

*i-Perception* (2011) volume 2, pages 1063–1075

dx.doi.org/10.1068/i0435

ISSN 2041-6695

perceptionweb.com/i-perception

# Effect of speed overestimation on flash-lag effect at low luminance

#### Maryam Vaziri-Pashkam

Vision Sciences Laboratory, Department of Psychology, Harvard University, Cambridge, MA, USA; e-mail: mvaziri@fas.harvard.edu

#### Patrick Cavanagh

Vision Sciences Laboratory, Department of Psychology, Harvard University, Cambridge, MA, USA; and Laboratoire Psychologie de la Perception, CNRS UMR 8158, Université Paris Descartes, Sorbonne Paris Cité, Paris, France; e-mail: patrick.cavanagh@parisdescartes.fr

Received 12 April 2011, in revised form 7 December 2011; published online 19 December 2011

**Abstract.** When a brief flash is presented at the same location as a moving object, the flash is perceived to lag behind the moving object to an extent that increases with the speed of the object. Previous studies showed that moving objects appear faster at low luminance as a result of their longer motion trace. Here we examine whether this faster perceived motion also affects the amount of the flash lag at low luminance. We first verified that speed was overestimated at low luminance with our stimulus. We then asked subjects to align a briefly flashed dot with the moving target. Results showed that the flash-lag effect increased with physical speed at both high and low luminance, but there was no additional increase due to the perceived increase of speed at low luminance. We suggest that although motion blur contributes to perceived speed, it does not contribute to the speed information that influences its perceived position.

Keywords: flash lag effect, Pulfrich effect, low luminance, speed perception, position perception, motion perception.

## 1 Introduction

Accurate perception of the position of moving objects is a challenging but critical task for the visual system. Avoiding obstacles while driving, hitting a ball in tennis, catching a moving target, all require precise localization of the moving objects. Moreover, we have to maintain this precision over a range of luminance levels that covers 10 orders of magnitude in natural settings (Land and Nilson 2002). Here we want to investigate whether changes of luminance affect the localization of moving objects. It is already well known that motion affects judgments of position (Eagleman and Sejnowski 2007; Whitney 2002) and that luminance affects estimates of speed (Hammett et al 2007; Vaziri Pashkam and Cavanagh 2008); will luminance therefore affect judgments of position?

The visual system, through specialized visual areas dedicated to the analysis of motion (Tootell et al 1995), can extract the motion of objects independent of their position (Wertheimer 1912; Zeki 1991; Addams 1834); however, motion affects the perception of the position of moving objects (Whitney 2002). One example of such interference is demonstrated by the well-known flash-lag effect. When a brief flash is presented at the same location as a moving object, the flash is perceived to lag behind the moving object (MacKay 1958). The underlying mechanism of this phenomenon is still controversial. Some attribute it to the difference in the perceptual latency of the flash and moving objects (Purushathaman et al 1998; Whitney and Murakami 1998), and some refer it to the extrapolation of the location of the moving object in the direction of motion to compensate for the delay in the neural response (Nijhawan 1994). In either case, stimulus properties such as speed (Wojtaj et al 2008) and change of motion direction (Whitney and Murakami 1998; Whitney et al 2000) can affect the flash-lag effect. More important for the purpose of our experiment here, it has been shown that the magnitude of the flash-lag effect increases as the speed of motion



increases (Wojtaj et al 2008). We will use the flash-lag effect to examine the nature of speed information that influences the perception of position.

It has been previously shown that the perceived speed of moving objects increases at low luminance (Hammett et al 2007; Vaziri Pashkam and Cavanagh 2008). This overestimate increases as a function of the speed, reaching a maximum effect of about 30% around 11 hz of temporal frequency. We have attributed this effect to the lengthening of the motion blur that occurs due to the increased visual persistence at low luminance (Di Lollo and Bischof 1995). As an object moves faster at a given luminance, it has a longer motion trace so that the length of the trace can be a cue to speed. At low luminance, persistence increases so the motion trace for a given speed will be longer, contributing to an impression of higher speed. Does this speed cue contribute to all processing that depends on speed or just to the perception of speed itself? To determine whether the flash lag is influenced by perceived or actual speed, we varied both speed and luminance in our flash-lag display. In the first experiment, we measured the speed overestimation effect across three different speeds and replicated the results of our previous study but now using a linearly translating patch of random dots. In the second experiment, we measured the magnitude of the flash-lag effect with similar stimuli and found that despite a significant modulation of the flash lag by actual speed changes, it was not significantly modulated by the perceived speed changes created by different light levels.

