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Fröhlich Effect and Delays of Visual Attention

Nika Adamian
Laboratoire Psychologie de la Perception

Patrick Cavanagh
Dartmouth College

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Nika Adamian
Laboratoire Psychologie de la Perception, Université Paris Descartes, Centre Biomédical des Saints Pères, Paris, France

Patrick Cavanagh
Laboratoire Psychologie de la Perception, Université Paris Descartes, Centre Biomédical des Saints Pères, Paris, France
Department of Psychological and Brain Sciences, Dartmouth College, Hanover, New Hampshire, USA

In the Fröhlich effect, the initial position of an object that suddenly appears in motion is perceived as being shifted in the direction of its motion. Here we establish that this shift is not an obligatory consequence of motion, but it is driven by focused attention. In Experiment 1 using different cueing conditions, we found that invalid cues produced larger perceptual shifts, although the Fröhlich effect was still present for valid and neutral cues. These results support Müsseler and Aschersleben's (1998) proposal that the Fröhlich effect is the result of the time it takes to shift focal attention to the moving stimulus. In Experiment 2 we found that the Fröhlich effect increased when the valid cue arrived more than 100 ms after the start of motion, suggesting again that a delay in attention's arrival shifted the location of the perceived motion onset. In Experiment 3 we compare the motion-induced shifts when the subjects attended to a set of moving stimuli as a group and when they attended to an orientation singleton. We showed that Fröhlich effect was only present when the target was individuated and disappeared when the stimulus was perceived globally. We conclude that the Fröhlich effect is a predictive spatial shift produced and modulated by focal attention.

Introduction

Localizing objects in space is one of the central functions of the visual system. When an observer or a target is moving, the motion of the eye or the object can be taken into account to compute the current object locations. Indeed, it has been shown many times that visual motion can strongly influence the perceived position of an object. For example, a stationary patch containing moving texture (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990), a flash presented on (Cavanagh & Anstis, 2013) or next to (Whitney & Cavanagh, 2000a) a moving texture, and even the onset and offset positions of the moving targets (Freyd & Finke, 1984; Fröhlich, 1923) are perceived as shifted in the direction of motion. In this paper we address attention's role in producing these motion-induced position shifts.

One of the most basic and longest known motion-induced position shifts—a shift of the perceived onset position of a moving stimulus—is now referred to as the Fröhlich effect (Fröhlich, 1923). The original finding showed that a strip of light travelling across a screen is not seen first at the edge of the screen, but farther into it. Over the decades a number of explanations for this effect have been presented, including attention delay (Müsseler & Aschersleben, 1998) and metacontrast masking (Kirschfeld & Kammer, 1999; see Kerzel, 2010, for a review). The attention delay explanation claims that the Fröhlich effect results from the lack of conscious representation of the stimulus before attention arrives so that any delay in shifting attention to the moving stimulus creates a displacement in its perceived starting location. To test this, Müsseler and Aschersleben cued one of two locations briefly (120 ms) before motion onset and then presented a moving stimulus at only one of the locations. A valid cue decreased the Fröhlich effect compared to an invalid cue and a no-cue condition. Note that Müsseler and Aschersleben (1998) do not assume that the invalidly cued location is unattended, but instead that attention is delayed in getting there as it starts first at the cue location and then switches to the uncued location. Their result was therefore in line with attention delay explanation. Additionally, Whitney and Cavanagh (2000b) showed that when a static object is

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presented for 2500 ms, then removed for 30 ms and immediately presented in motion, the "invisible" part of its trajectory is significantly reduced. Both these results suggest that if attention is already at the position where the motion is about to start, there is less motion-induced position shift.

Nevertheless, some studies of motion-induced position shifts show a different effect: smaller or no illusion in the case where attention is not focused either initially or eventually on individual moving stimuli. For instance, Linares and López-Moliner (2007) tested mislocalizations of moving dots relative to static ones (flash lag) when attention was directed to the global shape created by a field of many dot pairs. In each dot pair of the 400 that were presented, one dot was in motion and the other one was static and flashed briefly. When their participants attended to the global shape created by all the dot pairs, they did not report any illusory misalignment. Cavanagh and Anstis (2013) reported a similar loss of motion-induced position shift with multiple stimuli. When observers had to judge the length of the trajectory of a single moving dot, they consistently underestimated it. However, when this same judgment was made about multiple, asynchronously moving dots that could not be individually tracked, no such underestimation happened. Both of these studies compared focused attention to an individual item to attention distributed across a group of items and both reported improved localization performance (decreased illusion) with distributed attention. These results suggest that the effect of motion on position is not obligatory but arises only when attention is focused on individual trajectories. This would seem to be at odds with the results of the cueing experiment where a longer delay in attention's arrival at the motion onset position leads to more motion-induced position shift. With global attention to a set of trajectories, attention never actually focuses on any individual motion path, and one prediction might therefore be that a very large position shift should be seen in this case, rather than the absence of any shift that is observed.

Given these apparently contradictory results, the question of whether and how attention modulates the localization of motion onset remains open. The current paper attempts to reconcile the two accounts by exploring how the Fröhlich effect varies as a function of attentional delay and as a function of group versus individual attention using the same stimuli for both manipulations. In Experiment 1 we replicate the cueing results of Müsseler and Aschersleben (1998), showing that invalid cues produce a stronger Fröhlich effect, supporting the attention delay hypothesis. In Experiment 2 we vary the delay between the cue and the motion onset, showing a larger Fröhlich effect for cues arriving more than 100 ms after the motion onset. Finally, in Experiment 3 we test multiple Fröhlich stimuli and show that with attention to the group of stimuli, no motion-induced position shift is seen whereas, with attention to one of the stimuli, the effect is present.

Based on our results, we suggest that the shift in the perceived onset of a moving stimulus is an active process that is engaged only when attention is directed to an individual target in motion. We will link this to the corrections in position necessary whenever eye movements must be made to a moving stimulus. We call this the "saccade intercept hypothesis" where every attended target is naturally a potential saccade target, linking covert attention to overt attention. As a practical detail, any eye movement to a moving target must compensate for the movement of the target after the saccade has been programmed as the target keeps moving during the saccade. So its position representation must be extrapolated ahead along the path of movement. We assume that this extrapolation along the motion path is made for each tracked target whether or not a saccade is eventually made to it. Previous studies of simple moving targets have shown that the perceived location and saccades to the target both show this extrapolation effect (Etchells, Benton, Ludwig, & Gilchrist, 2010; Khurana & Nijhawan, 1995; Nijhawan, 1994).

This predictive shift extrapolates the perceived location to match the position to which the saccade must be targeted in order to accurately intercept the moving object. We assume that this extrapolation is the origin of the Fröhlich effect. When attention is delayed in reaching the target to begin tracking it, additional extrapolation is required and the Fröhlich effect increases. In contrast, when attention is directed to a set of moving stimuli, none of the trajectories is attentively tracked, none of them can be individual saccade targets without further processing, and the predictive shift is not engaged. These suggestions and the evidence behind them are presented in more detail in the General discussion section.

