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An illusory distortion of moving form driven by motion deblurring

Welber Marinovic, Derek H. Arnold *

Perception Laboratory, School of Psychology, The University of Queensland, Australia

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ABSTRACT

Many visual processes integrate information over protracted periods, a process known as temporal integration. One consequence of this is that objects that cast images that move across the retinal surfaces can generate blurred form signals, similar to the motion blur that can be captured in photographs taken with slow shutter speeds. Subjectively, retinal motion blur signals are suppressed from awareness, such that moving objects seem sharply defined. One suggestion has been that this subjective impression is due to humans not being able to distinguish between focussed and blurred moving objects. Contrary to this suggestion, here we report a novel illusion, and consequent experiments, that implicate a suppressive mechanism. We find that the apparent shape of circular moving objects can be distorted when their rear edges lag leading edges by ~60 ms. Moreover, we find that sensitivity for detecting blur, and for discriminating between blur intensities, is uniformly worse for physical blurs added behind moving objects, as opposed to in-front. Also, it was easier to differentiate between slight and slightly greater physical blurs than it was to differentiate between slight blur and the absence of blur, both behind and in-front of moving edges. These 'dipper' functions suggest that blur signals must reach a threshold intensity before they can be detected, and that the relevant threshold is effectively elevated for blur signals trailing behind moving contours. In combination, these data suggest moving objects look sharply defined, at least in part, because of a functional adaptation that actively suppresses motion blur signals from awareness.

1. Introduction

Some visual operations are so successful that their existence and necessity can either go unnoticed or underappreciated. A possibly uncontroversial example is compensation for our own eye movements. Like an unsteady hand-held camera our eyes are constantly moving, even when we try to maintain fixation (Martinez-Conde, Macknik, & Hubel, 2004). But this is typically unnoticed, at least in part because of a visual operation that identifies retinal image motions that are caused by involuntary eye movements. While fundamental, the existence of this operation was only recently discovered (Murakami & Cavanagh, 1998). Another somewhat controversial example involves moving objects. These seem sharply defined despite the considerable image blur that is associated with retinal image motion (Burr, 1980).

To some extent, human vision can be thought of as a camera with a slow shutter speed. As visual information is integrated over an expanse of time (~100 ms), images that move across the retina can generate a considerable blur signal. Moving objects, however, usually seem sharply focussed. This has been linked to an active deblurring process, wherein motion blur signals are suppressed from awareness (Anderson & Van Essen, 1987; Burr, 1980; Burr, Ross, & Morrone, 1986). The nature of this suppression has, however, been a point of controversy. Here we will report on a novel visual illusion, and on the results of experiments conducted to clarify the causal mechanisms of this illusion, which seem to speak to the nature of motion deblurring.

While subjectively invisible, motion blur signals can be detected in recordings of brain activity (Geisler et al., 2001). Moreover, these 'unseen' motion blur signals can modulate perceptual judgments, for better and worse. For instance, motion blur signals seem to *enhance* direction discriminations, as their elongation signals the axis of motion (Apthorp & Alais, 2009; Apthorp, Cass, & Alais, 2011; Badcock & Dickinson, 2009; Burr & Ross, 2002; Edwards & Crane, 2007). Conversely, when physical blur is added to moving inputs, motion blur seems to have an adverse impact, making it harder to identify the more blurred input. It is as if retinal motion blur signals summate with physical blur signals, resulting in people having to differentiate between two very blurred inputs, as opposed to two less blurred objects (Burr & Morgan, 1997; Morgan & Benton, 1989). Accordingly, an influential suggestion has been that retinal motion blur signals are not actively suppressed, but are merely unapparent as the human visual system is unable to perform the requisite discrimination to decide if a moving object is sharply focussed or blurred (Burr & Morgan, 1997).

Recently, while conducting an experiment on the impact of motion adaptation on the ability to track moving objects (Marinovic,

* Corresponding author.
E-mail address: d.arnold@psy.uq.edu.au (D.H. Arnold).

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Pearce, & Arnold, 2013), we noticed a novel visual illusion that might be a consequence of motion deblurring. At some speeds, circular moving elements seemed to have an altered shape. As one might expect from the involvement of a deblurring process, it was the trailing edge of physically circular moving elements that seemed deformed, as if they had a crescent cut out of them, or a flattened trailing edge (see Fig. 1 and Supplementary Movies). As these perceptual distortions seemed to involve an apparent suppression of the trailing extremities of moving elements, we felt that they spoke in favour of an active inhibitory account of deblurring (see Paakkonen & Morgan, 2001), as opposed to a simple failure to distinguish between different blur magnitudes (Burr & Morgan, 1997). According to the former account, form signals trailing behind moving contours might become hard to detect at certain combinations of lag and speed as they will be subject to a time dependent inhibitory process.

2. Experiments 1 and 2 – Distortion of moving form

In Experiments 1 and 2 we sought to determine the stimulus conditions that give rise to a subjective distortion of moving form.

Six volunteers participated in Experiments 1 and 2, including the authors and four additional observers who were naïve as to the experimental purpose. All had normal or corrected-to-normal visual acuity. Visual stimuli were generated with Cogent 2000 Graphics running in MATLAB 7.5 software, and displayed on a 19″ Sony Trinitron G420 monitor (1280 × 1024 resolution at 60 Hz). Stimuli were viewed from 57 cm with the head placed in a chin rest. Responses were recorded via mouse button presses.

