# Malleable Temporal Integration of Positional Information for Moving Objects

Paul A. Miller and Derek H. Arnold
The University of Queensland

One of the primary functions of visual processing is to generate a spatial mapping of our immediate vicinity, in order to facilitate interaction. As yet it is unclear how this is achieved, but the process likely involves an accrual of information over time—a temporal integration of positional information (Eagleman & Sejnowski, 2000; Krekelberg et al., 2000). Temporal integration is a common computational process evident in diverse settings, such as electrical engineering (Bryson & Ho, 1975) and neural coding (Rao, Eagleman & Sejnowski, 2001; Usher & McClelland, 2001). In the later context it is sometimes assumed that integration dynamics are immobile, and consequently that they can be diagnostic of a sensory system (Arnold & Lipp, 2011; Krauskopf & Mollon, 1971; Snowden & Braddick, 1991). Other data suggest that integration times can be flexible, varying in concert with the properties of a stimulus (Bair & Movshon, 2004) or environment (Ossmy et al., 2013). Our data provide behavioral support for malleable integration times. We examine a motion-induced illusion of perceived position linked to temporal integration, and use prolonged exposure to motion of different speeds (sensory adaptation) to modulate the dynamics of neural activity. Results show that perceived position is governed by a weighted average of positional estimates from multiple channels with distinct, fixed integration times. Postadaptation channel contributions are reweighted, resulting in coding that is optimized to the dynamics of the prevailing environment.

Keywords: temporal integration, Fröhlich effect, spatial coding, human vision

A common assumption in visual psychophysics is that the dynamics of an integration process underlying a particular perceptual experience are immobile and determined by the dynamics of the sensory mechanism used to encode the signal. Consequently, the dynamics of temporal integration have been used to infer when perceptual judgments rely on a common or on discrepant sensory processes (Arnold & Lipp, 2011; Krauskopf & Mollon, 1971; Snowden & Braddick, 1991). An alternate possibility is that the dynamics of a temporal integration process are dynamic, adaptable to suit the prevailing conditions. This seems plausible as integration times for V1 and MT neurons can vary as a function of input signal strength (Bair & Movshon, 2004), and recent evidence suggests human observers adjust temporal integration times to suit the prevailing environment (Ossmy et al., 2013). Here we provide evidence in support of this proposition, by establishing that the dynamics of positional information integration is malleable. We do so by using a striking visual illusion—the Fröhlich effect (Fröhlich, 1923).

In the Fröhlich effect, when a moving target suddenly appears it is not seen in its initial physical location. Instead, it appears to have onset at a location extrapolated along its trajectory (Fröhlich, 1923; Kirschfeld & Kammer, 1999). This has been ascribed to instanta-

neous position being derived from an averaging of positional information over time (a temporal integration of position). Information regarding the initial physical location is averaged with information pertaining to later locations, with perception necessarily being delayed by an extent equivalent to the averaging window, in sum resulting in the moving element seeming to have onset at an extrapolated location (Whitney & Murakami, 1998; Krekelberg & Lappe, 1999; Eagleman & Sejnowski, 2000; Krekelberg et al., 2000; Patel, Ogmen, Bedell, & Sampath, 2000).

To examine the possibility of the Fröhlich effect being impacted by a malleable integration process, we use visual motion adaptation to modify the dynamics of visual coding (Smith, 1985, 1987; Thompson, 1981). We find that the magnitude of the Fröhlich effect is *increased* via adaptation that *slows* perceived motion. This observation is counterintuitive as the magnitude of motion-induced positional illusions can scale with physical speed (Durant & Johnston, 2004; Fröhlich, 1923; Müsseler & Aschersleben, 1998; Nijhawan, 1994; although see Vaziri-Pashkam & Cavanagh, 2011 for an exception with perceived speed). We show that these data can be well accounted for via a weighted average of positional estimates from multiple mechanisms with distinct integration times. Accordingly, adaptation to fast motion would bring about a reweighting that favors positional estimates from mechanisms with relatively protracted integration times.

## Experiment 1

### Fröhlich Task

Eleven volunteers (three female) participated in the Experiment 1, including the first author (PM) and 10 participants who were

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Paul A. Miller and Derek H. Arnold, School of Psychology, The University of Queensland.

