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**USE YOUR ILLUSION:
THE FLASH-LAG EFFECT AS A TOOL
FOR PSYCHOPHYSICS**

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Declaration

This thesis conforms to an ‘article format’ in which the first chapter presents a synthetic overview and discussion. The remaining chapters consist of discrete articles written in a style that is appropriate for publication in peer-reviewed journals in the field.

All three articles (henceforth referred to as Papers I, II, and III) are written in the style of an article appropriate for the Journal of Experimental Psychology: Human Perception and Performance.

Under the supervision of Romi Nijhawan, the author was responsible for the conception, design, execution, and analysis of all experiments reported in this thesis.

I hereby declare that this thesis has not been and will not be, submitted in whole or in part to another University for the award of any other degree.

Signature:.....

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UNIVERSITY OF SUSSEX

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Doctor of Philosophy in Psychology

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Summary

The flash-lag effect is an illusion in which a moving object is perceived advanced beyond an aligned flash. The majority of research into the effect has been directed at specifying its source, though a small body of literature simply makes use of flash-lag to answer diverse questions about perception – without necessarily arbitrating between competing accounts of its nature. The current thesis expands on this little-explored potential of the flash-lag effect with the presentation of three papers reporting programmes of research that exploit the phenomenon to address issues unrelated to its cause. In the first paper it is shown that, like in visual flash-lag, a similar motion direction based anisotropy is evident in the motor version of the effect, in which one's unseen limb is perceived ahead of a flash. Specifically, the effect is greater for motion towards, rather than away from fixation. Furthermore, Paper I also demonstrates for the first time a motor flash-drag effect, in which one's unseen moving hand 'drags' the perceived position of a nearby flash. It is argued that both of these findings are evidence of parallels between vision and action systems. Paper II takes advantage of the explicitly perceptual nature of the flash-lag effect to investigate whether the visuospatial perception of threatening objects is different to that of non-threatening objects. It is ultimately shown that when a moving stimulus is threatening, the flash-lag effect is greater, regardless of its direction of motion. Paper III shows that gamma movement (the apparent contraction of disappearing stimuli) adds to and subtracts from the forward displacement of contracting and expanding stimuli, respectively. Prior to these papers, however, an overview chapter reviews the flash-lag literature, and argues that the effect can be a useful tool for psychophysics, even without a consensus on its origin.

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Thesis overview

1.1 Introduction

This overview chapter aims to place the research reported in the remainder of the thesis within a coherent framework. While the great majority of work on the flash-lag effect is aimed at arbitrating between explanations of its cause, the experiments described herein are held together by their mutual circumvention of the topic. As such, lengthy arguments in favour of one or the other account will not be presented, though the debate may come up from time to time as a side issue. Instead, it will be claimed that flash-lag can be a powerful tool in the arsenal of psychophysicists, with or without reference to its underlying nature. More specifically, it will be highlighted that one can use it to distinguish between retinal and perceptual positioning, or else to make predictions and draw conclusions about differences in its magnitude between conditions. These two perspectives are derived from digesting a small subsection of research that uses the effect in one of these ways, and focuses only indirectly on the flash-lag debate. To date, this literature has received scant attention, and certainly no overarching review. After such a treatment, a summary will be given of the research communicated in the three papers of this thesis, and it will be highlighted that they embody this same approach of using flash-lag to scrutinise unrelated issues. Prior to this, however, the flash-lag effect will be introduced, with special attention given to its diversity across modalities, and then coverage of some of the more prominent theories put forward to explain it shall follow.

1.1.1 The flash-lag effect and its diversity

It has long been known that a flash, aligned for an instant with a moving stimulus, is perceived to lag behind it (for an historical overview, see Maus, Khurana, & Nijhawan, 2010). A prominent early example of this phenomenon came from MacKay (1958), who produced a motion percept by applying intermittent pressure to observers' eyeballs

while they viewed a room containing several continuously lit objects. Each press of the eye made the continuously visible stimuli seem to move, while the rest of the room was lit stroboscopically, and appeared to remain relatively static and lagging behind. This illusion occurred in spite of subjects' knowledge that the sources of the external stimuli were not changing in position relative to one another. Interest in this basic phenomenon was reignited by Nijhawan (1994), who showed subjects a rotating luminous bar, with end segments that were occasionally flashed for 5ms. The percept at the time of each flash was of the continuously visible section being rotated beyond the briefly presented sections, despite their physical alignment. Nijhawan (1994) named this illusion the *flash-lag effect* and it has since been of considerable interest to vision scientists. Figure 1.1 shows an example of another type of flash lag display, in which two translating bars appear ahead of a flash aligned between them.