Experiment 1

Müsseler and Aschersleben (1998) showed that delay of arrival of endogenous attention at the location of the motion shifted the visible onset of the motion ahead along its path. Here we extend this finding using the stimulus based on the one used by Kirschfeld and Kammer (1999), namely, a rotating rod inside a circular placeholder. We arranged eight placeholders in a circle, as shown in Figure 1, which allowed us to cue the placeholder where the stimulus was about to appear (by briefly changing the color of the ring) without

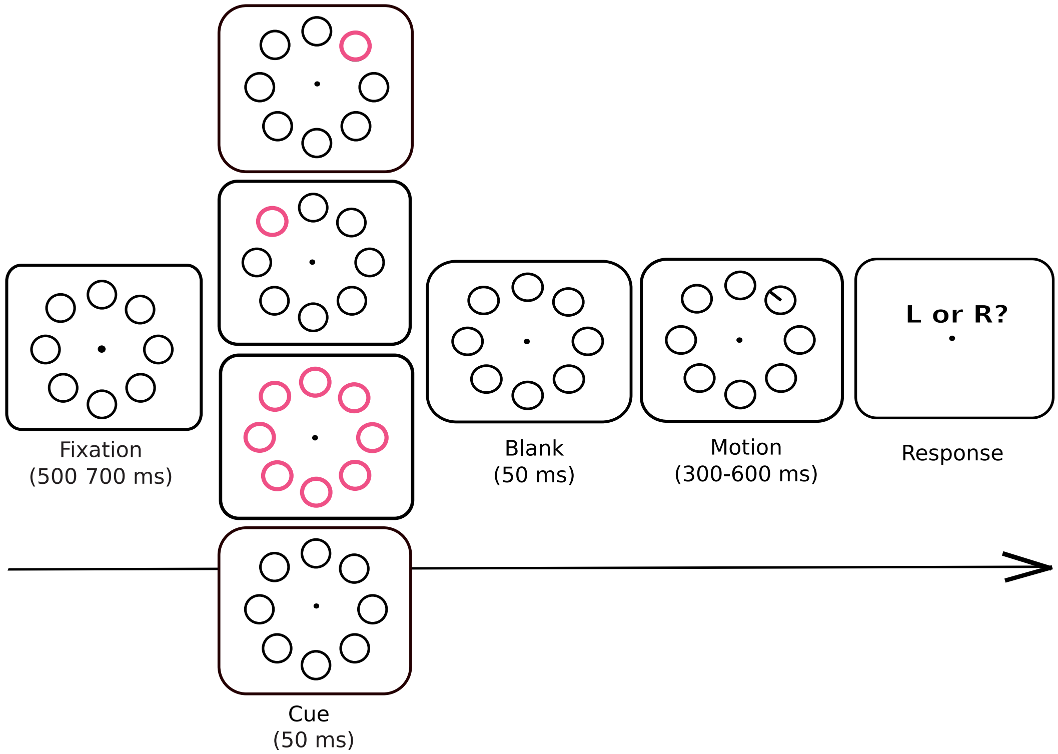

Figure 1. Experiment 1 trial schematic. Each trial started with a jittered fixation period, followed by a cue (a brief change in color of one or more placeholders). The cue could be predictive of a future target location (valid cue, 75% trials) or invalid (25% trials). In the separate blocks, the cue could be uninformative (all placeholders cued) or absent (no change in any of the placeholders). Following a 50 ms blanking period, one rotating target was presented, its onset angle varied according to the method of constant stimuli. The target was on until it reached the lower vertical radius of the placeholder; after that it disappeared, and subjects were asked to judge the onset angle of the target. Stimuli are not drawn to scale; in the real experiment the contrast was reversed (white stimuli on black background).

cueing the onset angle itself. Independent control over the to-be-reported feature (onset angle) and the direction of cueing is a major advantage of this stimulus. We tested the onset localization accuracy with valid, invalid and uninformative cues. In line with the attention-shifting explanation we predicted that invalid cues would yield larger localization errors than valid and neutral cues.

Method

Participants

Eight healthy adults took part in the experiment (three male, five female; mean age = 26.2 years, *SD* = 2.4, range = 22–34), including one author (S3). Two subjects (S3 and S5) were experienced psychophysical observers.

A power analysis was carried out in order to determine the sample size we used for the experiments. On the basis of the mean effect size (in the attentional manipulation) from the study of Müsseler and Aschersleben (1998) and our own pilot data ($\eta 2 = 0.5$) a minimal sample size of four is required to obtain statistical power of 0.95 in a within-subject ANOVA with four levels of dependent variable. However, since we also planned to run pairwise comparisons of conditions, we chose a sample size of eight, which allowed us to detect the expected effect (dz = 1.6) in a two-tailed *t* test with the power of 0.95.

All participants in this and following experiments reported normal or corrected-to-normal vision. All participants gave informed consent in writing prior to participation, and the protocols for the study were approved by the Université Paris Descartes Review Board, CERES, in accordance with French regulations and the Declaration of Helsinki. They were compensated 10€ per hour for their time.

Stimuli

In all the experiments, stimuli were displayed on a gamma-corrected LaCIE Electron monitor (100 Hz, 1024 × 768 resolution) controlled by a Mac Pro running MATLAB 7.1 (The MathWorks, Inc.) using Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Head position was held constant using a chin rest and a forehead bar at a viewing distance of 57 cm.

Experiments were conducted in a darkened room. On each trial participants fixated a small point in the middle of the screen filled with black background (CIE Yxy 2.3 cd/m^2, 0.2, 0.19), and covertly monitored eight white circles (placeholders) each subtending 5° of visual angle evenly distributed around the fixation point at an eccentricity of 8° (CIE Yxy 75.6 cd/m^2, 0.28, 0.30). After a random delay (500–700 ms) either none, one, or all placeholders briefly (for 50 ms) changed color from white to pink (CIE Yxy 13.0 cd/m^2, 0.35, 0.22). After a 50 ms blank period, a target—a sector covering 1° rotation—appeared inside one of the placeholders and rotated clockwise. The starting position of the target varied from −60° to 60° relative to the upper vertical radius of the placeholder, and the target disappeared once it reached the lower vertical radius. With the rotation speed of 0.9 revolutions per second, the average target presentation time was 450 ms. A response screen appeared immediately after target offset. Participants indicated whether they saw the target appearing to the left or to the right of the upper vertical (regardless of the placeholder) by choosing one of two response keys on the standard keyboard.