Correspondence concerning this article should be addressed to Paul A. Miller, School of Psychology, The University of Queensland, St. Lucia, Queensland 4067, Australia. E-mail: paul.miller@uqconnect.edu.au

naïve as to the purpose of the experiment. All had normal or corrected to normal visual acuity. Stimuli were generated using a ViSaGe stimulus generator from Cambridge Research Systems, driven by MATLAB 7.5 software. Stimuli were displayed on a Samsung Syncmaster 1100pp monitor (resolution $1280 \times 1024$, refresh rate 120 Hz). The display was viewed from 57 cm with the participant's head placed on a chin rest. Responses were made using left and right mouse buttons.

## Stimuli

Throughout the experiment participants fixated on a white (luminance = 102 cd/m2) disk positioned in the center of the display. This had a diameter subtending 0.2 degrees of visual angle (dva) at the retina. The display background was black. Throughout the experiment there were also three pairs of static white lines (each 0.3 dva long) separated by 1.8 dva and centered at an eccentricity 5 dva from fixation. These lines were oriented orthogonally to the positions they marked at 0, 45 (upper markers) and 315 (lower markers) angular degrees relative to fixation (see Figure 1A).

The adapting stimulus was comprised of multiple disks, each with a diameter subtending 0.5 dva and centered 5 dva from fixation, with a radial frequency of 14. This configuration rotated at a speed of either 0.1 (slow) or 0.6 (fast) revolutions per second (RPS). Five participants adapted to clockwise fast motion and counterclockwise slow motion, whereas other participants adapted to the opposite contingency. Element color was either red (CIE x = 0.612 y = 0.327 Y = 16) or green (CIE x = 0.282 y = 0.599 Y = 52), determined at random on a trial-by-trial basis.

## Procedure

Participants completed three blocks of trials; a baseline without adaptation, and one each following adaptation to fast and slow motion. During adaptation blocks of trials the adaptor was shown for 30 s before tests on the first and middle trials, and for 6 s before tests on other trials. When shown, there was a 500-ms inter-stimulus-interval between adaptation and test stimulus presentations.
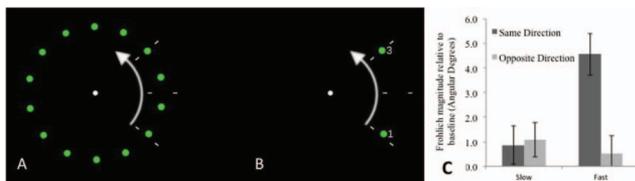


*Figure 1.* Depiction of visual display. (A) The adapting stimulus. Adapting elements rotated at either 0.1 (slow) or 0.6 (fast) revolutions per second, clockwise or counterclockwise. (B) Depiction of a test display. A moving target onset within +/− 6 angular degrees of a pair of static white flanking elements, which marked positions at 315° (position 1) or 45° (position 3) from fixation. Participants judged if it had onset before, or after, the flankers. (C) Results of Experiment 1; the perceived onset location of tests moving in the same direction as a fast adaptor was further shifted in the direction of motion, relative to tests moving in the opposite direction or following adaptation to slow motion. Error bars are S.E.M. See the online article for the color version of this figure.

Test presentations involved a single disk, matched in terms of its spatial dimensions to elements in the adaptation display. Test element color was set to red or green, determined at random on a trial by trial basis. Test elements onset at a position proximate to either the upper or lower markers. After onset test disks moved, either clockwise (if onset was proximate to upper markers) or counter clockwise (if onset was proximate to lower markers), at a fixed speed of 0.3 RPS. Tests presentations persisted for 750 +/− 83 ms, determined at random on a trial-by-trial basis. Test onset location (−6, −4, −2, 0, 2, and 4 angular degrees from proximate markers) was manipulated during a block of trials according to the method of constant stimuli, with each position sampled 8 times for each test direction—a total of 96 individual trials per block, all sampled in a random order.

Participants were required to report, by pressing one of two mouse buttons, if the moving element had appeared to onset at a position before or after the most proximate set of markers, understood in terms of the test trajectory. We fit cumulative Gaussian functions to individual data from each block of trials, one for each direction of motion, taking 50% points as an estimate of the physical onset location at which tests seemed aligned with static markers.