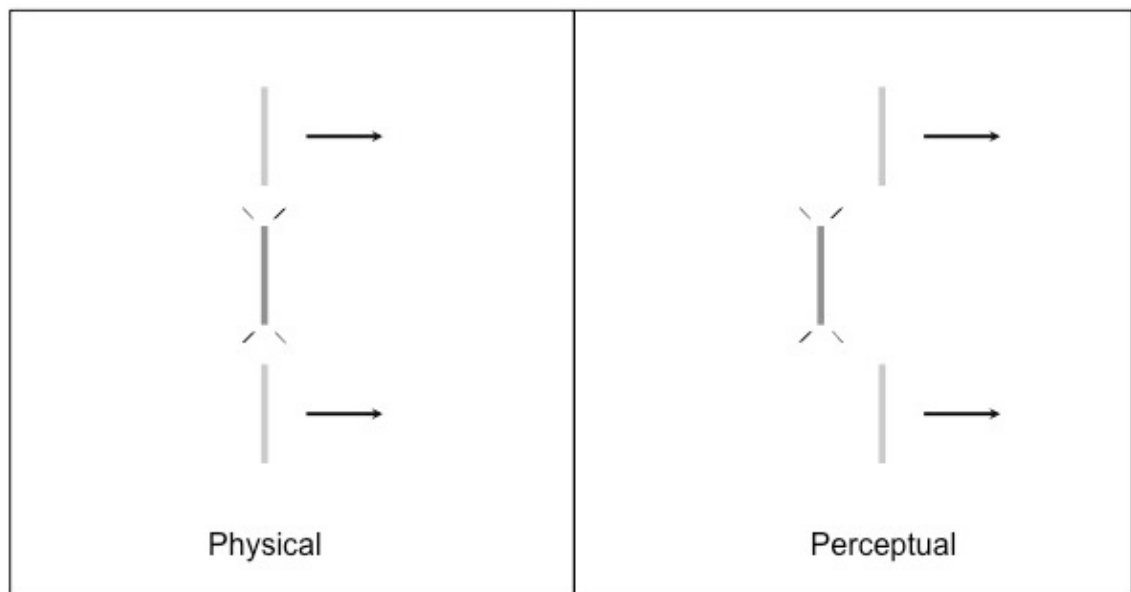


Figure 1.1. The flash-lag effect: Flashes physically aligned with moving stimuli appear to lag behind them.

Flash-lag has now been replicated extensively and demonstrated to occur with diverse kinds of stimuli (for reviews, see Hubbard, 2014; Krekelberg & Lappe, 2001; Maus et al., 2010; Nijhawan, 2002; Schlag & Schlag-Rey, 2002; Whitney, 2002). Notably, it has been shown that the display need not necessarily comprise of moving and flashed visual

components, per se. For instance, Sheth, Nijhawan, and Shimojo (2000) showed that the flash-lag effect occurs when the ‘moving’ stimulus is actually static in space, but varies continuously in a feature dimension over time. In the first of their experiments, a coloured disk changed gradually from green to red, or from red to green while its position in space was held constant. As the disk transitioned through colour space, another coloured disk was flashed adjacent to it. Here it was found that the flashed disk needed to be approximately 400ms’ worth of colour-change ahead in order to be perceived as the same. Further experiments revealed similar (though smaller) effects with spatially static stimuli that changed continuously in luminance, spatial frequency, and pattern entropy (Sheth et al., 2000). In light of previous work on flash-lag, the broadest implication of these findings is that the illusion is not limited to stimuli that change in spatial dimensions, but also occurs when something is varying in a feature dimension.