Procedure

We tested four conditions—Valid Cue, Invalid Cue, All Cued, and None Cued. All Cued and None Cued conditions were presented as separate experimental blocks, while the trials with Valid and Invalid Cues were presented in a randomly permuted order as one block. The trial sequence is shown in Figure 1. During the Valid/Invalid cueing block, only one placeholder was cued on a given trial. In 75% of the trials the cue was valid, that is, the target subsequently appeared in the cued placeholder. In 25% of the trials the cue was invalid, and the target appeared in one of the seven uncued placeholders. In All Cued condition all eight placeholders were simultaneously cued on each trial, followed by only one target. In None Cued condition no cues were presented. Given that the initial fixation period was jittered (500–600 ms), our None Cued condition represented the situation when neither location nor timing of the motion onset was cued. It is important to note that the cues only specified information about the location of the target, not about its onset angle.

For all conditions the target position (one of the eight placeholders) and the onset angle (−60° to +60° off the vertical in 20° increments) were counterbalanced within blocks. Following a two-alternative forced choice (2AFC) method of constant stimuli, observers were asked to judge whether the target appeared to the left or to the right of the upper vertical radius, regardless of the position of the target on the screen. Conditions were presented in separate blocks within one testing session; the order of the blocks was randomized between subjects.

In total, participants ran 280 trials per condition for the Invalid Cue, All Cued, and None Cued conditions, and 840 trials for Valid Cue condition. Participants were encouraged to take short breaks between the blocks and every 40 trials.

Results

The perceptual onset shift (Fröhlich effect) was measured individually for each condition, resulting in four estimates: (a) Valid Cue, (b) Invalid Cue, (c) All Cued, and (d) None Cued. Participant responses as a function of onset angle were fitted with logistic functions using *quickpsy* package for R (Linares & López-Moliner, 2016), and points of subjective equality (PSEs) were calculated for each condition. Here we assume that PSE reflects the onset angle that is perceived as vertical (however, see Weiß & Scharlau, 2011, for a discussion of whether PSEs are an accurate measure of temporally uncertain percepts).

Figure 2A shows individual data from one observer. All but one of the eight observers demonstrated the same pattern of results. If attention shifts are a part of the mechanism generating Fröhlich effect, the localization error should be larger (PSE will be shifted further away from zero) in the Invalid Cue condition compared to the Valid Cue condition and baseline conditions (All Cued and None Cued), and/or smaller (PSE closer to the zero) in the Valid Cue condition compared to the baseline.

As shown on the Figure 2B, the "Invalid Cue" condition yielded the largest localization shift. A one-way, repeated-measures ANOVA revealed a significant difference between conditions, $F(3, 21) = 9.54$, $p < 0.001$, $\eta^2 = 0.58$. Posthoc pairwise comparisons confirmed that invalid cues resulted in larger Fröhlich effect compared to valid cues, and to "All Cued" (but not "None Cued") baseline conditions ($p = 0.009$, $p = 0.007$ and $p = 0.65$ respectively, with Bonferroni corrections). The magnitude of shift in the Valid Cued condition did not differ significantly from either of the baselines ($p = 0.72$, $p = 0.99$ for "None Cued" and "All Cued" respectively); however, it did differ significantly from zero ($M = -13.94$, $t = -3.65$, $p < 0.001$). These findings replicate the original Müsseler and Aschersleben (1998) results, providing additional information regarding the source of the attentional effect. Taking the uninformative cue ("All Cued" condition) as baseline, we confirm that it is the cost of the invalid cue rather than the benefit of the valid cue that drives the observed difference. Additionally, the "None Cued" condition demonstrates that temporal predictability of motion onset is an important factor in localization

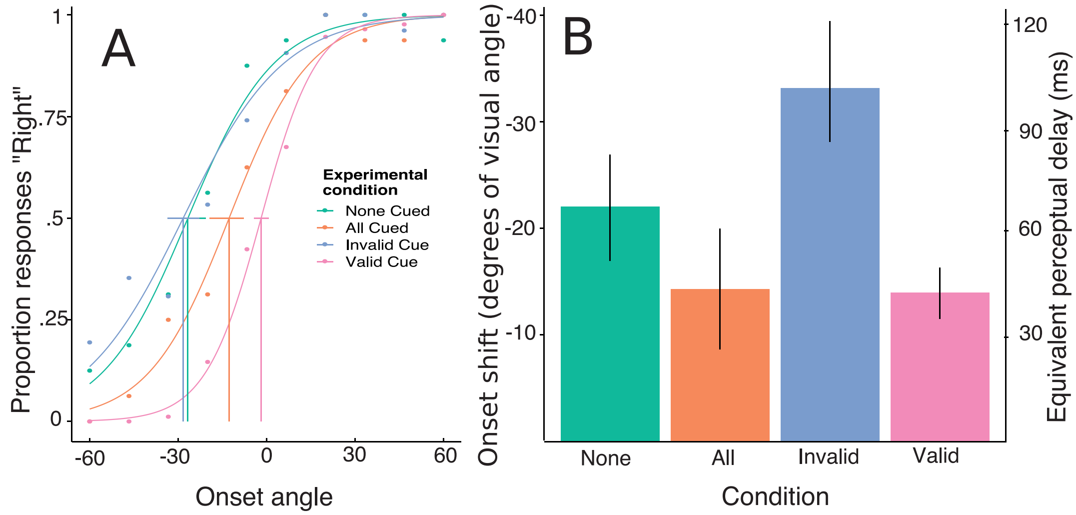

Figure 2. Results of Experiment 1. Panel A shows example Fröhlich effect measurement data from one subject; Panel B shows Fröhlich effect sizes for all conditions ($n = 8$). The shift (error) in degrees is the distance travelled by the target at the speed of 0.9 revolutions per second. Error bars on both panels represent 95% CIs.

accuracy—when the start of the trial is not well defined temporally, localization is shifted. However, even in the Valid Cue condition, Fröhlich effect was still present.

Discussion

We find that invalid cues increase the magnitude of the Fröhlich effect compared to the neutral (All Cued) condition. We reproduced the attentional effect first reported by Müsseler and Aschersleben (1998) in a paradigm that allowed cueing of spatial location (placeholder) but not the exact representation (onset angle) of the upcoming stimulus.

Alongside the cue-to-baseline comparisons, we replicated another previously reported finding. Although reduced by the cueing manipulation, the Fröhlich effect was not eliminated in any of the conditions. Even a validly cued target onset was perceived as shifted by about 14° of rotation (equal to a perceptual delay of 35 ms). If the delay of attention's arrival is the cause of the shift in the moving target's onset, our result suggests that this delay is longer than 100 ms (the cue-target stimulus onset asynchrony, SOA, which we used). Since our placeholder cue only indicates the region of the moving stimulus but not its actual start position, there may be a small additional delay as attention moves in from the overall region to the specific start location. As explained in the Introduction, we assume that the critical delay in producing the Fröhlich effect is not just the delay of attention in arriving at the target but also the time a saccade would then need to land on the target, if one were executed. This extra delay to compensate for (potential) saccade programming is in addition to any attentional delay in selecting the target and may be part of the explanation of the residual Fröhlich effects when the target is already attended. To examine the time course of attention-modulated position shifts, we next manipulate the timing of attention shifts by the means of different cue-to-motion onset intervals. According to the strict attention delay hypothesis, the later attention arrives, the larger the portion of the trajectory that will be omitted.