## Perceived Speed Task

Ten participants (four female) completed a perceived speed task, nine of these were naïve to the purpose of the study. Two had completed the previous task, including the first author (PM). Participants viewed the same adapting stimulus, for the same durations, but with the left half of the display omitted (see Figure 2). Following adaptation there was a 250-ms inter-stimulus-interval, before participants viewed two sequential 500-ms presentations of a single rotating disk (separated by a 250-ms inter-stimulus-intervals). The spatial properties of test stimuli were identical to those in the preceding task.

One of the two test elements (the standard) was positioned in the same location as the adapting stimulus and moved at 0.3 RPS (the test speed in Experiment 1). A comparison stimulus was offset at a position centered 7.5 dva to the left of fixation in order to match the average eccentricity of the two stimuli. It moved in an arc, in the same direction as the standard. Order of presentation (standard–comparison or comparison–standard) was randomized on a trial-by-trial basis.

Comparison speed (.22, .24, .26, .29, .33, .38, .44, .53, or .66 RPS) was manipulated during a block of trials according to the method of constant stimuli. Each comparison speed was sampled eight times for each direction (clockwise and counter clockwise), for a total of 72 individual trials, all completed in a random order. On each trial the participant indicated which test array had seemed fastest. We fit cumulative Gaussian functions to individual data from each block of trials, taking 50% points as an estimate of the point at which tests seemed to have a matched speed.

## Results

**Fröhlich Task.** Analysis revealed a significant increase in Fröhlich effect magnitude following adaptation to fast motion (5.16° +/− 0.85°) relative to baseline (0.59°, +/− 0.6°; paired $t_{10} = 4.05$, $p = .002$). This, however, only held for tests moving

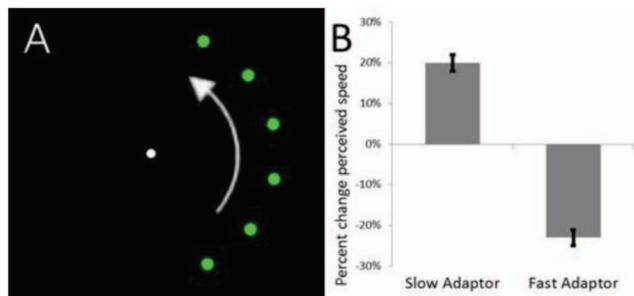*Figure 2.* (A) Depiction of adapting stimulus for Experiment 2. (B). After adaptation to a slow adaptor, there was a ~20% increase in perceived speed. Error bars show S.E.M. See the online article for the color version of this figure.

in the same direction as the adaptor. There was no evidence for a difference in Fröhlich effect magnitude, relative to baseline, for opposite direction tests (fast adaptation $1.11° +/- 0.73$; paired $t_{10} = 0.656$, $p = .527$).

Changes in Fröhlich effect magnitude were specific to fast motion adaptation. There was no evidence for different Fröhlich effect magnitudes following slow motion adaptation, relative to baseline, either for same ($1.46° +/- 0.78$; $t_{10} = 0.94$, $p = .370$) or opposite ($1.68° +/- 0.70$; $t_{10} = 1.145$, $p = .179$) direction tests.

**Perceived speed.** Following adaptation to fast motion, participants experienced a ~23% decrease ($0.26^{RPS} +/- 0.01$) in apparent test speed relative to baseline ($0.31^{RPS} +/- 0.01$, $t_9 = 4.43$, $p = .002$). After adaptation to slow motion, participants experienced a ~20% *increase* ($0.39^{RPS} +/- 0.01$) in apparent test speed ($t_9 = 8.675$, $p < .0001$).

## Discussion

Experiment 1 examined a common motion-induced positional distortion, following adaptation to either fast or slow motion. We found that tests seemed to onset at a *later* location after viewing a fast adaptor rotating in the same direction (see Figure 1c). This represents an *exaggeration* of the Fröhlich effect.