We also ran a control to address the effects of luminance on latencies to the moving and flashed stimuli. It has been previously shown that the flash-lag effect can be modulated by a change in the relative luminance of the flash and the moving target (Purushuthuman et al 1998; White et al 2008). We measured the latency of the flash, using a simultaneity judgment, and the latency of the moving stimuli, using the Pulfrich effect (Pulfrich 1922). These control conditions showed that latency effects cannot account for the observed data in our main experiment.

We conclude that the perceived position of a moving object is not affected by the blur cue that contributes to its perceived speed.

## 2 Experiment one

This experiment was designed to measure the degree of speed overestimation at low luminance in linearly moving patches of random dots.

#### 2.1 Methods

2.1.1 *Participants*. Five subjects participated in this experiment. Their ages ranged between 18 and 35. All subjects had normal or corrected-to-normal vision.

2.1.2 *Apparatus*. Stimuli were generated on a Macintosh computer with Matlab 7.7 and Psychtoolbox software (Brainard 1997; Pelli 1997) and were presented on a CRT monitor (SUN microsystem, 1024x768, 120 Hz). Subjects were positioned in a dark room in front of the screen, while the distance between the monitor and their eyes was 57 centimeters.

2.1.3 *Stimuli*. The moving stimulus consisted of 50 randomly positioned circular white dots that formed an illusory square of size 3.8 degrees on each side, which moved over a stationary random dot background consisting of 2000 dots of similar shape and size (Figure 1a). Each dot had a diameter of 0.2 degrees. The luminance of the dots was 88 cd/m<sup>2</sup>, and they were presented on a dark grey background with the luminance of 5 cd/m<sup>2</sup>. A small red fixation point was presented in the center of the display, and two square-shaped random dot patterns moved at 5.7 degrees on the top and bottom of the fixation point.

To achieve lower luminance levels without changing contrast, half of the screen was covered with two layers of 1.2 log unit neutral density filters to reduce the light reaching the eyes in both light and dark areas for the display by 2.4 log units. The luminance levels of the dots and the background in the low luminance condition were 0.35 and 0.02 cd/m<sup>2</sup>, respectively.

2.1.4 Procedure. On each trial subjects had to fixate the red "+" and adjust the speed of the "match" random dot square until it appeared the same as that of the "target" random dot square. In the beginning of the trial, the target random dot pattern appeared randomly on one side of the screen and moved with a linear motion of constant speed until it reached 11.4 degrees on the other side of the screen. After that the target was removed and the match square was presented and moved linearly in the opposite direction compared to the target (Figure 1b). This alternating presentation between target and match continued until the subjects reported the completion of the matching procedure. On each presentation, the starting point of the target and match was randomly jittered from 7.6 to 15.4 degrees on either sides of the screen. This was to ensure that the subjects did not use any information other than the speed of the stimuli (such as the duration of the presentation) to perform the match. The "match" square was initially presented at a random speed, and the subjects changed its speed on each repeated presentation by moving the computer mouse to the left or right to decrease or increase the speed respectively, and pressed the mouse button when they were satisfied that the speed of the match was similar to that of the "target" square. The speed of the target square was chosen pseudo randomly among three possible values: 9.12, 18.24, and 27.36 degrees/second. Subjects completed four experimental blocks of 15 trials with 5 trials for each target speed. In two of the experimental blocks the top half of the screen, and in the other two the bottom half, was covered with neutral density filters to reduce the luminance.



**Figure 1.** (a) A depiction of the moving stimuli used in all three experiments. A square-shaped patch of random dots moved on a stationary field of random dots. The dashed red outline shows the illusory borders of the stimulus and was not shown in the experiment. The red arrow shows the direction of motion. The red cross shows the fixation point. (b) The procedure used in the first experiment. The target and match stimuli were presented in alternation while the subjects used the mouse to change the speed of the match to be the same as the target. The dark area shows that half of the screen was covered with neutral density filters to reduce the luminance.