3. Experiment 1

Stimuli consisted of a circular rotating pattern, which comprised either of 3, 6 or 12 individual white (CIE, White: $x = 0.27$, $y = 0.27$, $Y = 75$) circular elements radially arranged about a central fixation point. Diameters of the individual white elements subtended 0.73 degrees of visual angle (dva) at the retina, and were displayed against a black background. The distance between fixation and the centre of individual rotating elements was 3.25 dva.

On each trial participants were asked to fixate a central white fixation point (0.43 dva) as the test rotated at one of 8 speeds. During a block of trials test speed was manipulated according to the method of constant stimuli (0.08–0.66 revolutions per second, in steps of 0.08 revolutions per second). Each speed was sampled 10 times for each of three test stimulus configurations for a total of 240 individual trials, which were completed in random order. Direction of rotation, clockwise or counter-clockwise, was reversed on a trial-by-trial basis to mitigate the build-up of directional adaptation. In the supplemental materials we have provided some sample Matlab code, that can be used in conjunction with Cogent (http://www.vislab.ucl.ac.uk/cogent_2000.php) and a CRT monitor, to gain a good impression of the appearance of this stimulus under experimental conditions.

At the end of each trial participants reported on the apparent shape of elements within the moving pattern by responding to a seven alternative classification task by pressing one of 7 buttons on a keyboard (see Fig. 2). Alternatives were: (1) Crescent – a distorted trailing edge with a missing crescent, (2) Flat – a distorted trailing edge with a flat edge, (3) Blurred – a blurred trailing edge, (4) Normal – an apparently sharply defined circular shape, (5) Blurred leading edge, (6) Flat leading edge, and (7) Crescent shaped leading edge.

When a distorted appearance was reported, participants were able to adjust the appearance of a subsequent static element centred 3.25 dva above fixation, a position coinciding with the apex of element trajectories during animation. When a Flat or Crescent shaped appearance was reported, participants could eliminate part of either the leading or trailing edge by progressively obscuring the static white element with a black circular (Crescent) or square (Flat) element of matched dimensions. The position of the occluding black element could be manipulated left and right by pressing the left or right mouse buttons. The initial position of the occluder abutted the left or right edge of the static white element (to the left when elements that had rotated clockwise had been said to have distorted trailing edges, to the right when elements that had rotated counter-clockwise had been said to have distorted trailing edges).

When a Blurred appearance was reported, participants could extend the static element in the appropriate direction by pressing the left or right mouse buttons, so as to make the blurred side elongated or contracted. When participants were satisfied that the

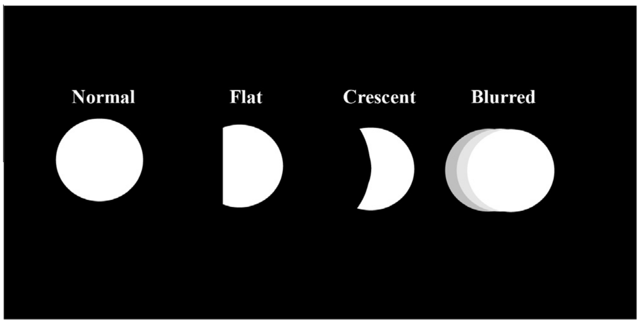

Fig. 1. Depictions of the subjective appearance of physically circular moving elements. These could seem circular and sharply defined (Normal), as if they had a flattened trailing edge (Flat), as if they had a crescent missing from the trailing edge (Crescent), or as if they had a blurred tail trailing behind (Blurred). Participants could report which of these configurations moving elements had most resembled and then, in all cases except for a 'Normal' appearance, adjust the extent of the distortion in a static element until they felt it matched the appearance of the rotating test elements.

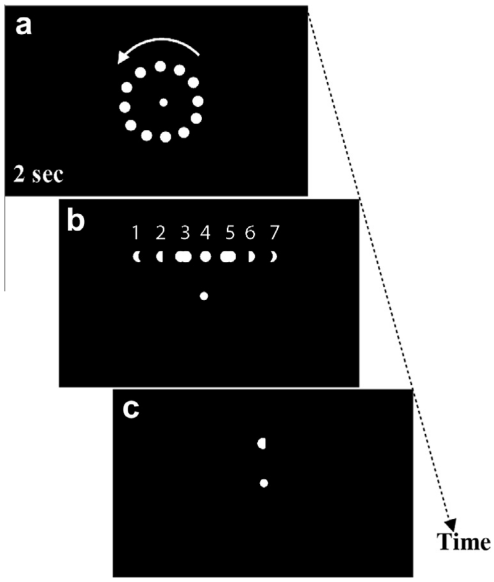

Fig. 2. Sequence of events during a trial in Experiments 1 and 2. (a) Participants first viewed an array of rotating circular elements. (b) Then they completed a 7-alternative classification task, cued by an array of 7 numbered elements. (c) If a distorted appearance was reported, they then completed an adjustment procedure (see Experimental Procedures for further details). This illustration depicts a trial in which the participant reported a flat trailing edge.

static reference matched the appearance of moving elements during the trial, participants terminated the adjustment procedure by pressing the middle mouse button.

4. Results and discussion

While participants could report that it had been the leading edge of moving elements that had seemed distorted, this only happened on 6 of 1440 trials completed by all participants, as opposed to the 520 trials wherein a distorted trailing edge was reported. Consequently, we have only analysed data relating to trailing edges. In Fig. 3 we have depicted the proportion of trials wherein participants reported Crescent shaped or Flattened trailing edges (Fig. 3a), Blurred trailing edges (Fig. 3c), or a Normal moving element appearance (Fig. 3b).