This adaptation-induced exaggeration of the Fröhlich effect is counterintuitive, as adapting to fast motion typically slows apparent test speeds (Smith, 1985; Thompson, 1981) and illusory motion-induced positional shifts usually scale with physical test speed (Fröhlich, 1923; Müsseler & Aschersleben, 1998) We therefore verified that our adaptor had had a typical impact on perceived speed by contrasting tests in an adapted location with comparisons in an unadapted location (see Figure 2). Doing so revealed that same direction fast motion adaptation slowed apparent test speeds by ~23%.

Finding an exaggeration of the Fröhlich effect following sensory adaptation to fast motion could be explained by changing the dynamics of the accrual of positional information. There are different scenarios by which this could happen. One possibility is that there is a single process that integrates positional information linearly, and this process has a malleable integration time. Such a mechanism would predict a linear increase in Fröhlich effect magnitude as a function of test exposure, up until the limit of the

single processes' integration time. Accordingly, doubling integration time should double the size of the Fröhlich effect (see Figure 3a). Another possibility is that there are multiple processes, or channels, that each provide a positional estimate, and each channel has a different, fixed, integration time. Perceived position could then be given by a weighted average of positional estimates, in a similar manner to how positional estimates are combined across different sensory modalities (Alais & Burr, 2004). This predicts a nonlinear decelerating increase in Fröhlich effect magnitude as a function of test exposure time, with a saturation point coinciding with the integration time of the most protracted channel that contributes to the positional average. Postadaptation, in this coding scheme the Fröhlich effect could be exaggerated by increasing the weightings given to positional information from channels with relatively protracted integration times. Note that although this would increase the magnitude of the Fröhlich effect, it would not change the saturation point as a function of test exposure time (see Figure 3b). In Experiment 2 we examine these possibilities by evaluating the microgenesis of the Fröhlich effect.

## Experiment 2

Ten participants (two female) completed Experiment 2, including the first author (PM), one person who had participated in Experiment 1 and nine additional volunteers who were naïve as to the purpose of the study.

Test displays were identical to Experiment 1, with the exceptions that we varied the test display duration and that tests only moved in the *same* direction as the adaptor (given the direction specificity found in Experiment 1). To simplify test presentations for our participants, test elements in Experiment 2 were gray (luminance = 51 cd/m2) rather than colored. Half the participants adapted and were tested using clockwise motion, the other half with counterclockwise motion.

## Procedure

Tests were viewed either in isolation, or following adaptation to fast motion (identical in detail to fast adaptation in Experiment 1). During a block of trials test duration was manipulated (8.3, 25, 50, 100, 200, or 400 ms), as was the test onset position relative to the lower (counter clockwise tests) or upper (clockwise tests) markers. During a block of trials each of seven relative onset positions was sampled four times for each of six test durations, a total of 168 individual trials, all completed in random order. Each participant completed three blocks of trials, and resulting data were collated for each participant. We fitted cumulative Gaussian functions to collated individual data for each test duration, and took 50% points as an estimate of the physical onset location at which test elements seemed aligned with static markers.

We examined two plausible explanations for our results. The first is a single channel integrator with a flexible integration time:

