no longer moving but has actually disappeared in a certain position. This process works retroactively, that is, it changes the percept of an earlier time point, although the physical process underlying this percept occurs later, namely when the transient signal is registered.

Similar retroactive changes of percepts are apparent in a number of visual phenomena (Dennett & Kinsbourne, 1995; Grush, 2005), most prominent of which is backward masking (Alpern, 1953; Breitmeyer, 1984), in which a visual target is rendered invisible by a subsequently presented mask. In masking, the transients of both the onset and offset of the mask elicit lateral inhibition that renders the target less visible or invisible (Macknik et al., 2000). Lateral inhibition, elicited by the offset of the moving object, might suppress the extrapolated neural representation. Figure 6 schematically shows the neural activity in a retinotopic map in response to the abrupt offset of a moving object. The grey dashed curve represents the traveling wave of activity in response to a moving object (cp. Kanai et al, 2004; Kirschfeld & Kammer, 1999). Its peak is shifted forward by the mechanisms suggested above. Trailing behind the peak is a wake of inhibitory activity. The black dashed curve represents the transient off-signal from the sudden offset of the moving object, accompanied by lateral inhibition (Macknik et al, 2000). The peak of the transient is accurately localized and less spread out than the traveling wave. Assuming a linear interaction of these two signals, the resulting summed activity pattern is displayed by the solid black line. The lateral inhibition of the transient leads to an attenuation of the traveling wave's peak. The global maximum peak of the resulting pattern is accurately localized near the true offset position of the stimulus. The trailing inhibitory wake might in fact lead to a small undershoot of the disappearing object, as we experimentally found in

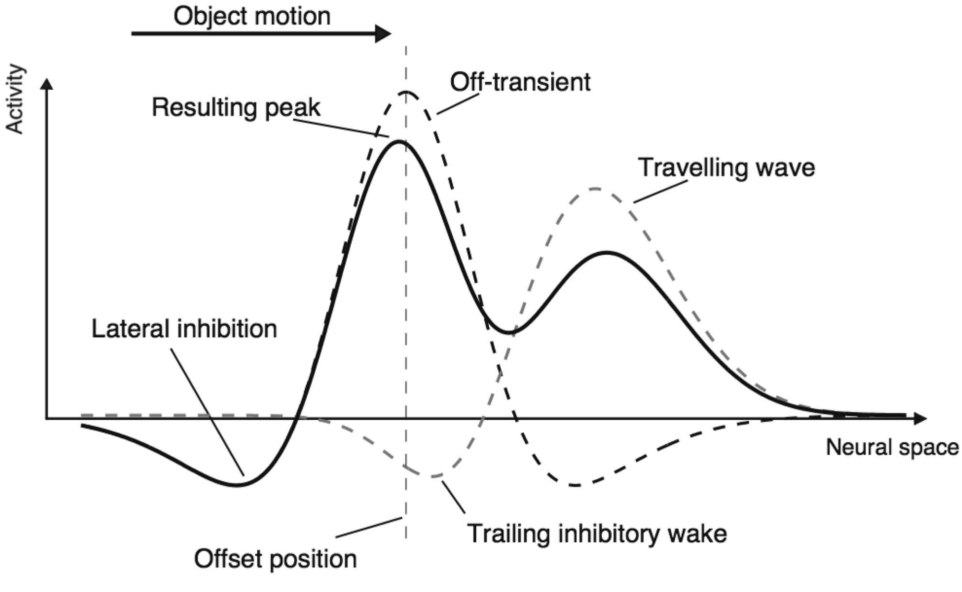

Figure 6. Schematic illustration of the pattern of neural activity in a cortical retinotopic map in response to the abrupt offset of a moving object. The graph depicts a snapshot of neural activity at the time when the off-transient has been fully registered by neurons at this site. The abscissa denotes space in the retinotopic map, the ordinate neural activity. Object motion is indicated by the large arrow; the abrupt offset occurs at the dashed vertical line. The grey dashed line depicts a traveling wave of activity (Erlhagen, 2003), shifted forward from the object's position in the direction of motion to compensate for temporal delays in neural pathways. Neurons in the wake of this wave are being inhibited to reduce motion smear (Burr, 1980; Kirschfeld & Kammer, 1999). The black dashed line depicts the neural response to the transient off-signal. It is centered around the true offset position and features symmetric lateral inhibition. The black solid line is the resulting neural activity produced by adding the two activity patterns. The peak of the traveling wave is attenuated, rendering the resulting maximum close to the true offset position. Due to the inhibitory wake, the peak could actually be shifted slightly in the opposite direction of motion.

Experiment 2B. However, physiological evidence (Borg-Graham, Monier, & Fregnac, 1998; Shu, Hasenstaub, & McCormick, 2003) and computational considerations (Gutkin, Laing, Colby, Chow, & Ermentrout, 2001) give reasons to believe that the transient's inhibitory effects are nonlinear, resulting in a shunting of the self-sustained activity of the traveling wave. In this case, the resulting activity pattern would feature a more complete suppression of the traveling wave and directly reflect the perceptual outcome of an accurately perceived offset position. Manipulating the relative strengths of the two signals (the dashed curves in Figure 6) might lead to the perception of intermediate positions, as found in Experiment 3.

Limitations and Future Directions

The theory presented in this article has one important limitation: The experiments focused on abrupt offsets. Abruptly stopping objects that remain visible or abrupt changes of direction have similar effects on the localization of moving objects (Eagleman & Sejnowski, 2000; Whitney & Murakami, 1998). However, it is known that changes in the direction or speed of a moving stimulus elicit strong electrophysiological responses in the visual system stemming from motion-sensitive areas (Ahlfors et al, 1999; Clarke, 1972; Pazo-Alvarez, Amenedo, & Cadaveira, 2004). Moreover, it has recently been shown that the abrupt reversal of direction of a moving object can even elicit a strong synchronized peak of activity in retinal ganglion cells (Schwartz, Taylor, Fisher, Harris, & Berry, 2007). These "change transients" can probably elicit similar mechanisms as an off-transient does. This proposal remains to be tested in further detail.

A strong argument for a predictive mechanism for localization of moving objects can be made from findings where moving objects are seen in unstimulated retinotopic space after disappearing without providing a transient for correction of position (Maus & Nijhawan, 2006). We recently investigated the final perceived position of a moving object disappearing in the blind spot and found that the object is visible well into the blind area (Maus & Nijhawan, in press). This finding can be explained only by a spatial shift of perceived position based on past motion signals, as there is no bottom-up position (or motion) information from within the retinal blind spot.

Our proposal that off-transients play an active role in the localization of final positions of moving objects entails a special involvement of the M-pathway. This could be further investigated by using isoluminant stimuli. Additionally, the advent of more advanced techniques, for example, neuro-navigated transcranial magnetic stimulation (Sack et al, 2006), will make direct study of the involvement of cortical feedback from motion-sensitive areas to earlier retinotopic maps possible.

Conclusions

Abrupt offsets of moving objects have profound effects on their localization by the visual system. In a display where two identical aligned objects move and one of them disappears abruptly, the offset is perceived in its veridical position, whereas the object in continuous motion is perceived displaced forward. We propose that the forward shift can be explained by an internal model entailing predicted positions of coherently moving objects and a correction mechanism for the forward shift based on the retinal transient when the object disappears. When the relative strengths of these two mechanisms are manipulated, intermediate positions are perceived. Such a two-process model of object motion perception is advantageous for an organism because it maximally reduces spatio-temporal localization errors of the visual system.

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Received October 20, 2007
Revision received January 31, 2008
Accepted March 10, 2008 ■