#### 2.2 Results

The speed of the match is plotted as a function of the speed of the target in Figure 2. The dashed line shows the veridical match (match speed = target speed), and the solid line demonstrates the final speed of the match stimulus. Results show that the perceived speed of the moving patch at low luminance is overestimated. A one-way repeated-measures ANOVA with target speed as the factor and the amount of speed overestimation calculated as the difference between the target speed and match speed as the dependant variable showed a significant effect of speed on the overestimation of speed at low luminance (F(2,6) = 27.6, p < 0.01). We also ran a regression analysis with target speed as the predictor and matched speed as the dependant variable on each individual subject's data and then compared the slope values from this analysis to the slope of 1 using a one-sample *t*-test (otherwise known as a random effect analysis). Results showed a significant overestimation of speed: the slope of the regression line was significantly greater than 1 (slope = 1.3, t(4) = 7.87, p < 0.01). Individually, only the speed increase at the highest speed, 27.36, was significantly greater than the veridical speed (t(4) = 5.98, p < 0.05, corrected for multiple comparisons using the Bonferroni method). In conclusion, the results of this experiment replicate our previous findings (Vaziri Pashkam and Cavanagh 2008) with new stimulus parameters. We used these stimuli in the next experiment to investigate the effect of speed overestimation at low luminance on flash-lag effect.



**Figure 2.** Results of experiment one. The final matched speed is plotted as a function of target speed. The dashed line shows the veridical value. Results showed that perceived speed is overestimated at low luminance and that this effect increases with stimulus speed. Error bars show standard error of mean.

### 3 Experiment two

This experiment was designed to investigate whether the overestimation of speed at low luminance affects the perceived *position* of a moving target when compared to a flashed reference. Using moving stimuli with different speeds and different luminance levels, we explored the extent to which the flash-lag effect is modulated by the perceived and real speed of the moving patterns. If the flash-lag effect is modulated by the perceived speed we predict an increase in the perceived flash-lag effect at low luminance; however, if the target speed that determines the flash-lag effect is not affected by the blur cue, there should be no change in the amount of flash-lag effect at low luminance.

#### 3.1 Methods

3.1.1 Participants. Five subjects from previous experiment participated in this experiment.

3.1.2 Apparatus. Same set up as the previous experiment was used for this experiment.

3.1.3 *Stimuli*. A square-shaped patch of random dots moved on a stationary random dot background as in the previous experiment. The target started randomly at 7.6 degrees on one side of the screen and moved horizontally until it disappeared at 7.6 degrees on the opposite side and then reappeared again at the starting point. Each time the target patch reached the vertical meridian a small white square with the side of 0.76 degrees in size was flashed on the screen. The horizontal target trajectory was randomly presented above or below the fixation point at 5.7 degrees eccentricity. The flash was presented for 33.3 milliseconds (4 frames) along a horizontal line 3.4 degrees from fixation and on the opposite side of the fixation point from the target. During the four frames in which the flash was present, it was moved with the same velocity as the moving target. This movement was minimal, yet it was necessary to ensure that the physical distance between the target and flash was kept constant.

3.1.4 *Procedure*. In each trial, subjects were asked to fixate on the red "+" and adjust the location of the flash after each trial until it was perceived to be vertically aligned with the target. The adjustment was made by moving the computer mouse to the left or right (Figure 3). The final adjusted location was registered when the subjects pressed the mouse button. The target was pseudo randomly selected to have one of three possible speeds (9.12, 18.24, or 27.36 degrees/second), two possible directions (leftwards or rightwards), and two possible locations (below or above the fixation point). Each subject completed 4 blocks of 36 trials. In two of these blocks the top half of the screen was covered with 2.4 log unit neutral density filters and in the other two the bottom half was covered with 2.4 log unit neutral density filters.

## 3.2 Results

**Figure 4** shows the results of the second experiment collected from all subjects. The amount of flash-lag effect is plotted as a function of the speed of the moving target. The solid red line shows the amount of flash-lag effect at high luminance, and the solid blue line demonstrates the amount of flash lag at low luminance. A two-way repeated-measures ANOVA with speed and luminance as the two factors showed a significant effect of speed (F(2,8) = 43.54, p < 0.001) and no significant effect of luminance (F(1,4) = 3.01, p = 0.158) on the observed flash-lag effect and no interaction (F(2,8) = 1.5, p = 0.278). The dashed line shows the flash-lag effect that would be expected if the speed overestimation at low luminance had modulated the flash lag to the same extent as variations in the real speed. To calculate the expected values for each subject, we fitted a linear function to each subject's flash-lag data at high luminance. Then the effective speed was increased to match the overestimates measured at low luminance from the previous experiment. These adjusted speeds were then entered into the linear functions to predict the flash lag that should have



**Figure 3.** Procedure of experiment two. A random dot patch moved from one side of the screen to the other, and at the middle of its path a dot was flashed just above it. The subjects had to move the position of the dot using the computer mouse so that it appeared vertically aligned with the target. The red cross shows the fixation point.