$$P(t) = \bar{x}(Ps(t - i))$$

Where perceived position $p$ at time $t$ is derived from an average $\bar{x}$ of physical positions $Ps$ occupied by an element during an integration period $i$, prior to time $t$. By varying the size of the integration window ($i$), the positional estimate can be changed.
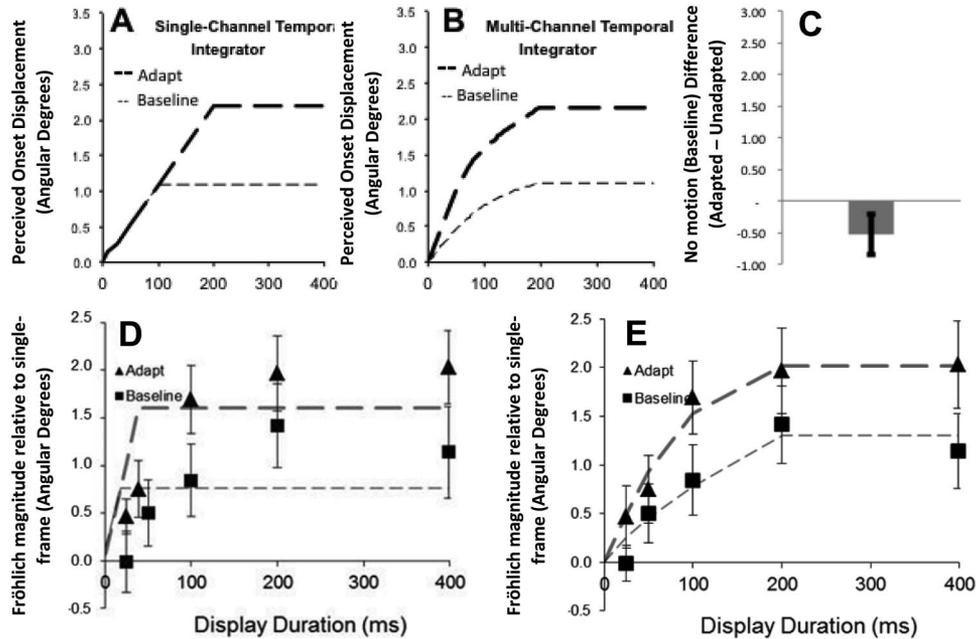
*Figure 3.* (A) Changes in Fröhlich effect magnitude as predicted by a single channel, with a malleable integration window. (B) Changes in Fröhlich effect magnitude as predicted by a weighted average of positional estimates from distinct mechanisms, that each accrue positional information linearly over different time spans. (C) Difference between perceived onset location of single frame trials, for the adapted and unadapted conditions. (D) Results of Experiment 2, showing onset displacement magnitude for different display durations, plotted relative to a single flashed frame. Lines represent best-fit functions from a one-channel coding scheme with a malleable integration time either pre (dotted line; $R^2 = 0.29$) or post- (bold dotted line; $R^2 = 0.42$) adaptation to fast motion. (E) As in C, but with best-fit functions from a three-channel coding scheme (channel integration times 1, 80, and 200 ms) to data from unadapted baseline (dotted line; adjusted $R^2 = 0.62$) and adapted (bold dotted line; adjusted $R^2 = 0.89$) trials. Error bars indicate S.E.M.

An alternative explanation is a process wherein perceived position is given by a weighted average of multiple positional estimates from different channels with distinct integration times:

$$P(t) = \frac{\sum w_n EST_n}{C}$$

Where $p(t)$ refers to perceived position, $w_n$ is the weight given to the $n$th single-channel estimate, $EST_n$ refers to the positional estimate from the $_n$th channel, and $c$ is the total number of channels. Individual channel estimates can be determined as per Equation 1, with progressive channels having progressively longer integration times.

The processes by which humans determine estimates of spatial position, particularly for moving inputs, remain largely mysterious, and so it is difficult to constrain assumptions regarding plausible integration times for different channels. There are pertinent integration time estimates, but these vary widely. The extent by which the trajectory of a moving element that reverses seems to be shortened, relative to its physical magnitude, suggests a brief integration of positional information for moving objects (~50 ms, see Whitney, Murakami, & Cavanagh, 2000). A slightly longer integration is suggested by the time taken for an illusory motion-induced spatial distortion to saturate after a trajectory reversal (~80 ms; see Eagleman & Sejnowski, 2000), and an even longer

integration period is suggested by the optimal time for the application of disruptive brain stimulation to disrupt a motion-induced distortion of perceived position (~200 ms, see Maus, Ward, Nijhawan, & Whitney, 2013). Finally, a very protracted integration is suggested by the extent of time that a transient moving input has to persist in order to look aligned with more persistent moving elements (~500 ms; Krekelberg & Lappe, 1999; also see Zimmermann, Morrone, & Burr, 2013 for estimates of positional integration around the time of saccades). One possibility is that all of these estimates reflect the operation of relatively independent mechanisms that integrate information over different time spans, with the specifics of the experimental protocol dictating which has the most profound impact on perception.

Guided by a consideration of various estimates for the integration of positional information for moving objects, we have chosen to assess how well a weighted average of multiple positional estimates from different channels with distinct integration times can account for our data. We have assumed channel integration times (*i*) of 1 ms (to reflect the contribution of an online monitoring of retinotopically mapped input), 80 ms (to reflect the contribution of intermediate integration times, see Eagleman & Sejnowski, 2000; Whitney, Murakami, & Cavanagh, 2000), and of 200 ms (to reflect the contribution of a protracted integration of positional information, see Maus, Ward, Nijhawan, & Whitney, 2013).