Experiment 2

In Experiment 2 we measured the Fröhlich effect as a function of cue to motion onset SOA. Having established in Experiment 1 that invalid cues increase the shift in localization, we now explore whether this effect is linearly associated with attentional delay using only validly cued targets. We manipulated cue-target SOAs such that the cues could appear both before (precues) and after (postcues) the target onset. If the Fröhlich effect is the result of the delay in attention reaching the cued moving stimulus, it should also increase with the additional cue-motion delay, now for the validly cued target.

Method

Participants

Nine healthy adults took part in the experiment (two male, seven female; mean age = 23.9 years, $SD = 2.36$, range 18–30). Three subjects (S1, S3, and S4) were experienced psychophysical observers, but were naive

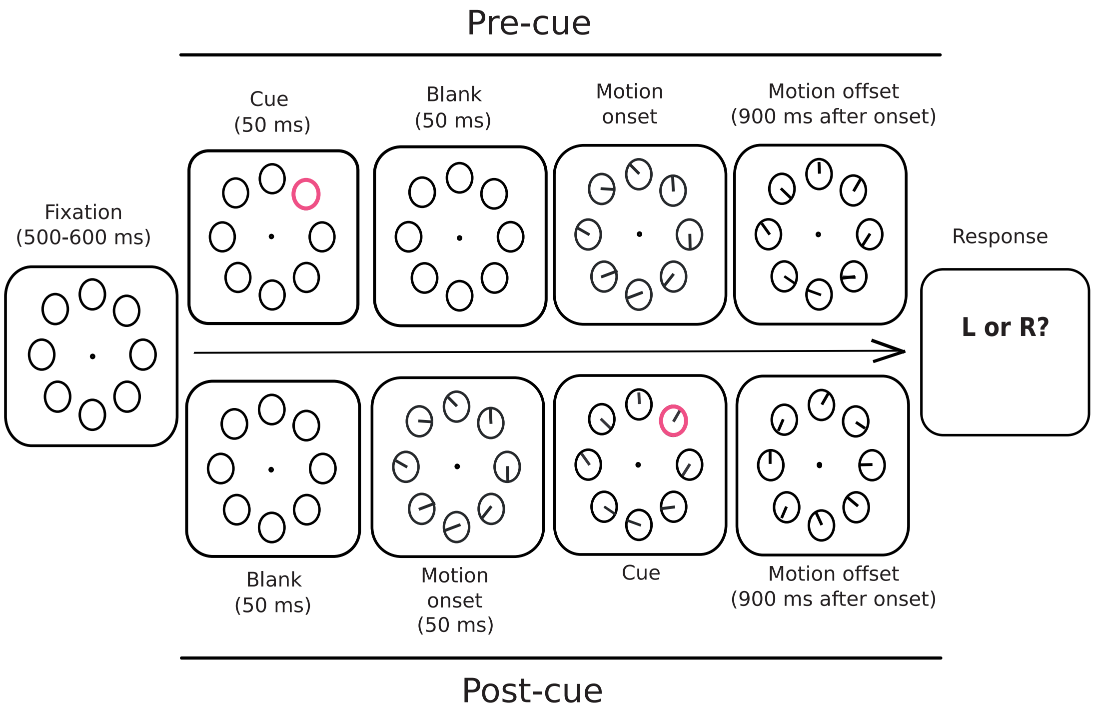

Figure 3. Experiment 2 trial schematic. Upper row shows the "precue" cases; lower row shows the "postcue" cases. In all the trials the task was to report the onset angle of the cued target. In the precue cases, the cue (identical to those of Experiment 1) preceded the onset of eight moving targets by a fixed SOA, thus allowing to selectively attend to one item. In the postcue condition, the to-be-attended target was revealed only after the motion onset (again, after a fixed SOA).

to the purposes of the experiment; two subjects (S1 and S2) also participated in Experiment 1. Data of two subjects were removed because of the self-reported failure to understand the instructions, leaving data of seven subjects for analysis. As noted in the Participants section of Experiment 1, this sample size allowed us to detect the effect of attention with enough statistical power.

Stimuli

Stimuli were the same as in Experiment 1 with the following changes. As shown in Figure 3, moving bars appeared in all the placeholders on each trial. However, only one of them was the target, the others served as distractors. The target placeholder was cued at one of the tested SOAs (–300–300 ms relative to motion onset in the increments of 100 ms), signaling to the subject which of the moving objects they have to report.

Negative SOAs mean that the cue was presented before motion onset, which is identical to the cueing used in Experiment 1. However, with the positive SOAs the cue appeared after the motion onset, which means that observers had to attend to all eight stimuli for some time before being able to focus on the target. Onset angles varied from –80° to 80° relative to the upper vertical of the placeholder, whereas in Experiment 1 we used the range of –60° to 60°. The expanded range was necessary for the more difficult late SOAs, where the participants' responses covered a larger range of angles. Another difference from Experiment 1 was that all stimuli disappeared from the screen simultaneously 900 ms after the motion onset (having travelled 290°), and not when they reached the lower vertical position. Thus, the duration of motion was not predictive of the onset angle.

Procedure

The procedure was similar to that of Experiment 1. On each trial subjects were asked to fixate the central dot, observe the rotation and then respond with the button press whether the cued stimulus started moving from the left or from the right relative to the upper vertical radius of the placeholder. Subjects were aware that the timing of the cues varied unpredictably. Trials with pre- and postcues were presented in a pseudorandom order. On average, subjects had 1700 trials, with 240 trials per SOA.

Results

The size of the Fröhlich effect was estimated in the same way as in Experiment 1. Individual PSEs were

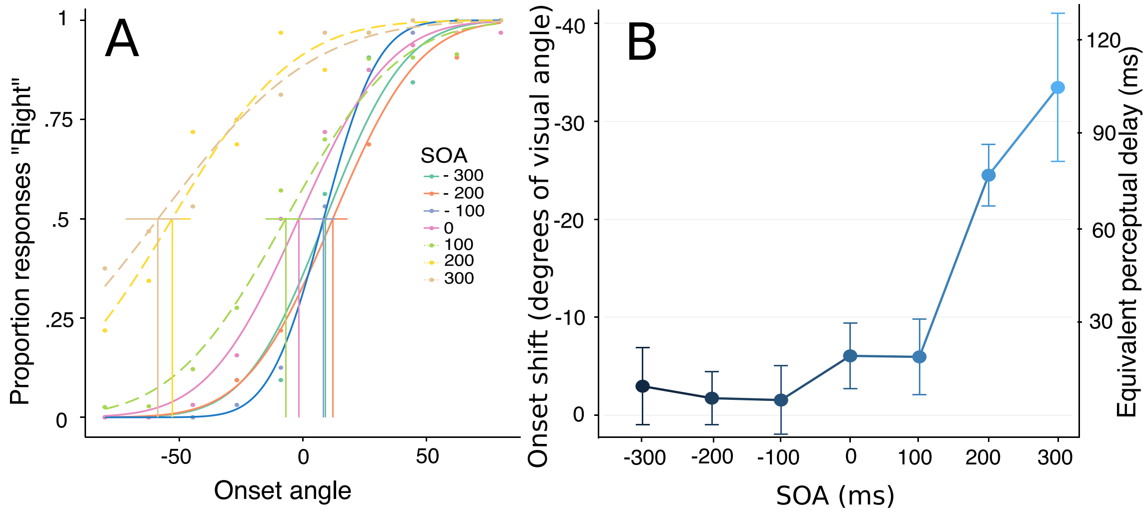

Figure 4. Results of Experiment 2. Panel A shows example data from one participant across the seven SOAs. Negative SOA conditions are plotted in dashed lines, positive SOA condition—in solid lines. Panel B shows average Fröhlich effect size as a function of SOAs for all subjects ($n = 7$). Error bars represent 95% CIs.