The optimal speed for inducing illusory distortions of moving form was estimated by fitting Gaussian functions to proportions of illusory distortion reported by each individual for each of 8 test speeds for each of 3 test configurations (see Fig. 3a and Table 1). Estimates were 0.44 (SE: 0.03) revolutions per second (rps) for tests containing 12 circular elements (95% confidence intervals: 0.36–0.52 rps), 0.44 rps (SE: 0.02) for tests containing 6 elements (95% confidence intervals: 0.37–0.50), and 0.43 rps (SE: 0.09) for tests containing 3 circular elements (95% confidence intervals: 0.33–0.53). An analysis of the means of the fitted Gaussian functions found no evidence for a main effect of stimulus configuration (Repeated measures Anova $F_{2,10} = 0.385$, $p = 0.69$, $\eta_p^2 = 0.07$). These data were re-analysed without the author data, and results were qualitatively matched (Repeated measures Anova $F_{2,6} = 1.114$, $p = 0.39$, $\eta_p^2 = 0.27$). Although we have not included further analyses of this type, analyses without author data were done as a routine precaution for all subsequent analyses, and in no case did this produce a qualitatively discrepant result. Readers can assess this for themselves by inspecting individual data provided in Table 1.

A further analysis concerning the full-width-half-heights of the fitted Gaussian functions also found no evidence for a main effect of stimulus configuration (Repeated measures Anova $F_{2,10} = 0.145$, $p = 0.87$, $\eta_p^2 = 0.03$). These data suggest that trailing edge shape distortions are tuned for element velocity (~0.44 rps or 8.98 dva/s), rather than for the rate at which individual moving elements repeatedly occupy the same positions – the local temporal frequency of the stimulus. Note also that these data suggest that the spatial proximity of stimulus elements is not critical for this illusion, as the inter-element spacing in the 3-element display was much greater than in the 12-element display, and yet the optimal speed for illusory distortion was matched for these two configurations (see Fig. 3a).

At the optimal test speed for inducing illusory distortions ~25% (SE: 0.04) of individual moving elements, located toward trailing edges, were suppressed from awareness. This was evident from how much of a static reference participants removed via adjustment in order to match the appearance of circular elements that seemed to have either a 'Flat' or 'Crescent' shaped appearance while rotating (see Fig. 1). The magnitude of this effect did not vary across our three stimulus configurations (Repeated measures Anova $F_{2,10} = 0.542$, $p = 0.59$, $\eta_p^2 = 0.09$). This implies a suppressive mechanism targeting portions of moving elements trailing leading edges by a fixed temporal interval of ~60 ms (SE: 3.4). A plausible mechanism would be backward meta-contrast masking (Breitmeyer, 1984), with the leading edge of moving elements masking the trailing extremities of the same elements. Accordingly, illusory distortions of elements within our stimulus might not have happened at greater speeds, as at these speeds all sections of a moving element would have moved beyond the zone targeted for suppression once 60 ms had elapsed.

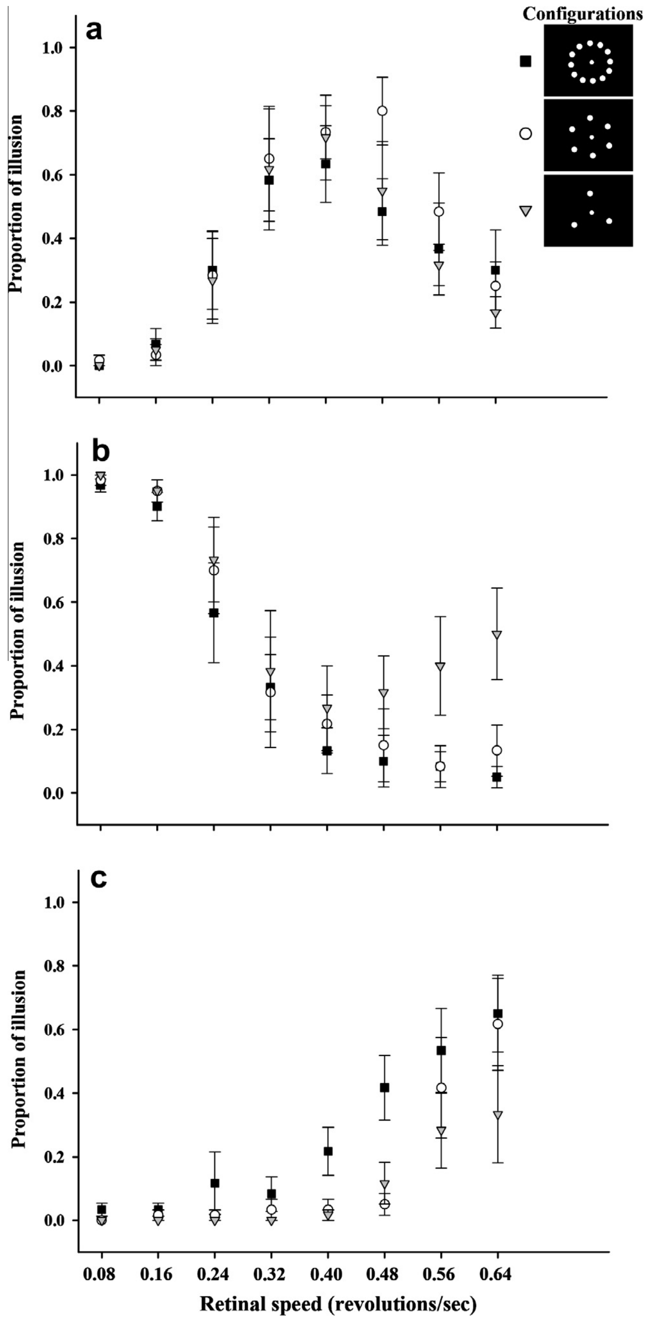

Fig. 3. Proportion of trials in which rotating circular elements were reported to have a distorted trailing (a), normal (b) or blurred edge (c) as a function of element revolution speed. Data are shown for test configurations comprising of 3, 6 or 12 elements. Error bars depict the standard error of the mean.