Both explanations were determined via Matlab scripts. The linear fit searched for the lowest squared residuals between the observed data and time constants from 1 ms to 400 ms, in 1-ms increments. The multichannel explanation followed the same procedure across all possible weighting combinations (between 1% and 100%) for the three channels chosen. The reported fits were the best found via these procedures.

According to our proposed coding scheme, the extent to which the apparent onset position of a moving element is extrapolated will vary if positional estimates from different channels are reweighted. Greater illusory position shifts should result when relatively greater weightings being given to channels with protracted integration times, but this would not impact on the physical stimulus exposure time at which illusory positional shifts maximize, as this will be determined by the largest integration time for any of the channels that contribute to the weighted average. We therefore determined estimates of point at which Fröhlich effects saturate as a function of stimulus exposure time by estimating of time constants for best-fit single-phase exponential decay functions fitted to baseline and fast motion adaptation data, averaged across observers.

## Results

A repeated measures ANOVA revealed a significant main effect of adaptation, such that participants reported *larger* distortions following adaptation to fast motion ($M = 1.40 +/- 0.38$) relative to baseline ($M = 0.37 = +/-0.30$; $F(1, 9) = 9.10$ $p = .015$, $\eta^2 = 0.5$). A best-fit function, from a model assuming a single channel that integrates positional information linearly over time, explained 29% of the variance in baseline data, and 42% of variance in adaptation data (see Figure 3d). The single free parameter in this model is the extent of time across which positional information is linearly integrated. These fits estimated integration time at 18 ms for unadapted data, and at 39 ms for adapted data. In this coding scheme, these values set the test presentation time at which the Fröhlich effect saturates. Note that neither of these times correspond with the time at which the Fröhlich effect saturated (~230 ms, see Figure 3d).

Once accounting for the number of free parameters, a dynamically weighted three-channel code could explain 62% of the variance in baseline data, and 89% of variance in adaptation data (adjusted $R^2 = .62$ and $.89$, respectively). This model consists of three channels that each integrate positional information linearly over time, across three different fixed integration times. There are three free parameters in this model—the weightings given to positional estimates from each of the three channels. A best-fit model to baseline data had channel weightings of 0.81, 0.06, and 0.13, whereas a best-fit model to fast motion adaptation data had channel weightings of 0.57, 0.31, and 0.12—therefore, a greater Fröhlich effect magnitude postfast motion adaptation was predicted via a greater relative weighting being given to positional estimates from the channel with an integration time of 80 ms, as opposed to the channel that has an integration time of 1 ms.

In addition to providing a better description of the data, relative to a linear integration of positional information, a dynamically weighted multichannel code makes some important qualitative predictions. First, this coding scheme predicts that the maximum possible saturation point, as a function of test presentation time,

should equal time corresponding to the integration period of the longest integrator contributing to the positional estimate. Thus, reweighting channel estimates will vary the magnitude of the Fröhlich effect, but will not impact on the saturation point as a function of presentation time. Another qualitative prediction is that the increase in Fröhlich effect magnitude as a function of time should be nonlinear, with a decelerating increase as progressively more fixed-channel-integration times are exceeded.

To assess the proposition that Fröhlich effects of different magnitude can share a common temporal saturation point, we assessed the time constants for best-fit single-phase exponential decay functions to our baseline and fast motion adaptation data sets. Doing so revealed no significant difference between time constant estimates ($0.013 +/- 0.013$ ms for baseline and $0.015 +/- 0.010$ ms for same-directional tests postfast motion adaptation; $F(1, 6) = 0.063$, $p = .810$). There was, however, a significant difference in the magnitude of Fröhlich effects in baseline and fast motion adaptation conditions, as reflected by the discrepant amplitudes at which cumulative function fits plateaued ($1.3° +/- 0.59°$ and $2.1° +/- 0.40°$, respectively, $F(1, 6) = 9.455$, $p = .022$). These data are therefore consistent with our proposal, that the perceived position of moving elements is determined via a weighted summation of positional estimates from multiple channels that each integrate positional information linearly, but over different periods of time.