then plotted against the SOAs to reveal the time course of attentional modulation of Fröhlich effect.

Figure 4B represents the average time course of the Fröhlich effect modulation. Overall, SOA had little effect on the perceived onset position except at the two late SOAs (+200 and +300 ms) where the Fröhlich effect increased compared to the other SOAs, $F(6, 36) = 53.1$, $p < 0.001$, $\eta^2 = 0.87$). This pattern of results was shared by all subjects.

This increase is consistent with the attentional explanation of the Fröhlich effect, as the later attention arrives at the moving target, the bigger the mislocalization. As in Experiment 1, the mislocalizations after precues (–300, –200, and –100 ms), although smaller than seen in Experiment 1, were still significantly greater than zero, $M = -4.12$, $t(20) = -2.26$, $p = 0.04$, again confirming that Fröhlich effect was present even when attention was shifted towards the target area prior to motion onset. Note, however, that in Experiment 1, a valid cue at –100 ms SOA yielded mislocalization of –22° in Experiment 1 but only –3.9° in Experiment 2. A few differences between the tasks may account for this reduction of the position shift. First, the range of starting angles was larger in Experiment 2 (–80°:80° compared to –60°:60°), possibly helping the discrimination performance. Second, in Experiment 2 the stimuli were simultaneously presented in all the placeholders, whereas in Experiment 1 stimuli were presented one at a time. This presence of irrelevant but perceptually similar distractors could enhance the effectiveness of the cue. Additionally, the irrelevant stimuli could provide references for the judgment about the starting angle of the target. Third, the offset angle of the stimulus was predictive of its onset angle, since the motion duration was fixed. However, participants were not aware of this association and never received response feedback.

We also analyzed the slopes of the psychometric curves as a function of SOAs (Figure 5). Slopes were calculated by fitting logistic functions to participants' responses as a function of onset angle for each SOA condition. Cueing delay could affect not only the magnitude of the perceptual effect, but also the memory of the percept, making the onset locations at later SOAs more difficult to report. In this case we would expect the slope of the psychometric functions to be shallower for the later cues. One-way, repeated-measures ANOVA with SOA as a factor did show a significant main effect, $F(6, 36) = 19.2$, $p < 0.001$, $\eta^2 =$

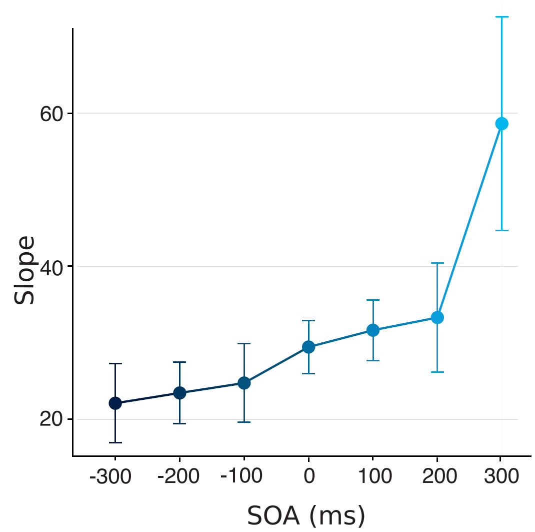

Figure 5. Slopes of the psychometric curves as a function of SOAs, averaged across all participants ($n = 7$). Error bars represent 95% CIs.

0.58, meaning that the task indeed became more difficult with increasing SOA.

Discussion

The results of this experiment showed that the Fröhlich effect increased when cues arrived after motion onset, as would be predicted by a delayed attention explanation. The later attention arrives at the moving target, the more the start position is shifted along its path. However, participants were surprisingly good at reporting the onset location of one of the eight simultaneously attended moving targets even when the cue indicating which to report came 100 ms after the onset of the motions. The results suggest that the simultaneous onsets may be held in iconic memory and the cued motion trajectory can be retrieved if the cue arrives soon enough. If this interpretation is correct, it suggests that iconic memory is not simply a static memory but a dynamic one. This is in line with the previous accounts of multiple layers of iconic memory (Rensink, 2014) or multiple systems of visual memory (Sligte, Vandenbroucke, Scholte, & Lamme, 2010).

The increasing shifts with more delayed postcues (>100 ms) might be caused by factors other than simple delay of attention. A late SOA implies a longer memory retention period, and that means that the reported shifts could arise from working memory limitations and might not be perceptual in nature. This could explain why the Fröhlich effect observed with late cues is much bigger than one observed with simple invalid cue in Experiment 1 and why, as evident from the analysis of slopes (Figure 5), the task is harder with late SOAs.

Additionally, these data again suggest that the Fröhlich effect is not solely explained by the delay in attention reaching the cued position from the fixation point. The size of the Fröhlich effect is largely unchanged for precues, and we can safely assume that attention would reach the cued location at or prior to motion onset if the cue preceded the motion onset by 300 ms (Egeth & Yantis, 1997; Posner, 1980; however, see Purushothaman, Patel, Bedell, & Ogmen, 1998). Rather than the absence of Fröhlich effect, we still see a significant shift. If there were an additional delay as attention moves from the general area cued by the flashed ring toward the actual start location of the motion, it might explain part of this Fröhlich effect for the precues as attention cannot make this final move until the motion actually starts. Another additional shift is required with the saccade intercept hypothesis (see General discussion) even if attention is already at the moving target. Programming a saccade to accurately intercept the target requires a position extrapolation to account for the unavoidable delays in taking the eye to the target.

Overall, this experiment showed that attentional shifts modulate Fröhlich effect within a specific time frame. If attentional selection of the target happens before the motion onset, a minimal (but significant) shift in the perceived motion onset is reported. If attention is shifted to the target later, this shift progressively increases, as expected from attentional delay account. However, in all these cases one target out of the group had to be selected at some point.