Our data also suggest a minimal stimulus speed in order for illusory distortions to occur, with little or no evidence of illusory distortions of moving elements at rotation speeds below ~0.24 rps (the speed coinciding with the lower limit of full-width-half-heights of fitted Gaussian functions, averaged across participants and stimulus configurations). Two factors might contribute to this. First, stimulus speed must be sufficient to excite a robust response from transient temporally band-pass tuned mechanisms while prompting low-pass filters to signal retinal-motion blur. Previously, it has been estimated that dots must move a distance greater than their' width every 100 ms in order for low-pass filters to generate a robust retinal motion blur signal, because of protracted temporal integration times (see Geisler, 1999). This would coincide

Table 1
Obtained results for individual data fits in Experiment 1 and 2.

ID	3 Elements			6 Elements			12 Elements		
	Peak	FWHH	G. Fit	Peak	FWHH	G. Fit	Peak	FWHH	G. Fit
Experiment 1									
SP	0.40	0.12	0.90	0.39	0.14	0.85	0.37	0.10	0.96
KS	0.41	0.10	0.79	0.45	0.13	0.89	0.43	0.13	0.92
RG	0.60	0.15	0.81	0.57	0.17	0.81	0.56	0.06	0.95
WM*	0.35	0.07	0.95	0.40	0.09	0.90	0.36	0.07	0.96
PM	0.48	0.08	0.93	0.46	0.04	0.98	0.46	0.11	0.91
DA*	0.36	0.12	0.87	0.43	0.14	0.87	0.49	0.24	0.69
Mean	0.43	0.11	0.88	0.45	0.12	0.88	0.44	0.12	0.90

ID	3 Elements			6 Elements		
	Peak	FWHH	G. Fit	Peak	FWHH	G. Fit
Experiment 2						
SP	0.84	0.26	0.86	0.59	0.14	0.99
KS	0.91	0.25	0.85	0.71	0.08	0.98
RG	0.94	0.19	0.93	0.76	0.20	0.98
WM*	0.71	0.15	0.99	0.61	0.17	0.81
PM	0.90	0.20	0.80	1.01	0.28	0.94
DA*	0.77	0.27	0.81	0.76	0.25	0.89
Mean	0.84	0.22	0.87	0.74	0.18	0.93

Peak = speed at which the fitted Gaussian function reaches maximum amplitude. FWHH = full-width-half-heights of fitted Gaussian function. G. Fit = Gaussian function Goodness of fit.
* Author data.

with a rotation speed of ~0.31 rps for our stimulus, which is reminiscent of the minimal speed for illusory distortions (~0.24) reported here.

Another factor that might shape the probability of illusory distortions of moving shape is the existence of a threshold encoded intensity for perceptual suppression (with sub-threshold intensities being successfully suppressed) coupled with a time-averaging of encoded intensity at each retinotopic location, such that encoded intensity at any given epoch will be unevenly distributed across a retinotopic mapping of responses associated with a moving stimulus. Hence we would only expect moving elements to appear 'shortened' when moving at a sufficient speed and when the encoded intensity of the trailing edge is sufficiently weak. In sum, we believe there will be an interaction involving the time course of the suppressive mechanism, stimulus speed and the size of moving elements. In combination these factors will dictate if an apparent distortion of moving form is likely to ensue.

5. Experiment 2

To test for an interaction involving element size and speed, in Experiment 2 we doubled the size and speed of the circular moving elements. Further details for Experiment 2 were as for Experiment 1, with the following exceptions. In this experiment we only used configurations with 3 or 6 elements, as doubling element sizes would have caused overlap in a 12-element display.

Gaussian function fits to individual data from Experiment 2 (see Table 1) suggest optimal average speeds of 0.84 rps (SE: 0.03) for tests containing 3 circular elements (95% confidence intervals: 0.76–0.92 rps), and 0.74 rps (SE: 0.06) for tests containing 6 circular elements (95% confidence intervals: 0.58–0.89 rps). Thus doubling element size approximately doubled the requisite speed for inducing illusory distortions to the shape of moving elements, from ~0.44 rps (Experiment 1) to ~0.79 rps (Experiment 2; paired *t*-test: $t_5 = 11.05$, $p < 0.001$, $r = 0.83$, see also Table 1).

At the optimal speed for inducing illusory distortions of physically circular moving elements in Experiment 2 ~25% (SE: 0.03) of the trailing extremities of moving elements were suppressed from awareness. The magnitude of this effect was very similar to that observed in Experiment 1 (paired *t*-test: $t_5 = 0.65$, $p = 0.95$, $r = 0.33$). Overall, these data are consistent with an active inhibitory process, that targets form signals trailing ~60 ms behind moving contours.