Other researchers have shown that the flash-lag effect even occurs in non-visual stimuli. Alais and Burr (2003), for example, had a source of constant auditory white noise move (invisibly) through space near to their subjects, and presented a brief white noise burst at some offset in the middle of the trajectory. Comparable to the standard visual flash-lag effect, the burst was perceived to lag behind the position of the moving auditory stimulus. Also, reminiscent of Sheth et al. (2000), it was shown in a separate experiment by Alais and Burr (2003) that when the time-varying stimulus changed in feature space (pitch, in this case), it was perceived to lead the instantaneous value of the ‘flashed’ stimulus.

A final example of the diversity of flash-lag, which is given more treatment in the first of the three papers that make up this thesis, comes from Nijhawan and Kirschfeld (2003). These authors found that if one holds a rod, and moves it side-to-side through space in complete darkness, a small flash of light presented in alignment with the end of the rod is perceived to lag behind it. That is, the felt position of the subject’s rod (and, by extension, their hand) is perceived ahead of an aligned flash. This was described as a ‘motor’ flash-lag effect, since the only input regarding the changing position of the rod in space could come from a combination of efferent motor commands and afferent proprioception.

We have seen so far that the flash-lag effect is not limited to visual motion through space, and also occurs in motor (Nijhawan & Kirschfeld, 2003) and auditory (Alais & Burr, 2003) space, as well as in visual (Sheth et al., 2000) and auditory (Alais & Burr, 2003) feature dimensions. Whatever mechanism it is that underpins the flash-lag effect, it appears to be guided by a general perceptual principle. We turn now to the debate regarding the mechanisms that produce the flash-lag effect.

1.1.2 What causes the flash-lag effect?

1.1.2.1 Visual prediction

Accompanying the flash-lag effect's rediscovery, Nijhawan (1994) put forth an explanation, claiming that the misalignment reflected the workings of a perceptual mechanism that compensated for sensory transmission delays (Nijhawan, 1994). This account starts with the uncontroversial proposal that, without compensation, the time taken for retinal input to reach perception should mean that the percept of a moving object will lag behind its true position in space. However, more radical is the subsequent claim that one or more mechanisms – perhaps at multiple levels of the nervous system – reduce this physical-perceptual discrepancy by using the prior trajectory of a moving stimulus in order to predict its future state (e.g., Nijhawan & Wu, 2009; Nijhawan, 1994, 2002, 2008). By estimating the position the moving object should occupy, it is suggested that neural delays can be at least partially cancelled out in the process of perception. This would allow organisms to interact effectively with moving objects by seeing them close to their real-world locations (Nijhawan, 1994). On this view, then, the flash-lag effect occurs because the percept of a predictably time-varying stimulus is more up-to-date than that of an unpredictable flash, which is subject to a necessary delay. The difference between the position of the flash and the extrapolated position of the moving stimulus is the flash-lag effect.

Two broad findings with so-called 'half-cycle' displays represent the principal difficulties for the visual prediction account (Nijhawan, 2002). Firstly, in the *flash-*