Both Experiment 1 and Experiment 2 show that there is a residual Fröhlich effect even when attention is already at the location of the target. We next examined whether the motion-induced shift depended on the mere presence of attention alone or if attention had to track individual targets to produce the shift. To address this we compared two modes of attention to the target: either a distributed attention to several targets or a focused attention on one.

Experiment 3

Experiment 1 and Experiment 2 confirmed the basic predictions of attention delay explanation. However, this explanation assumed a tight focus of attention that was either on the individual target or elsewhere. What would happen if attention were directed to several targets at once? Is the presence of distributed attention sufficient to generate the Fröhlich effect? Cavanagh and Anstis (2013) used multiple and single dots travelling back and forth to test the role of attention in illusory trajectory shortening. In a trajectory shortening stimulus, a dot travels back and forth along a linear path and there is a Fröhlich-like shift of the beginning of the visible path at both ends of the trajectory, shortening its apparent length. Importantly, when multiple stimuli are presented, moving asynchronously along parallel paths, they are not unattended, but rather attended as a group, which allows reporting of the end-points of all the trajectories without engaging focused attention on individual trajectories. It was shown that trajectory shortening only exists for individually attended trajectories, but not for those attended as a group. This is similar to the finding by Linares and López-Moliner (2007) where flash lag was eliminated with a group display. Here we use this logic to test the occurrence of the Fröhlich effect with distributed attention to multiple rotating line segments.

For this experiment we created a new stimulus display and a new task. First, we added more items to the display and increased the eccentricity (as shown in Figure 6B, and Movies 1 and 2). To ensure distribution of attention to all items throughout the trial, we presented synchronised motion in all the placeholders simultaneously and we asked subjects to report a

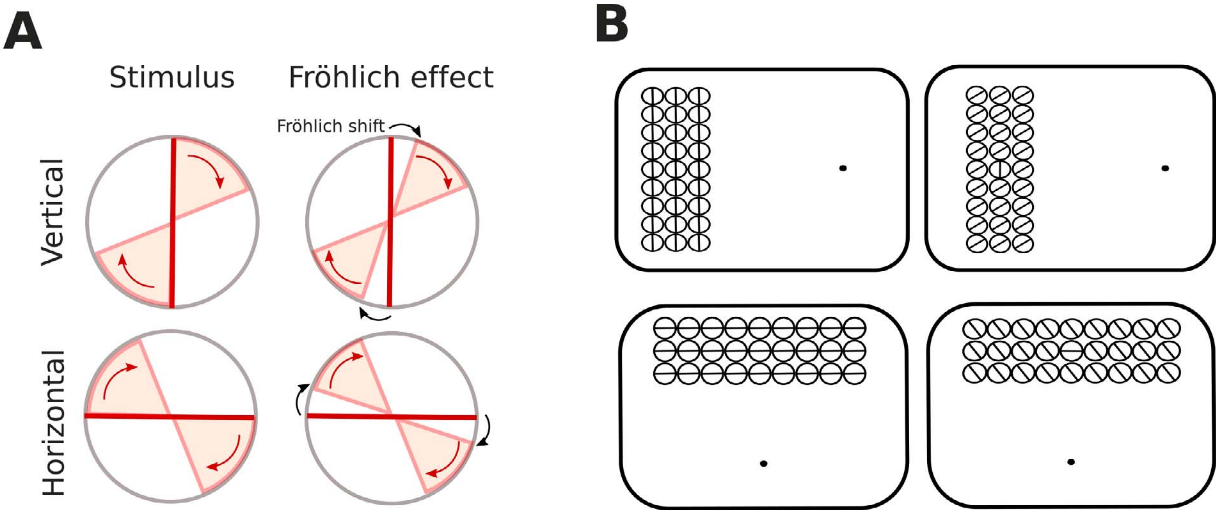

Figure 6. Panel A. A schematic showing the orientations covered by a single rotating line starting at vertical (top left, 0° onset trial) or horizontal (bottom left). To the right of each is the hypothetical range of perceived orientations given a 15° Fröhlich shift. The thick red bar within each circle (not actually shown on screen) indicates the to-be-detected orientation, either vertical (top) or horizontal (bottom), respectively. Physically, the stimulus contains the to-be-detected orientation right at the start of the motion (left), but the illusion then renders it invisible (right). Panel B. Stimuli arrangements at the to-be-detected orientations in Experiment 3. The upper row shows the Vertical condition; lower row shows the Horizontal condition. The left column shows the alignment to be detected in the "Group" condition. The right column shows the orientation of the singletons to be detected in the "Single target" condition

feature of the display created by all the items on the screen—their alignment. At the moment when all the stimuli were aligned, they are grouped together as three distinctive lines, either vertically (Figure 6B, top left panel) or horizontally (Figure 6B, bottom left panel). Vertical and horizontal configurations were tested in separate blocks. We took advantage of this momentary grouping to probe motion perception under distributed attention. If the Fröhlich effect persists for each individual rotating segment, all of their perceived onset angles will be shifted. Therefore, if the segments start from alignment, this alignment would not be perceived, as the Fröhlich effect would render them visible with some additional rotation (Figure 6A). By estimating the maximal onset angle that results in perceived alignment, we were able to measure the simultaneous Fröhlich effect for the entire group of elements.

For our control condition, we introduced focused attention to a single moving element in this display (Figure 6B right hand panels). To do so, we took advantage of another well-known phenomenon—attentional capture (Yantis, 1996). We rotated one of the items of the display relative to the others, making it an orientation singleton, and asked participants to report whether this singleton is seen as either horizontal or vertical at any point during the trial. This question is essentially the same as the one we asked about the group alignment (since the alignment was only present when the segments were either all vertical or all horizontal); only here the judgment had to be done on a single, attended item.

Participants

Eight healthy adults took part in the experiment (four male, four female; mean age = 21.8 ± 2.2 years, range 19–28), three of them (S3, S5, and S7) participated in Experiments 1 or 2. Two participants (S3 and S4) were experienced psychophysical observers, but were naive to the purposes of the experiment.

Stimuli

The stimulus consisted of 27 placeholders lined up in the periphery as shown in Figure 6B, arranged in three rows of nine. Each placeholder was 2.5° wide. The whole stimulus set was 22.5° long and 7.5° wide, and its center was 21° away from the fixation point. Targets (bars covering placeholders' diameters, 0.2° thick) were presented in all the placeholders simultaneously, and moved in the same direction and in synchrony. Motion started at a randomly selected angle from –30° to 36° relative to the vertical or horizontal (in respective blocks) in the increments of 6°, and rotated 60° clockwise with the speed of 0.83 revolutions per second.