been seen at low luminance if the perceived speed determined the effect. The dashed line in Figure 4 shows the average of these predicted low-luminance values for all subjects. A two-way repeated-measures ANOVA showed a significant difference between the observed flash lag (solid blue line) and predicted flash lag from the perceived speed (dashed blue line) at low luminance (F(1, 4) = 8.076, p < 0.05). Moreover the predicted low-luminance flash lag (dashed blue line) was also significantly greater (F(1, 4) = 14.195, p < 0.05) than the observed flash lag at high luminance (solid red line). This shows that if the flash-lag effect had been modulated by the perceived speed, our statistical test would be able to detect the difference. A statistical power analysis for this comparison between the high luminance results and the predicted low luminance results (dashed blue line) found an observed power,  $\beta$ , of 0.801, above the accepted criterion of 0.8 (Cohen 1992). This indicates that 5 subjects were sufficient for the effect of speed overestimation at low luminance to be significant if it had had the predicted strength. In conclusion, this experiment shows that the flash-lag effect is not modulated by changes in perceived speed at low luminance.

#### 4 Experiment three

At low luminance the processing time required to perceive a visual object increases. If this increase in the perceptual latency at low luminance is different for the flash than for the moving patch, this could lead to a change in the flash-lag effect. One could claim that the flash lag indeed increases at low luminance due to an increase in perceived speed, but the differential change in the latency of the flash and the moving target could counteract it. To control for this, a further experiment was designed to compare the delay in the perception of the flash and the moving target caused by a reduction in luminance. To measure the delay of the flash, two dots were presented on the screen one at high and one at low luminance, and the subjects were asked to judge their simultaneity in time. To determine the delay in the perception of the moving patch, we measured the Pulfrich effect (Pulfrich 1922) on a moving



**Figure 4.** Results of experiment two. The magnitude of the flash-lag effect is plotted as a function of target speed for high luminance (blue line) and low luminance (red line) stimuli. Results showed that reducing luminance did not significantly change the flash-lag effect. The dashed blue line shows the predicted flash lag if the magnitude of the lag had been modulated by the speed overestimation at low luminance. Both red line and blue line are significantly different from the dashed line. Error bars show between-subjects standard error of mean. Stars represent significant differences between the dashed blue lines and the red line, and the dashed blue line and the solid blue line.

target that was presented at different luminance levels in the two eyes. The longer latency for the eye with low luminance generates a spatial lag of the moving target seen by that eye. When combined with the other eye's view, this spatial lag generates a binocular disparity that results in a depth percept. The amount of depth is a measure of the luminance-dependent delay.

### 4.1 Methods

4.1.1 *Participants*. Four subjects, two from the previous experiment and two new subjects, participated in this experiment. Their ages ranged between 18 and 35. All subjects had normal or corrected-to-normal vision.

4.1.2 *Apparatus*. Same set up as the previous experiment was used for this experiment. For measuring the Pulfrich effect, a mirror and prism were used to separate the image that was presented to the left and right eye in order to induce stereovision.

4.1.3 *Stimuli and procedure*. For comparing the delay in the perception of a flash at high and low luminance two flashes were presented, one above and one below the fixation point with the same size, eccentricity, and duration as the flashes presented in the second experiment (0.76 degree, 3.4 degree, and 33 ms, respectively). Half of the screen was covered with neutral density filters, and thus one of the flashes was presented at low and one at the high luminance area of the screen. Subjects were asked to change the relative timing of the two flashes until they were perceived to appear simultaneously on the screen. The relative timing was changed by moving the mouse to the left and right to change the timing of the dot below the fixation point to be earlier or later than the dot above the fixation point. The final match was registered when the subjects pressed the mouse button. Each subject completed four blocks of 10 trials. In two of these blocks the top half of the screen and in the other two the bottom half was covered with neutral density filters.

For comparing the delay in the perception of the moving patch of random dots at high and low luminance, two patches were presented, one to the left and one to the right eye on a background of stationary dots. The display was divided into two halves and each half of the display was presented to one eye using a mirror and prism. Two moving patches were presented to the left and right eve so that the subjects would perceive a single square moving above the fixation point at 5.7 degrees eccentricity. The speed of the two moving patches was chosen pseudo randomly from three possible speeds: 9.12, 18.24, or 27.36 degrees/s. The relative disparity of the two patches could be changed so that the fused patch would appear at different depth planes relative to the stationary background. On each trial the moving patch was presented at a random location in depth relative to the background, and the subjects were asked to change the relative depth so that the target was perceived to be at the same depth plane as the background. Subjects changed the depth plane of the target forward and backward by moving the mouse to the left and right, respectively, and the final match was registered when they pressed the space button on the keyboard. Each subject was trained on this task with equal luminance in both eyes for ten trials. In the actual experiment the right eye was covered with neutral density filters of 2.4 log units and each subject completed two blocks of 15 trials, with 5 trials for each target speed.