A nonlinear decelerating increase in Fröhlich effect magnitude could also be predicted by a leaky single-channel linear integration of positional information. In this coding scheme changes in Fröhlich effect magnitude could be predicted by changing the amount of time across which positional information is integrated. This would, however, also predict a change in the presentation duration at which the Fröhlich effect saturates. Our data are inconsistent with this premise.

Another potential explanation for an enhanced Fröhlich effect postfast motion adaptation would be if a motion aftereffect selectively influenced the adapted baseline condition (single-frame presentations post adaptation). If adaptation had caused the perceived position of a single flashed frame to be shifted in the direction of a motion-aftereffect signal (see McGraw, Whitaker, Skillen, & Chung, 2002), but had had little or no impact on multiframe presentations, then the apparent exaggeration might simply reflect a distorted baseline, rather than an exaggerated Fröhlich. There was, however, no evidence for a significant difference between adapted ($0.25° +/- 0.27°$) and unadapted baselines ($-0.28° +/- 0.23°$, $t_9 = -1.657$, $p = .132$), and the direction of the difference (adapted baselines were associated with positional estimates that were relatively advanced along the trajectory for moving tests relative to unadapted baselines) would actually have encouraged *mitigated* Fröhlich effects post adaptation. We are therefore confident that our data cannot be accounted for via a selective distortion of our baseline measures (see Figure 3c).

## Discussion

Experiment 2 examined Fröhlich effect magnitude as a function of test duration, with and without prior adaptation to rapid motion. We replicated the main result of Experiment 1, in that the Fröhlich effect was exaggerated post adaptation (see Figure 3d). Results also revealed a nonlinear decelerating increase in Fröhlich effect

magnitude, both for tests conducted with and without preadaptation to fast motion. Moreover, as predicted by a dynamically weighted multichannel account of positional estimation, while fast motion adaptation resulted in exaggerated Fröhlich effects, adapted and nonadapted Fröhlich effects saturated at a *common* presentation time (see Figure 3e). Note that this pattern differs *qualitatively* from the predictions of a single channel mechanism that integrates positional information linearly over variable amounts of time (see Figure 3a and 3d).

Readers should note that our data, describing how the Fröhlich effect increases as a function of presentation time, is consistent with positional averaging. This type of hypothesis predicts that *any* period of movement will be subject to a Fröhlich effect, with a magnitude that scales with exposure duration until a saturation point is reached (which is determined by the extent of the averaging window). Our data are consistent with this, as they suggest an effect that increases smoothly, at least initially, as a function of exposure duration. We find no evidence for a change in the point in time at which the Fröhlich effect asymptotes, even when the Fröhlich effect is exaggerated by adaptation to fast motion. Readers might note that, at baseline, no Fröhlich effect was apparent at the shortest movement presentation time (25 ms), which is inconsistent with positional averaging. However, the very small Fröhlich effect predicted by positional averaging at this presentation time might not be easily detected, and we did measure a Fröhlich effect at this presentation time post adaptation to fast motion.

Another plausible coding scheme, that could predict how the Fröhlich effect should change with increasing test presentation times, would be if positional information were encoded via a single channel that leaks information progressively as a function of time (Fredericksen, Verstraten, & Van de Grind, 1994; Ossmy et al., 2013). Such a coding scheme is similar to a weighted average of estimates from multiple channels, in that it predicts a nonlinear decelerating increase in Fröhlich effect magnitude as a function of time, due to progressively less information being accrued. However, in order to predict a systematic change in Fröhlich effect magnitude, such a coding scheme would have to assume either a change in absolute integration time or a change in the degree to which information leaks. A change in absolute integration time would again predict a shift in the Fröhlich effect saturation point—an observation not supported by our data. Equally, while varying leak magnitude in isolation would maintain the point of saturation, the data observed here could only be fit by assuming that leakiness decreases following exposure to a noisy signal (fast adaptation), an assumption in direct contrast to existing evidence (Ossmy et al., 2013). As our data provide no evidence for a shift in the point at which the Fröhlich effect saturates, and effects become more pronounced following adaptation, we can dismiss this as a plausible explanation for our data (see Figure 3d).