The results of Experiments 1 and 2 suggest an alternate explanation for previous findings. For example, differentiating between the magnitudes of luminance ramps, which differ in physical intensity, can be more difficult when the luminance ramps are positioned behind moving contours as opposed to in front. Moreover, this enhanced difficulty increases with stimulus speed (Burr & Morgan, 1997). The interpretation of these data must be considered in conjunction with the fact that it is *harder* to differentiate between different blur magnitudes when both blur signals are strong, as opposed to weak. So a plausible interpretation of these data, favoured by the authors, is that retinal motion blur signals that trail behind moving contours summate with physical blur signals, whereas there is no such summation in advance of moving contours. This would result in more intense combined signals trailing behind moving contours, which are consequently harder to distinguish. According to this view there would be no active suppression of retinal motion blur signals. Rather, these signals would persist within the visual system and impact perceptual judgments. The subjective 'invisibility' of retinal motion blur signals was attributed by these authors to humans being unable to differentiate between moving stimuli that are sharply defined or somewhat blurred (Burr & Morgan, 1997).

An alternate explanation for enhanced difficulty when differentiating between physical blurs trailing behind moving contours, as opposed to in-front, is that while retinal motion and physical blur signals might summate, these combined signals are targeted for suppression by a common active inhibitory process. Less intense combined signals might then be entirely suppressed from awareness, whereas stronger combined signals might only be mitigated.

To tease these possibilities apart, in Experiment 3 we examine the ability to discriminate between different intensities of physical blur placed at either the leading or trailing edges of moving contours (see Fig. 4). If blur signals positioned behind moving contours tend to be subjectively invisible because they are suppressed via an active process, blur signals will need to be more intense when trailing behind moving contours, as opposed to in front, before they reach a threshold for visibility. Alternatively, if motion blur signals simply summate with physical blur, physical blur signals at trailing edges should be visible at lower physical intensities.

6. Experiment 3 – Leading and trailing edges sensitivity

Details for Experiment 3 were as for Experiments 1 and 2, with the following exceptions.

Six volunteers participated in Experiment 2, including the first author (WM) and five additional participants who were naïve as to the experimental purpose. All had normal or corrected-to-normal visual acuity and reported having normal colour vision. Stimuli consisted of an array of 4 circular elements radially arranged about the central fixation point (see Fig. 4). The individual elements had a diameter subtending 0.7 dva. The outer diameter of the test configuration subtended 3.6 dva. Two of the rotating elements were red ($x = 0.63$, $y = 0.33$, $Y = 24$), whereas the other two were green ($x = 0.28$, $y = 0.61$, $Y = 24$). The different colours were used as an identification cue, making a two-alternative forced choice paradigm possible.

On each trial participants were required to look at the fixation point (0.4 dva) as the four stimulus elements rotated at 0.4 rps (the optimal speed to evoke shape distortions, as determined in Experiment 1). The luminance of stimulus elements increased

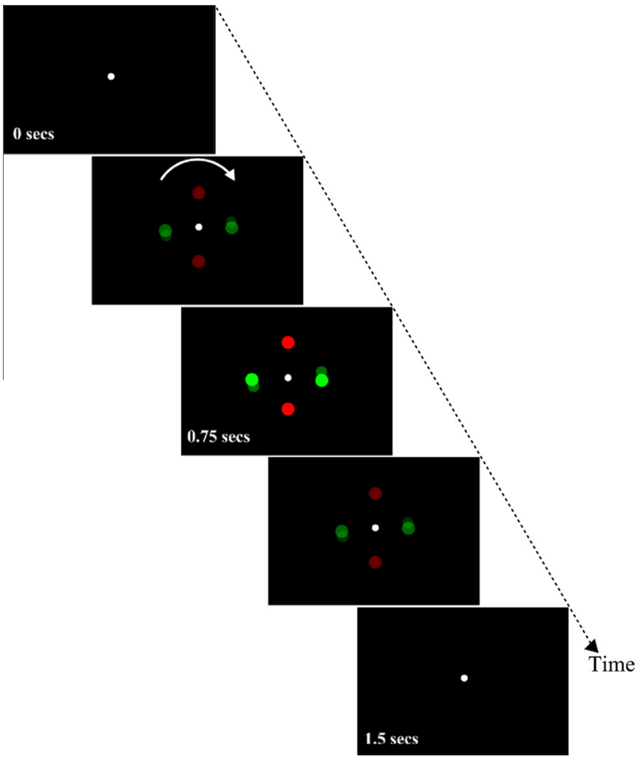

Fig. 4. Sequence of events in Experiment 3. The illustration shows a trial in which physical luminance ramps were added to the trailing edge of green elements. The intensity of the moving elements, and associated blur signals, was linearly ramped on and off over 0.75 s, for a total 1.5 s presentation. Participants chose which pair of elements (red or green) had seemed more blurred. See Experimental Procedures for further details. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

linearly, reaching a peak of 24 cd/m^2 0.75 s into the presentation, then decreased linearly for the same duration, resulting in a 1.5 s presentation (see Fig. 4).

Physical luminance ramps (which simulated retinal motion blur when positioned at the trailing edges of moving elements) were added to one of the two pairs of differently coloured rotating elements. These were generated by setting crescent shaped regions, being the difference between element positions on the current and last frame of the animation (for trailing blur) or the difference between element positions on the current and next frame of the animation (leading blur), to a multiple of element luminance intensity. Intensity was then linearly reduced (to 0) across crescents coinciding with the next 11 preceding (trailing blur) or succeeding (leading blur) positions, simulating a 100 ms blur signal matched in colour to the relevant rotating elements (see Fig. 4). Note that the increasingly faint crescents positioned in advance of moving elements did not resemble the effects of retinal motion blur in any way (motion blur necessarily lags moving contours), but were included as a control for the trailing edge condition.