## 4.2 Results

Figure 5 shows the amount of the delay of the flash and moving target at low luminance compared with high luminance. The blue dot shows the perceptual delay of the flash at low luminance compared with high luminance. The red line shows the perceived delay of the moving target at low luminance compared with high luminance for the three target speeds. The delay of the moving target was calculated as:

$$Delay = Ds/V$$

Where *Ds* is the final disparity between the stimuli presented to the left and right eye in degrees of visual angle that was required to null the depth, and *V* is the speed of the moving target in degrees/s.

The results showed that as the speed of the stimulus increased, there was a significant decrease in the delay of the moving stimulus at low luminance (F(2,6) = 35.57, p < 0.001) relative to high luminance. Consistent with these results, Nickalls (1996) has shown a decrease in Pulfrich effect at faster angular velocities with a rotating stimulus.

The reason for the decrease in the latency at faster speeds is not well understood. In a neurophysiological study Anzai et al (2001) demonstrated that most neurons of the striate cortex jointly code motion and depth and that the response profile of these cells can account for the Pulfrich effect. One possibility is that these cells might be relatively more responsive (ie, have a higher firing rate and shorter response latency) to faster speeds at low luminance. This could be a consequence of the increasing contribution of magnocellular relative to parvocelluar responses at higher temporal frequencies and low luminance.

One point that is worth noting is that even though the differential latency is the most widely accepted account of the Pulfrich effect, it is not the only one. Morgan (1977) has attempted to explain the Pulfrich effect based on the differential visual persistence and spatial averaging of the position information. According to this account, the position of the stimulus in each eye is shifted behind its actual position due to the spatial averaging of the actual object position and the motion smear introduces by visual persistence. An increase in persistence at low luminance introduces a disparity between the positions of the stimuli in the two eyes. The only way to reconcile this account with our data is to assume that the difference of the motion smear between high and low luminance is smaller at faster speeds

(1)



**Figure 5.** Relative delay for low luminance versus high luminance stimuli as a function of speed. The blue dot shows the relative delay of the flashed stimulus, and the red line shows the relative delay of the moving stimuli for three speeds. The perceptual delay of the dim relative to bright moving stimuli decreased as the speed increased. The purple area above the dotted line through the relative dim-bright delay for the flash shows the delay values for the moving stimuli that will decrease the flash-lag effect, and the cyan area below the dotted line shows the delays that will increase the flash-lag effect. Error bars show standard error of mean.

compared with slower speeds. We find this unlikely given that the motion blur increases at faster speeds, but this could be tested with further experiments.

Regardless of the underlying mechanism, what we observe here is that the relative delay for the moving stimulus was similar to or less than that observed for the flash alone, showing that, if anything, these changes of relative latencies should have increased the flash-lag effect at low luminance, at least at higher speeds. However, in the second experiment, low luminance and the increased perceived speed did not increase the flash lag. Consequently, the lack of effect in Experiment 2 cannot be attributed to the change in differential latencies at high and low luminance. Note that from the data of the second experiment the average time lag of the flash relative to the moving stimulus at high luminance is approximately 23 ms. Therefore, if the flash-lag effect were purely determined by the time difference between the flash and moving stimulus, at low luminance we would have observed a significant increase in the magnitude of flash lag. These data suggest that the relative delays do not contribute to the flash lag or that some other factor has cancelled their effect.

## 5 Discussion

The first experiment showed that a linearly translating stimulus is perceived to move faster at low luminance than an otherwise identical stimulus at high luminance. This replicates earlier findings (Vaziri Pashkam and Cavanagh 2008) but importantly demonstrates that this effect is seen on the compact stimuli we needed for our flash-lag experiments. Our earlier experiments had used full-field or rotating stimuli. We also show again that the speed overestimation is larger at faster speeds of motion. The second experiment demonstrated that a standard flash-lag effect was seen with our moving patch of random dots and that the magnitude of the flash-lag effect increased as the speed of the moving target increased. However, decreasing the luminance of the stimuli did not significantly change the magnitude of the flash-lag effect. Importantly, we showed that the expected change in the perceived speed due to low luminance was sufficient to produce a significant increase in the flash lag. Since it did not, we concluded that the blur cue that contributes to perceived speed does not contribute to the speed that determines the flash lag. In the third experiment it was shown that the differential change in the perceptual latency of the moving target and the flash at low luminance could not account for the results observed in the second experiment.