initiated cycle, when the initial appearance of the moving stimulus coincides with the flash, the flash-lag effect is undiminished (Khurana & Nijhawan, 1995; Nijhawan, Watanabe, Khurana, & Shimojo, 2004; Nijhawan, 1992; Watanabe, 2004). If a moving object's position is predicted on the basis of its prior trajectory, it seems on face value that this display, in which the moving object has no pre-flash history, should result in no flash-lag. Secondly, in the *flash-terminated cycle*, when the flash occurs at the moment the moving stimulus disappears, no flash-lag is observed (Eagleman & Sejnowski, 2000a; Nijhawan, 1992; Whitney, Murakami, & Cavanagh, 2000). This is awkward for the visual prediction account because it would be expected that an unpredictable cessation of motion should result in a perceptual overshoot of the extrapolated moving stimulus. Further, in accordance with both of these findings, when the moving object changes direction at the time of the flash, it does not overshoot the change-point, but is forwardly shifted in the post-flash direction (Eagleman & Sejnowski, 2000a; Whitney, Murakami, et al., 2000; Whitney & Murakami, 1998). In response to finding a flash-lag in the flash-initiated cycle, Nijhawan and colleagues have defended the visual prediction model, arguing that the processes underlying it could set up an extrapolation very rapidly (Khurana & Nijhawan, 1995; Nijhawan, 2008; Shi & Nijhawan, 2012). Indeed, if this process were complete significantly before either stimulus was registered in perception, it would explain why the moving stimulus is perceived ahead of the flash even when both appear simultaneously. To address the lack of a flash-lag effect in the flash-terminated cycle, it has been claimed that highly salient motion offset signals might correct for the extrapolations of recently halted stimuli (Nijhawan, 2008). This perspective suggests that there is no flash-terminated flash-lag because the ongoing position prediction applied to the representation of a moving stimulus is interrupted and backwardly masked by a strong offset transient signal. A series of studies have supported this proposition by showing that reducing the salience of motion offset transient signals leads to previously unobserved forward shifts of motion endpoints (Maus & Nijhawan, 2006, 2008, 2009; Shi & Nijhawan, 2012). For example, forward displacements are seen when the moving stimulus is made to fade out before disappearing (Maus & Nijhawan, 2006), when it moves into the blind spot (Maus & Nijhawan, 2008), or when it is either dim or blue and moves into the central fovea, which is insensitive to such stimulation (Shi & Nijhawan, 2012). The visual prediction account thus remains on the table in spite of the results from the flash-initiated and flash-terminated cycles.

1.1.2.2 Motion averaging and postdiction

Two other explanations have their own, somewhat similar account of the flash-initiated and flash-terminated results. According to the temporal averaging model, the perceived position of a moving object equates to its mean position sampled over a period of time (Krekelberg & Lappe, 1999, 2000a, 2000b; Lappe & Krekelberg, 1998). The position of the visibly persisting flash is similarly averaged, though since it does not move, its mean location is somewhere behind that of the moving stimulus. Slightly different is the postdiction account, which agrees that position signals are averaged over time, but contends that the salience of the flash resets the averaging process (Eagleman & Sejnowski, 2000a, 2007). Once the averaging process is complete, the percept is said to be “postdicted to the time of the flash” (Eagleman & Sejnowski, 2000, p. 2038). This explanation could therefore be seen as the opposite of the visual prediction account outlined above, since the suggestion is that future events bias the perception of earlier events, rather than the other way around. The suggestion is, then, that the pre-flash trajectory has no impact on the perception of flash-lag. Both the temporal averaging and postdiction accounts sit well with the flash-initiated and flash-terminated results because they allow for post-flash events to affect the percept of the flash relative to the moving stimulus.

These positions, however, are not without their difficulties. Take for instance, that both accounts suggest that the forward displacement of a moving stimulus depends on its position comparison with a flash. It has been shown subsequently, however, that forward displacements can occur without comparison flashes, both in perception (Fu, Shen, & Dan, 2001; Maus & Nijhawan, 2006, 2008, 2009; Shi & Nijhawan, 2012), and in retinal physiology (Berry, Brivanlou, Jordan, & Meister, 1999). These displays produced forward shift effects despite the lack of a flashed stimulus to either persist in vision (as claimed by temporal averaging) or reset motion integration (as claimed by postdiction). Furthermore, Nijhawan (2002, 2008) has noted that both of these spatiotemporal integration theories argue that the neural delay for the moving and flashed stimuli are the same. The issue here is that for both stimuli to arrive in perception at the same time, and for the flash-lag effect to occur, the moving stimulus

should be perceived to speed up around the time of the flash – a phenomenon that has not been observed (Nijhawan, 2002).

1.1.2.3 Differential latencies

A third perspective argues, like visual prediction, that the flash-lag effect occurs because the moving object's representation is more up-to-date than that of the flash, but due to a 'passive' difference in perceptual latency, instead of an 'active' prediction process (Kafaligönül, Patel, Ögmen, Bedell, & Purushothaman, 2010; Ögmen, Patel, Bedell, & Camuz, 2004; Patel, Ögmen, Bedell, & Sampath, 2000; Purushothaman, Patel, Bedell, & Ögmen, 1998; Whitney, Cavanagh, & Murakami, 2000; Whitney & Cavanagh, 2000b; Whitney & Murakami, 1998). Two findings provided the initial justification for this position over the visual prediction account. Firstly, there was the aforementioned lack of an overshoot of the moving object at abrupt motion reversal points (Whitney & Murakami, 1998), which was initially troublesome for visual prediction. Secondly, there was the finding that increasing the luminance of the moving stimulus relative to the flash increased the effect (Purushothaman et al., 1998). The authors of this latter study argued that, since higher luminance stimuli are subject to shorter delays, and that increasing the luminance of the moving stimulus enhances flash-lag, the misalignment must be the result of differential latencies.