In a baseline condition physical luminance ramps were only presented adjacent to one pair of 'target' elements (red or green). This allowed us to determine thresholds for detecting physical luminance ramps at leading and trailing edges. In subsequent conditions all elements were accompanied by physical luminance ramps (pedestal blur). Non-target elements had pedestal signals set to either 1, 2 or 4 times the participants' detection threshold for the relevant edge (leading or trailing), whereas target elements had one of 8 more intense (relative to non-targets) signals. This allowed us to determine luminance increment thresholds for identifying which pair of elements had the brighter physical luminance ramp.

At the end of each trial participants reported which pair of elements (red or green) had the more intense physical luminance ramp by pressing one of two mouse buttons. During a block of trials each of 7 target ramp intensities was presented 12 times in a pseudo random order, according to the method of constant stimuli. Participants performed two blocks of trials for each of the four experimental conditions, baseline and pedestal ramps set to 1, 2 or 4 times the relevant threshold (with distinct thresholds for ramps at leading and trailing edges). Data were collated across the two blocks of trails for each experimental condition. The six non-baseline conditions were completed in a pseudo-randomised order.

7. Results

We found that physical luminance ramps (which simulated blur when placed at the trailing edges of motion) had to be more intense when trailing behind a moving contour in order to be detected, relative to ramps positioned in front of leading edges (Baseline lead vs. Baseline trail, paired t-test: $t_5 = 5.061$, $p = 0.004$, $r = 0.71$). Moreover, at leading edges we found that it was easier to differentiate between slight and slightly greater physical luminance ramps than it was to differentiate between slight ramps and the absence of a ramp (compare Baseline with Threshold pedestal data in Fig. 5). Differentiating between ramp intensities then became progressively more difficult as physical ramp intensities increased. This pattern of results is a common finding, known as a dipper function (Nachmias & Sansbury, 1974). The presence of a 'dip' in this function explains why polynomial contrasts revealed that a quadratic trend provided a better description of these data ($F_{1,5} = 90.23$, $p < 0.001$, $\eta_p^2 = 0.95$) than did a linear trend ($F_{1,5} = 21.25$, $p = 0.006$, $\eta_p^2 = 0.81$).

If we analyse data in terms of multiples of threshold contrast, the only discrepancy between data for the leading and trailing edges is that sensitivity at trailing edges is uniformly worse than sensitivity at leading edges (see Fig. 5; main effect of blur location $F_{1,5} = 22.09$, $p = 0.005$, $\eta_p^2 = 0.81$; ramp location x pedestal intensity interaction $F_{3,15} = 1.27$, $p = 0.32$, $\eta_p^2 = 0.20$). This is inconsistent with what we would expect if ramp intensity discriminations at trailing edges of motion were more difficult purely because physical luminance ramps and retinal motion blur signals summate. If

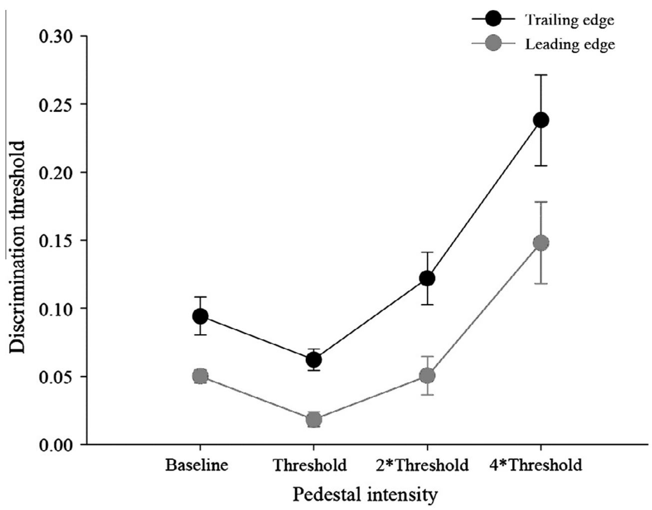

Fig. 5. Discrimination thresholds for physical luminance ramps as a function of the magnitude of the physical luminance ramp at corresponding edges of all elements (pedestals). Data are shown for physical luminance ramps at both the leading and trailing edges of moving elements. Error bars depict standard error mean.

one considers trailing edge baseline thresholds in relation to the leading edge function, performance suggests a position along the leading edge function in-between pedestal values of 2 and 4 times threshold. So one could surmise that this is the approximate magnitude of the retinal motion blur signals trailing behind moving contours in this stimulus, as this is the magnitude of *physical* luminance ramp that would need to be added to the leading edges of stimuli in order to match baseline performance at trailing edges. At this point of the leading edge function sensitivity declines for additionally intense luminance ramps, and yet the trailing edge function displays improved sensitivity (a dip) with the addition of a slight physical ramp pedestal relative to baseline. This would seem to suggest that something more than summation is needed to explain relative insensitivity at trailing edges of motion.

An alternate possibility is that both physical luminance ramps and retinal motion blur signals trailing behind moving contours are subject to an active inhibitory process, as suggested by Experiments 1 and 2, and that this process does not target signals in advance of moving contours. We could further assume that this inhibitory process is achieved via a divisive modulation of gain (Geisler & Albrecht, 1992; Meese & Holmes, 2002; Watson & Solomon, 1997; Wilson & Humanski, 1993; Wilson & Kim, 1998). We could then estimate the magnitude of the divisive gain modulation by expressing the average baseline threshold at leading edges (0.51 ± 0.04) as a fraction of the average baseline at trailing edges (1.07), resulting in an estimate of ~0.48.