The main finding of this series of experiments is that the flash-lag effect is independent of perceived speed when physical speed is held constant. This result has potential implications for both models of speed perception and the flash-lag effect.

Despite the importance of speed perception for visually guided action, there are no widely accepted models of speed perception. Some models propose a normalization of motion energy by the stimulus contrast (Adelson and Bergen 1985). Hammet et al (2007) make the related proposal that speed is defined as the ratio of activity of the cells in magnocellular and parvocellular pathways. Others propose that spatiotemporal filters perform a Fourier analysis on the input image and extract the speed (Van Santen and Sperling 1984, 1985; Watson and Ahumada 1985). A number of articles have pointed out the secondary effects of motion, such as that motion blur can act as a cue to the direction of motion (Barlow and Olshausen 2004; Burr and Ross 2002; Geisler 1999), and as we have recently shown (Vaziri Pashkam and Cavanagh 2008) have shown that the overestimation in the perceived speed at low luminance can be attributed to a longer motion blur due to an increase in the visual persistence at low light levels.

Our results here demonstrated that the effects of motion on perceived position are not determined strictly by perceived speed. This suggests that multiple dissociable signals contribute to the sense of speed and that some of these cues, such as motion blur, contribute to perceived speed but not to the speed-related distortions in position perception such as the flash-lag effect.

The underlying mechanism of flash-lag effect has been long debated in the literature. Here we will examine our results based on two of the most widely accepted models of flash lag—namely, latency difference and motion compensation.

## 5.1 Latency difference

Whitney and Murakami (1998) have suggested that the difference in the perceptual delay of a flash and a moving object causes the flash-lag effect. According to this account, if the time required for a moving object to reach perception is T, the time required for a flash to reach perception is longer  $(T + \Delta t)$ , as moving stimuli are processed more efficiently than flashes. Thus, by the time the flash is perceived the moving object has moved to a new location, and therefore the flash is perceived to lag behind the moving object. The magnitude of this lag ( $\Delta d$ ) will depend on the speed of moving objects ( $\Delta d = V * \Delta t$ , where V is the speed of motion), so with the same time difference  $\Delta t$ , an increase in speed would produce a larger perceived lag. According to this account, the speed of moving objects does not directly modulate the perceived flash lag, but it acts through the increased spatial lag seen for a constant temporal lag at faster speeds. In our last experiment we showed that the delay of the flash and the delay of the moving objects are both increased at low luminance. The amount of this increased delay was similar for both the flash and the moving objects at slow speeds, but the delay decreased as a function of speed for the moving stimulus. This would mean that the flash-lag effect, if it were solely a function of differential latency, should increase at higher speeds for the low luminance stimulus relative to the high luminance stimulus. However, we did not observe this, which means that a pure latency-based model of flash-lag effect cannot explain our results.

#### 5.2 Motion extrapolation

Nijhawan (1994) proposed that the flash-lag effect occurs because the position of the moving objects is perceived ahead of their veridical position in order to compensate for the neural delay between the presentation of the stimulus and perception to facilitate motor reactions to current rather than past locations of moving objects. According to this account, speed dependence of the flash-lag effect is crucial, as a faster moving object needs to be compensated more than a slow one. In terms of this theory, our results suggest that the magnitude of the motion extrapolation is calculated based on motion signals that do not include the blur cue that increases perceived speed at low luminance. If we assume that the flash-lag effect reflects an attempt to maintain precise motor interactions with moving objects, the fact that the magnitude of the lag is modulated by the real speed rather than the perceived speed at low luminance supports the dissociation of perception and action proposed by Goodale and Milner (1992).

## 5.3 Other models

Other models have been proposed for the underlying mechanisms of flash-lag effect. Baldo and Klein (1995) appeal to the attention capture caused by the flash and suggest that during the time it takes to shift attention from the flash back to the moving object the object changes position and appears to precede the flash. Our results cannot speak strongly for or against this account, as there is no clear prediction for the effect of luminance on the speed of attentional shift. However, if we take into account the visual delay in the perception of the position of the moving objects after the attention shifts from the flash to the moving object, we could speculate that this model predicts an increase in the flash lag at low luminance at all speeds, but that is not what we observe here.