In the Group condition, all the targets had the same onset angle. In the Single condition, one random target was rotated 45° counterclockwise relative to the rest of the targets, thus becoming an orientation singleton and breaking the alignment. The stimuli were presented in two spatial arrangements, with the stimuli in the upper visual hemifield (Vertical condition) and in the left

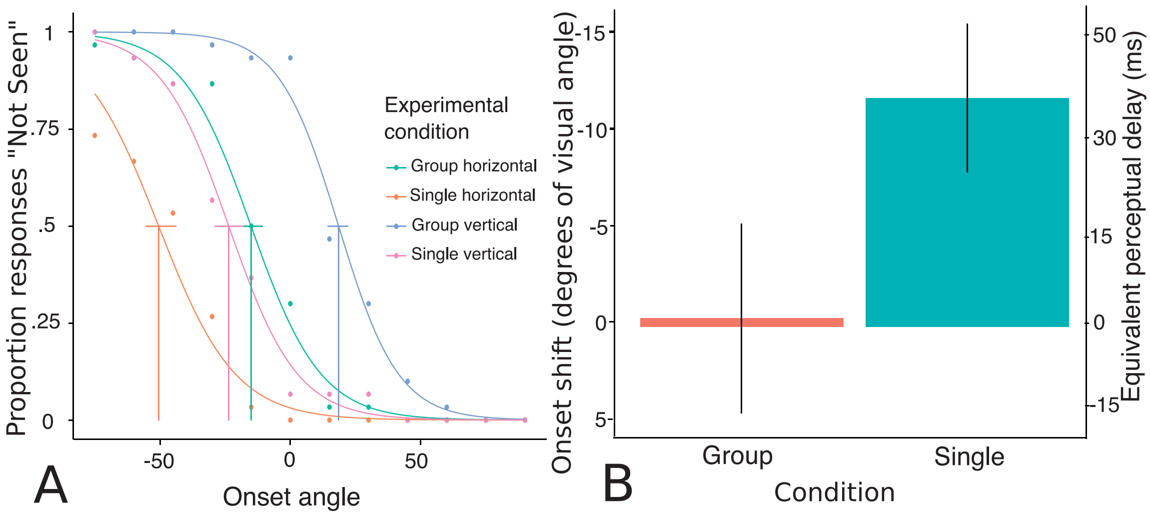

Figure 7. Results of Experiment 3. Panel A shows data from one participant. Panel B shows the average Fröhlich effect for Group and Single conditions for all participants ($n = 8$). Error bars represent 95% CIs.

visual hemifield (Horizontal condition). Stimuli for Horizontal condition were created by rotating the stimuli from the Vertical condition 90° counterclockwise.

Procedure

Each combination of conditions (Single/Group and Horizontal/Vertical) was tested in a separate block of 360 trials. The order of the blocks was counterbalanced across subjects. On each trial, subjects had to fixate, then observe the motion and respond by key press. Trials were separated by 500 ms–600 ms jittered ITI.

In the Group condition subjects had to report whether the targets were perceived in alignment at any point during the trial. In Single Target condition they had to report whether the stimulus that was different from the rest of the set was at horizontal (or vertical, in respective blocks) at any point during the trial. The to-be-detected orientation of the stimuli/stimulus was present at some point in all the trials with the starting angle lower or equal to 0°. Importantly, the to-be-detected orientation could only appear once per trial, since motion was restricted to 60° of rotation and so only passed through either horizontal or vertical (for starting angle of 0° or less), depending on the block. The singleton location changed from trial to trial.

To test our hypothesis that the Fröhlich effect is reduced in the Group condition, i.e., that alignment will be detected when the stimulus starts at 0° in the Group trials, we first calculate participants' performance on trials with 0° onset. These trials in both conditions are demonstrated in Movies 1 and 2. We then performed the analysis of the full psychometric curve to estimate the Fröhlich effect in both conditions in the same way that we did in Experiments 1 and 2.

Results

Psychometric curves were fitted individually for each observer and condition, and PSEs were estimated as the onset angle of motion that produced 50% reports of a horizontal or vertical alignment (Group conditions) or a horizontal or vertical singleton (Single condition). Therefore, negative PSEs reflect a shift in the perceived onset location in the direction of motion (Fröhlich effect).

The analysis of 0° onset trials showed that the starting angle was correctly detected as aligned to the vertical or horizontal on average in 78% (± 10.5) of the trials in the Group condition suggesting that the orientations of the line segments were perceived almost veridically with little if any shift when reported as a group. In contrast, only 7% (± 8.2) of Single trials were reported as aligned to vertical or horizontal. The analysis of the psychometric functions confirms these results. Figure 7 shows that PSEs were shifted to the left in the Single condition compared to the Group condition both in vertical and horizontal layouts, meaning that perceived onset locations were shifted further in the direction of motion in the Single condition. This pattern of results was observed in all participants. One-way, repeated-measures ANOVA revealed a significant main effect of condition, $F(3, 21) = 14.35$, $p < 0.001$, $\eta^2 = 0.32$. The PSE shift was significantly larger in Single compared to Group condition ($M_{Group} = -0.44$, $M_{Single} = -11.84$, $t = 3.05$, $p = 0.005$). The pattern of results was the same if vertical and horizontal cases were analyzed separately. Overall, the onset shift was significantly different from zero in the Single condition, $t(15) = -4.51$, $p < 0.001$, JZS $BF_{10} = 6.38$, but not in the Group condition, $t(15) = -0.17$, $p = 0.87$, JZS $BF_{10} = 0.26$.

Discussion

The main finding from this experiment is that Fröhlich effect is greatly reduced when the moving stimuli are attended as a group. Equally important, the effect was restored when focal attention was directed to an orientation singleton within the group. While it is true that distributed attention is enough to detect the presence of a singleton item, focal attention is then necessary to analyze its features (Sagi & Julesz, 1985), for example, as in our case, its orientation. The presence of focal attention then allows the motion of the target line segment to be individuated and tracked. By contrast, in the Group condition moving bars were attended as a group in order to detect the emergence of the global shape (alignment) and although the motions were clearly visible, no single trajectory could be isolated and tracked. This condition reveals that the full motion trajectory is not masked by some low-level property of the stimulus motion.

We propose that it is this focal attention to a specific trajectory that engages a predictive mechanism for that trajectory, advancing the location of the motion onset for purposes of targeting, as we explain in the General discussion section that follows. With multiple stimuli attended as a group, no one stimulus can be a saccade target without further processing. We suggest that when saccade programming is not possible, the predictive position shift is not engaged.

This result is in line with the finding by Cavanagh and Anstis (2013) who showed that attention to multiple trajectories does not result in trajectory shortening (a Fröhlich effect at both ends of a reversing trajectory), but attention to the individual trajectory does lead to the illusory shift. Here we show that focal attention shifts localization not only for motion reversals, but also for motion onsets. Again, this suggests that the Fröhlich effect is not an unavoidable consequence of motion, but it is driven by focused attention.

One important feature of the Single target task is that the target changed its position from trial to trial. Müsseler and Kerzel (2004) argued that Fröhlich effect is only observed when stimuli appear at a predictable position, possibly because moving targets require attentional disengagement from the previously attended space. However, our data show that although the orientation singleton had 27 possible locations, it still produced a Fröhlich effect, casting doubt on this hypothesis.