## General Discussion

Our data suggest two novel observations concerning the perceived position of moving objects. First, this reflects a weighted average of positional information from multiple channels with different integration times. Second, the weighting applied to estimates from different channels is malleable, with increased weighting given to channels with protracted integration times post adap-

tation to a dynamic environment. This shift in weighting, in favor of channels with more protracted integration times, could have a functional benefit in terms of supporting a more accurate sense of a moving objects' trajectory (Clifford, Arnold, Wyatt, & Wenderoth, 2001; Clifford & Wenderoth, 1999; Phinney, Bowd, & Patterson, 1997). In essence, this would imply more smoothing of motion in dynamic environments (see Rao et al., 2001), potentially resulting in enhanced trajectory estimates.

Our data are inconsistent with a different type of explanation for the Fröhlich effect. It has been suggested that onset distortions could happen because perception is effectively delayed, with the initial trajectory of a moving element *suppressed* from awareness via backward masking (Kirschfeld & Kammer, 1999). Hypothetically, the functional benefit of suppressing awareness of signals trailing movement would be to make moving elements appear more sharply defined than they would otherwise (Pääkkönen & Morgan, 2001). One of the authors has recently shown that this can result in an illusory distortion of moving form, with segments of a moving stimulus located at trailing edges of movement *erased* from awareness (Marinovic & Arnold, 2013; see also Arnold et al., 2010). Our present data, however, show that fast motion adaptation results in a Fröhlich effect that is exaggerated, but which saturates at the same presentation time as at baseline. This is inconsistent with an effect driven by a perceptual delay, as the only way to increase the magnitude of such an effect would be to extend the perceptual delay, and this should have a commensurate impact on the exposure time necessary to observe a maximal magnitude Fröhlich effect. Note that a protracted period of backward masking is also at odds with the fact that, postfast motion adaptation, the Fröhlich effect can be discerned at *shorter* presentation times relative to baseline. This suggests a curtailed masking period, which should result in smaller Fröhlich effects according to the theory—the opposite effect to that suggested by our data.

One aspect of our data that is curious is how the efficacy of fast motion adaptation (which exaggerates Fröhlich effect magnitudes) contrasts with ineffectual slow motion adaptation. One possible explanation for this is that participants were already adapted to what is predominantly a static environment, so further adaptation to slow movement had no impact. Another noteworthy aspect of our data is that the adaptation effects were direction-tuned. Adaptation to fast motion exaggerated the Fröhlich effect for tests moving in the *same* direction, but had no discernable impact on tests moving in the opposite direction (see Experiment 1). This suggests that positional information is provided by direction-tuned mechanisms, and the extraction of this information is changed by motion adaptation.

Our data reveal two hitherto unknown characteristics of the Fröhlich effect. Our data reveal that (a) the Fröhlich effect is exaggerated by adaptation to fast motion, and (b) that the postfast motion adaptation exaggeration of the Fröhlich effect does not seem to be accompanied by a shift in the point at which the Fröhlich effect asymptotes as a function of presentation time. These twin observations must now be accounted for by any adequate account of the Fröhlich effect. Both of these observations can be accounted for via a positional averaging account, which taps multiple channels that accrue positional information over different time spans, if we assume that adaptation can reweight contributions from the different channels to the positional estimate. We acknowledge that other types of model might equally account

for these data (see Grossberg, 1973), and look forward to such proposals.

The accrual of information over time is a common computational strategy, repeatedly demonstrated in diverse contexts (Arnold & Lipp, 2011; Fredericksen, Verstraten, & Van de Grind, 1994; Haberman, Harp, & Whitney, 2009; Singer & Sheinberg, 2006; Smith, Bowen, & Pokorny, 1984; Tanaka, Kaiser, Butler, & Le Grand, 2012; Wallis, & Bulthoff, 2001). We propose that multiple channels with different integration times contribute to the determination of perceived position for moving objects, and that the weightings given to positional estimates from the different channels is dynamic, shifting to suit the dynamics of the prevailing environment. We have established evidence for this by examining the perceived onset location of moving objects. We anticipate that this computational strategy will be evident and have utility in diverse settings.

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