In Fig. 6a we have plotted individual luminance increment thresholds, at both leading and trailing edges of motion, as a function of physical pedestal intensities. Data relating to leading and trailing edges are markedly different. If insensitivity at trailing edges is driven by divisive gain modulation, these discrepancies should be eliminated by compensating for the reduction in gain at trailing edges, by dividing individual trailing edge thresholds and corresponding pedestals by the denominator calculated from the grouped averaged data (0.48). A plot of adjusted trailing edge data, along with raw leading edge thresholds and associated pedestal values, are depicted in Fig. 6c. As can be seen, applying this adjustment to trailing edge data results in a good match between the two data sets.

Figure panels 6b and 6d consist of *XY* plots of luminance increment thresholds at leading and trailing edges, with data points representing individual data paired on the basis of pedestal intensity (multiples of baseline thresholds). Trailing edge increment thresholds in Fig. 6b are unadjusted, whereas trailing edge increment thresholds in Fig. 6d are adjusted to compensate for the estimated impact of divisive gain modulation. As can be seen, there is a significant correlation between leading and trailing edge increment thresholds ($r = 0.77$, $p < 0.001$) which gives rise to a slope that is markedly less than 1 for unadjusted data (see Fig. 5b; slope = 0.549, SE = 0.09, 95% Confidence Intervals 0.348–0.750) but to a slope that is consistent with a 1:1 relationship (slope = 1.12, SE = 0.19, 95% Confidence Intervals 0.71–1.53) for adjusted trailing edge data. This reflects the fact that increment thresholds at trailing edges are numerically greater than corresponding leading edge thresholds when data are expressed as a function of pedestal intensity (as multiples of baseline threshold, see Fig. 5), but threshold magnitudes are well matched when trailing edge data are adjusted to compensate for the estimated impact of divisive inhibitory gain control. Note that these analyses focus on increment thresholds, as opposed to pedestal values which by definition are matched by our adjustment (as individual pedestals were set to multiples of baseline thresholds, and our adjustment equates individual baseline thresholds).

8. Discussion

We believe we have found a situation wherein the processes that help suppress awareness of retinal motion blur signals result in an apparent distortion of moving form. This depends on the trailing edges of moving elements moving into a zone targeted by an inhibitory process ~60 ms after the element's leading edge had occupied the same position. Moreover, we have shown that the deblurring process is active, in that it results in an objective reduction in sensitivity for physical blur signals added behind

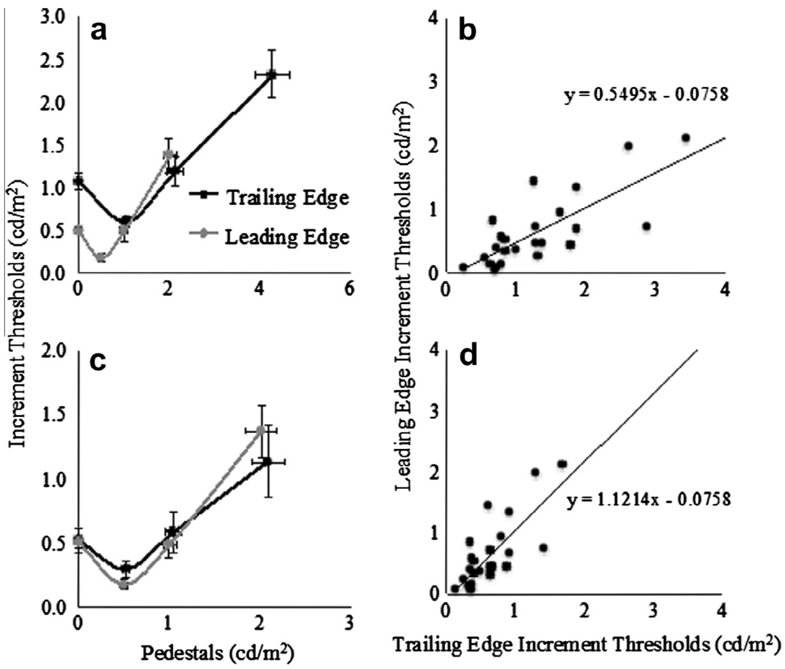

Fig. 6. Luminance increment thresholds as a function of pedestal intensity (a and c). Data are shown for raw leading and trailing edge datasets (a) and for raw leading edge and adjusted trailing edge datasets (c, see main text for an explanation). We have also depicted *XY* scatter plots depicting individual Leading edge increment thresholds relative to either raw (b) or adjusted (d) trailing edge increment thresholds. Here individual data points are paired on the basis of pedestal intensities (multiples of corresponding baseline increment threshold).

moving contours. These data are inconsistent with the notion that people simply fail to notice retinal motion blur because it is too hard to differentiate between moving elements that are blurred and sharply defined (Burr & Morgan, 1997). Instead, our data are consistent with a deblurring mechanism that does not differentiate between retinal motion blur and simulated physical blur signals (e.g. luminance ramps) – both are targeted for suppression.

To the best of our knowledge, the illusory distortion of moving form we have reported is novel. We believe this apparent distortion of moving form results from an inhibitory process of visual masking (Breitmeyer, 1984; Cass & Alais, 2006; Cass et al., 2009). In this instance it would seem that the trailing extremities of a moving element is masked be that elements' leading edge. We suggest that this illusory distortion results from a functional adaptation, which helps to create the impression that moving objects are sharply defined, despite the considerable retinal motion blur signals that can be associated with moving objects due to protracted temporal integration times in human visual processing (Apthorp & Alais, 2009; Apthorp, Cass, & Alais, 2011; Badcock & Dickinson, 2009; Burr & Ross, 2002; Edwards & Crane, 2007).