There are alternatives to our distributed attention explanation for the reduction of Fröhlich effect with multiple stimuli. It is possible that a summary or ensemble representation of all of the orientations is generated by a fast, automatic mechanism (Alvarez & Oliva, 2009; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). This ensemble representation would always be more accurate than the representation of a singleton, and possibly available earlier. Additionally, the to-be-detected alignment in Group condition was a property of a much larger stimulus, involving all the elements, than the single item, and this could also affect the speed of processing (Vogels, 2009). However, previous studies using comparably large stimuli (Kirschfeld & Kammer, 1999) successfully demonstrated large Fröhlich effect.

General discussion

In this series of experiments, we set out to disentangle the evidence regarding the role of attention in Fröhlich effect. Experiments using cueing paradigms (Müsseler & Aschersleben, 1998; Whitney & Cavanagh, 2000b) report that validly cued stimuli show less of a Fröhlich effect than invalidly cued stimuli. Müsseler and Aschersleben (1998) proposed a delay hypothesis wherein the later attention arrived at the stimulus, the further it was seen shifted along its path. In contrast, other experiments showed that the Fröhlich effect is absent when attention is directed to a group of moving stimuli (Cavanagh & Anstis, 2013; Linares & López-Moliner, 2007) and not to individual targets within the group. The group result indicates first that the position shift of the Fröhlich effect is not an obligatory consequence of stimulus movement. However, the group result does not easily match with what the attentional delay hypothesis would predict. Here we used similar stimuli in both cueing and group attention situations and we replicated these previous findings. We consider an alternative explanation of the Fröhlich effect based on the preparation of saccade programming to moving targets. This interceptive saccade conjecture is consistent with both results.

In Experiments 1 and 2 we varied the delays with which attention reaches the target with invalid versus valid cuing (Experiment 1) and with cue-motion onset delays for valid cues (Experiment 2). In both cases, we found increases in the Fröhlich effect associated with longer delays. Critically, following Müsseler and Aschersleben's (1998) proposal, we interpret the invalid cue condition as causing a delay in attention reaching the target rather than a condition of inattention or lack of attention. Our finding of a modulation of Fröhlich effect with attention cues is consistent with the previous research using single targets. Specifically, Müsseler and Aschersleben (1998) as well as Whitney and Cavanagh (2000b) showed that the Fröhlich effect could be increased by invalid attention cues.

We also found, in line with the previous cueing experiments, that the Fröhlich effect is small, but always present and significant when the location of the upcoming motion onset is attended. In some stimuli, including ours, part of this residual Fröhlich effect could be attributed to the additional delay of transferring attention from the cue to the actual start location of the motion within the cued area, as well as to the hypothetical execution delays of a potential saccade.

The execution delays refer to the "saccade intercept hypothesis" we propose to link covert attention to overt attention by treating every attended target as a potential saccade target. Any accurate eye movement to a moving target requires compensation for the distance travelled by the target after the saccade has been programmed but before it lands on the target (Ludwig, Mildinhall, & Gilchrist, 2007). Given how closely linked attention and saccade systems are (Corbetta et al., 1998; Krauzlis, 2014), we assume that this extrapolation along the motion path is engaged for every tracked target, whether or not it eventually engages a saccade. As long as the target is attentively tracked, we assume that its perceived location is extrapolated to match the location where the saccade will intercept it, the position to which the saccade must be targeted. Several studies with motion-induced position shifts with simple moving targets show evidence for a similar extrapolation for perception and saccades. All of these show matched shifts in perceived location and saccade landings (Etchells et al., 2010; Nijhawan, 1994). The one exception is for a stimulus with two motion components (double drift, Lisi & Cavanagh, 2015) where the internal motion of the stimulus appears not to be registered by the saccade system.

Note that this proposal has the target shifted in position so that its initial appearance is *displaced*, not masked as some have proposed (Kirschfield & Kammer, 1999). Evidence in favor of this shift as opposed to masking is clear when the initial target position is marked in some way, for example, with a unique color. In this case, that brief unique color does not disappear, as it should if the initial portion of the trajectory were masked to produce the Fröhlich effect. Instead, the color flash is seen displaced, still at the beginning of the trajectory, but that trajectory now starts further along the motion path (Cai & Schlag, 2001; Cavanagh & Anstis, 2013, figure 13b, flash at start of trajectory; Eagleman & Sejnowski, 2007).

The saccade intercept hypothesis provides a possible explanation for the residual Fröhlich effect seen with advanced cues in Experiment 2 as well as in other studies where the target is fully attended, including the original observation by Fröhlich (1923). Even if attention is already deployed to the upcoming target location, any potential saccade will only reach the target after a delay, which could be compensated in a predictive manner by perceptual extrapolation. Additionally, when attention is delayed in reaching the target to begin tracking it, more extrapolation is required and the Fröhlich effect increases, as demonstrated by several cueing experiments.

In contrast, when attention is directed to a set of moving stimuli, as in the Group condition of Experiment 3, no Fröhlich effect is seen. In this case, none of the trajectories is attentively tracked and none of them can be individual saccade targets without further processing, and the predictive shift is not engaged. There are other examples in the literature showing that motion-induced position shifts disappear with attention to the group (Cavanagh & Anstis, 2013), attention to the global shape (Linares & López-Moliner, 2007), or attention to a large space (Müsseler and Tiggelbeck, 2013). All of these conditions required a spatial spread of attention (20°–30° visual angle) to all items of the display, not to a few locations or objects within it. In other words, they implied diffusion of attention where no particular stimulus is attended individually and none could be targeted by a saccade without further processing to single them out.

However, once focal attention is directed to an individual target in the same group (Single condition), it becomes a potential target and the predictive shift is again seen. This result strongly suggests that whatever the mechanism creating the perceptual shift in position, it requires focal attention. When the target engages focal attention on one particular location, a moving object there gets shifted forward. Once attention is narrowly focused, the magnitude of the Fröhlich effect is determined by the time it takes to arrive at the moving object as well as, we suggest, any additional execution delay for a potential eye movement to it.

Conclusion

The findings of this study are two-fold. Our data confirm that attention delays are important predictors of the magnitude of the Fröhlich effect. More importantly, we show that focused attention by itself is a requirement—without it the Fröhlich effect disappears completely. We suggest that focused attention tracks the target motion and adjusts the perceived location to match the necessary targeting location for an accurate saccade, even if one is not made. When attention is deployed to a group of targets, they are not tracked individually and they could not be individual saccade targets without further processing, and so the position shift that produces the Fröhlich effect is not engaged. In this case, the initial portions of the motion traces are clearly seen showing that the Fröhlich effect is not an obligatory consequence of any motion, only of motion that is attentively tracked.

Keywords: perception, motion, attention, motion-induced position shift, localization

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Corresponding author: Nika Adamian.
Email: nika.adamian@parisdescartes.fr.
Address: Laboratoire Psychologie de la Perception, Université Paris Descartes, Centre Biomédical des Saints Pères, Paris, France.

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