Krekelberg and Lappe (2000) suggest that the flash-lag effect is caused by the position persistence of the flash and comparing the location of the moving object integrated over time with the last registered position of the flash. As in this model the temporal integration window is dissociated from and is presumed to be larger than the visible retinal persistence, it is hard to speculate about the predictions of this model for flash-lag effect at low luminance. If position persistence increases at low luminance (similar to visual persistence), then we would expect the flash-lag effect to increase at low luminance, but that is once again not observed here.

Eagleman and Sejnowski (2007) in their "Postdiction" model of the flash-lag effect propose that flash resets the mechanisms of position integration and the position of the moving object after the flash is integrated and averaged for a period of about 80ms. This average position is then compared with the position of the flash, resulting in the flash-lag effect. This model also does not have clear predictions for the flash lag at low luminance. If the duration of the temporal integration after the flash changes at low luminance, we would expect a change in flash lag in the same direction.

In summary, our data show that perceived location is not determined by perceived speed in the flash-lag effect. At low luminance the perceived speed is systematically overestimated, but the perceived location is not similarly affected. Among the current models of the flash-lag effect that make clear predictions for an effect of low luminance, none of them can fully account for this data. We suggest that there are multiple cues for the perception of speed, some of which are distorted at low luminance and others of which remain unchanged. A modified version of motion extrapolation model in which the extrapolation of position is calculated based on speed cues that are immune to luminance distortions would therefore be consistent with the observed flash-lag effect at low luminance. Acknowledgements. This work was supported by grant EY009258 to Patrick Cavanagh from National Institute of Health.

## References

- Addams R, 1834 "An account of a peculiar optical phenomenon seen after having looked at a moving body" *London and Edinburgh Philosophical Magazine and Journal of Science* **5** 373–374
- Adelson E H, Bergen J R, 1985 "Spatiotemporal energy models for the perception of motion" *Journal* of the Optical Society of America A **2** 284–299 doi:10.1364/JOSAA.2.000284
- Anzai A, Ohzawa I, Freeman R D, 2001 "Joint-encoding of motion and depth by visual cortical neurons: neural basis of the Pulfrich effect" *Nature Neuroscience* **4** 513−518 **◄**
- Barlow H B, Olshausen B A, 2004 "Convergent evidence for the visual analysis of optic flow through anisotropic attenuation of high spatial frequencies" *Journal of Vision* **4** 415–426 doi:10.1167/4.6.1
- Baldo M V, Klein S A, 1995 "Extrapolation or attention shift" *Nature* **378** 565–566 doi:10.1038/378565-a0 ◀
- Brainard D H, 1997 "The Psychophysics Toolbox" Spatial Vision 10 433–436 doi:10.1163/156856897-X00357 <
- Burr D C, Ross J, 2002 "Direct evidence that speedlines influence motion mechanisms" *Journal of Neuroscience* 22 8661–8664 ◄
- Cohen J, 1992 "A power primer" *Psychological Bulletin* **112** 155–159 doi:10.1037/0033-2909.112.1.-155 <
- Di Lollo V, Bischof W F, 1995 "Inverse-intensity effect in duration of visible persistence" *Psychological Bulletin* **118** 223–237 doi:10.1037/0033-2909.118.2.223
- Eagleman D M, Sejnowski T J, 2007 "Motion signals bias position judgments: A unified explanation for the flash-lag, flash-drag, flash-jump and Frohlich effects" *Journal of Vision* **7** 1–12 doi:10.1167/7.4.3
- Geisler W S, 1999 "Motion streaks provide a spatial code for motion direction" *Nature* **400** 65–69 doi:10.1038/21886 ◀
- Goodale M A, Milner A D, 1992 "Separate visual pathways for perception and action" *Trends in Neurosciences* **15** 20−25 doi:10.1016/0166-2236(92)90344-8 ◄
- Hammett S T, Champion R A, Thompson P G, Morland A B, 2007 "Perceptual distortions of speed at low luminance: evidence inconsistent with a Bayesian account of speed encoding" *Vision Research* **47** 564–568 doi:10.1016/j.visres.2006.08.013 <
- Krekelberg B, Lappe M, 2000 "A model of the perceived relative positions of moving objects based upon a slow averaging process" *Vision Research* **40** 201–215 doi:10.1016/S0042-6989(99)00168-6 ◀
- Land M F, Nilsson D E, 2002 Animal eyes (New York: Oxford University Press) <
- MacKay D, 1958 "Perceptual stability of a stroboscopically lit visual field containing self-luminous objects" *Nature* 181 507–508 doi:10.1038/181507a0 <
- Morgan M, 1977 "Differential visual persistence between the two eyes: A model for the Fertsch-Pulfrich effect" *Journal of Experimental Psychology: Human Perception and Performance* **3** 484–495 doi:10.1037/0096-1523.3.3.484
- Nickalls R W, 1996 "The influence of target angular velocity on visual latency difference determined using the rotating Pulfrich effect" *Vision Research* **36** 2865–2872 doi:10.1016/0042-6989(96)00039-9 ◀
- Nijhawan R, 1994 "Motion extrapolation in catching" Nature 370 256–257 doi:10.1038/370256b0 <