Previously it has been argued that detecting physical blur signals, and differentiating between different magnitudes of blur, is disproportionately difficult at trailing edges of motion because retinal motion blur signals summate with added physical blur (Burr & Morgan, 1997). The subjective invisibility of retinal motion blur signals was attributed to humans being unable to differentiate between moving contours that are blurred or sharply defined (Burr & Morgan, 1997). We do not believe this explanation can account for our observations. First, we have documented an illusory distortion of moving form perception, wherein a good proportion of a moving element's trailing extremities are erased from awareness. This seems to speak in favour of an active inhibitory process, rather than to an inability to distinguish between blurred and sharply defined contours. Second, if retinal motion blur signals act as a pedestal for physical luminance ramps, one could reasonably expect the latter to be detectable at lesser intensities at trailing edges than at leading edges. The results of Experiment 3 show that the reverse is true.

Our data show that it is harder to detect physical luminance ramps trailing behind moving contours than it is to detect luminance ramps placed in advance of moving contours. One could take this as evidence for there being discrepant perceptual thresholds at leading and trailing edges. Possibly a more nuanced interpretation would be that the perceptual thresholds for blur at leading and trailing edges of motion are equivalent, but due to there being an active inhibitory process at trailing edges, more intense physical inputs are required relative to leading edges in order to achieve a requisite level of encoded intensity for perceptual detection. This suggestion is consistent with our dipper functions.

The dips of dipper functions have been associated with the need for a signal to surpass a visibility threshold, thus adding a weak signal (known as a pedestal) to all elements can actually help people detect a weak additional signal at a given location, as the two signals at this location combine to exceed threshold (for a historical review see Solomon, 2009). When expressed in terms of physical input intensity, the dips in our leading and trailing edge functions are displaced (see Fig. 6a) but they are aligned when we adjust our data (see Fig. 5c) to estimate encoded signal intensities after the impact of an inhibitory divisive modulation of gain (Geisler & Albrecht, 1992; Meese & Holmes, 2002; Wilson & Humanski, 1993; Wilson & Kim, 1998) at trailing edges of motion.

An alternate interpretation of our data might be that the distortion of moving form perception results from localised neural adaptation, with encoded intensity gradually diminishing over the time that a given pixel is persistently lit as it signals the presence of a moving element. At the optimal speed to induce our illusion, this equates to a duration of approximately 50 ms. We believe this renders this explanation implausible, as fading due to neural adaptation usually requires a much longer exposition (Livingstone & Hubel, 1987), in the order of seconds rather than milliseconds. Moreover, while neural response rates can diminish over brief exposure durations (10's of milliseconds, see Baccus & Meister, 2002), perceived intensity is actually subject to temporal integration. Inputs of matched physical intensity can seem to be mismatched, with apparent brightness positively correlated with exposure duration up to a period of ~100 ms (Barlow, 1958; Legge, 1978).

The dynamics of our illusion are more consistent with the dynamics of the human temporal impulse response function, wherein an initial positive response to a flash is followed ~50 ms later by a negative response (see Watson, 1986). This can have a profound impact on motion coding. Time lagged negative responses to greyscale images can interact with an intervening mean grey input to create a vivid impression of coherent movement, which is not seen in the absence of the intervening input (see Mather, 2006 and http://www.lifesci.sussex.ac.uk/home/George_Mather/TwoStrokeFlash.htm). In this instance, motion coding treats delayed negative responses to flashed images as an input. In the case of our data and illusion, a delayed negative neural response might be interacting with persistent responses from low-pass temporal filters (see Paakkonen and Morgan (2001) for a model consistent with this proposal). If time lagged negative responses summate with persistent responses from temporally low-pass mechanisms, the extent of encoded retinal motion blur signals would be curtailed.

Overall, our data implicate an inhibitory process that can impact blur signals trailing behind moving contours. This process does not seem to differentiate between retinal motion blur and physical luminance ramps, suppressing both. We believe this results in blur signals (specifically linear luminance ramps, brightest immediately adjacent to moving elements) having to be more intense to reach a level required for perceptual awareness relative to signals positioned in advance of moving contours. This inhibitory process also seems to result in an illusory distortion of moving form when the physical dimensions and speed of a moving element combine to place its trailing edge ~60 ms behind its leading edge. We suspect that the precise characteristics of this relationship will vary according to the luminance intensity of the moving elements, the contrast between elements and background, and the adaptive state of the visual system. However, it would seem that it is reasonably easy to elicit this interaction in order to bring about an illusory distortion of moving form. Initially, we did so by accident.

Observations reported here extend an established line of investigation in our lab. Recently, lab members discovered a novel form of perceptual rivalry, dubbed spatio-temporal rivalry (Arnold et al., 2010). This phenomenon can be induced with a stimulus consisting of a square-wave, predominantly red-armed, windmill pattern with thin green stripes extending across the mid-points of each arm. When rotated at sufficient speed the thin green stripes can seem to form a solid static green ring. Moreover, the illusory static ring can seem to intermittently disappear, replaced by an impression of an entirely red rotating windmill pattern. The illusory static ring seen in these circumstances seems to be mediated by mechanisms with relatively protracted integration times, otherwise the physically segregated moving green elements would not seem co-joined. We have characterised this as a visible consequence of retinal motion blur signals, which seem to engage in an inhibitory interaction with signals pertaining to moving form (Arnold et al., 2010). This is consistent with our suggestion here, that both physical luminance ramps and retinal motion blur signals are targeted for suppression by a common inhibitory process, that results in physical simulations of blur being *harder* to detect when trailing behind a moving contour, as opposed to when they are positioned in advance.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2013.05.009.

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