Pelli D G, 1997 "The VideoToolbox software for visual psychophysics: Transforming numbers into movies" *Spatial Vision* **10** 437–442 doi:10.1163/156856897X00366

- Pulfrich C, 1922 "Die Stereoskopie im Dienste der isochromen und heterochromen Photometrie" Die Naturwissenschaften 10 569–574 doi:10.1007/BF01565573 <
- Purushothaman G, Patel S, Bedell H, Ogmen H, 1998 "Moving ahead through differential visual latency" *Nature* **396** 424–424 doi:10.1038/24766 <
- Tootell R B, Reppas J B, Kwong K K, Malach R, Born R T, Brady T J, Rosen B R, Belliveau J W, 1995 "Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging" *Journal of Neuroscience* **15** 3215–3230 ◀
- Van Santen J P, Sperling G, 1984 "Temporal covariance model of human motion perception" *Journal* of the Optical Society of America A 1 451–473 doi:10.1364/JOSAA.1.000451 <
- Van Santen J P, Sperling G, 1985 "Elaborated Reichardt detectors" *Journal of the Optical Society of America A* **2** 300–321 doi:10.1364/JOSAA.2.000300 <

- Vaziri Pashkam M, Cavanagh P, 2008 "Apparent speed increases at low luminance" *Journal of Vision* 8 1–12 doi:10.1167/8.16.9
- Watson A B, Ahumada A J, 1985 "Model of human visual-motion sensing" *Journal of the Optical Society of America A* **2** 322–341 doi:10.1364/JOSAA.2.000322 <
- Wertheimer M, 1912 "Experimentelle Studien uber das Sehen von Bewegung. Zeitschrift fur Psychologie" 61 161–265 ◀
- White A, Linares D, Holcombe A, 2008 "Visuomotor timing compensates for changes in perceptual latency" Current Biology 18 R951-53 <
- Whitney D, Murakami I, 1998 "Latency difference, not spatial extrapolation" *Nature Neuroscience* **1** 656–657 doi:10.1038/3659 <
- Whitney D, Murakami I, Cavanagh P, 2000 "Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli" *Vision Research* **40** 137–149 doi:10.1016/S0042-6989(99)00166-2
- Whitney D, 2002 "The influence of visual motion on perceived position" *Trends in Cognitive Sciences* 6 211–216 doi:10.1016/S1364-6613(02)01887-9
- Wojtach W, Sung K, Truong S, Purves D, 2008 "An empirical explanation of the flash-lag effect" *Proceedings of the National Academy of Sciences* **105** 16338–16343 doi:10.1073/pnas.0808916105
- Zeki S, 1991 "Cerebral akinetopsia (visual motion blindness): A review" Brain 114 811-824 doi:10.1093/brain/114.2.811



**Maryam Vaziri Pashkam** got her medical degree at Tehran Medical University in Iran in 2005, after which she moved to United States to study psychology. During her graduate school she worked on speed perception and action at low light levels at the Vision Sciences Laboratory. She got her PhD in 2011 and since then has been a post-doc at Harvard Psychology Department investigating perceptual decision-making in human Parietal cortex using fMRI. She is interested in a wide range of topics in vision science, including visuo-motor interactions, decision-making, and attention.



**Patrick Cavanagh** received a Bachelor of Engineering from McGill University in 1968. An interest in artificial intelligence led to a PhD in cognitive psychology from Carnegie-Mellon in 1972. He taught at the Université de Montréal in Psychology until 1989 and at the Department of Psychology at Harvard until 2007. He recently joined the faculty at the Université Paris Descartes.

Copyright © 2011 M Vaziri-Pashkam, P Cavanagh Published under a Creative Commons Licence Composition