It has been contended, however, that the latencies for moving stimuli might actually be greater than those for flashed stimuli, when measured physiologically (Raiguel, Lagae, Gulyàs, & Orban, 1989; though also see Jancke, Erlhagen, Schöner, & Dinse, 2004) and psychophysically (Nijhawan et al., 2004). Nijhawan et al. (2004), for example, showed that response times to moving and flashed stimuli were no different, and further, that temporal order judgments actually suggested a latency advantage for flashes over moving objects. Along similar lines, Eagleman and Sejnowski (2000b) found that temporal order judgments for moving and flashed stimuli did not differ. Other authors have presented findings suggesting that moving stimuli may have a shorter latency than flashes, but not to an extent sufficient to explain the magnitude of the flash-lag effect (Arnold, Durant, & Johnston, 2003; Arnold, Ong, & Roseboom, 2009; Arrighi, Alais, &

Burr, 2005). Finally, even if the latency of the moving stimulus is less than that of the flash, this account does not neatly explain the flash-initiated flash-lag effect; that is, how can a latency advantage be bestowed upon one stimulus when it appears in synchrony with another (Maus et al., 2010; Nijhawan, 2002)?

1.1.2.4 Attention

A final approach to explaining the flash-lag effect, espoused initially by Baldo and Klein (1995), was actually the first to be offered in the wake of Nijhawan's (1994) motion extrapolation model, and invoked the possible role of attention. In an experiment not unlike Nijhawan's (1994), subjects judged the relative positions of a linear rotating stimulus and flashed extensions (Baldo & Klein, 1995). The experiment differed, however, in that the stimuli were rows of dots, rather than lines, and their eccentricity could be varied. It was found that as the flashed dots were moved away from fixation, they appeared to lag further behind the moving stimulus. Further, when the stimuli were switched, so that the outer dots rotated, while the inner dots flashed, the magnitude of the flash-lag effect did not depend on the eccentricity of the outer (moving) dots. On the basis of these results the authors claimed that the flash perceptually lags the moving stimulus because it takes time to shift attention from one to the other in order to compare their relative positions. When the initial locus of attention is far from the flashed stimulus, it takes more time to shift attention, and so a larger lag is perceived.

Results contradicting the attentional allocation model were given by Khurana and Nijhawan (1995) in response to Baldo & Klein's (1995) findings. In this experiment the rows of moving and flashed stimuli were interleaved, rather than presented in separate locations, so that the shift in attention should presumably have been negligible (Khurana & Nijhawan, 1995). It was found in this case that the flash-lag effect was unaffected by the lack of a required attention shift. The attentional allocation theory has drawn further criticism for its inability to explain the presence of a full flash-lag effect in the flash-initiated cycle (Khurana & Nijhawan, 1995; Nijhawan, 2002). Specifically, it is unclear why there should be an attentional advantage for one stimulus over the

other when both appear simultaneously. Another set of experiments also explicitly manipulated (rather than inferred) attention by cueing the location of the flash, and found that doing so did not affect the flash-lag effect (Khurana, Watanabe, & Nijhawan, 2000). However, in response, it has been shown that attention can at least modulate the flash-lag effect, if not cause it outright (Baldo, Kihara, Namba, & Klein, 2002; Chappell, Hine, Acworth, & Hardwick, 2006; Namba & Baldo, 2004; Sarich, Chappell, & Burgess, 2007).

1.1.2.5 Summary of the flash-lag debate

There is no widespread agreement on the nature of the flash-lag effect. The preceding review has attempted to non-exhaustively sketch out the most influential theories put forward thus far, and to give the reader an impression of the state of the discussion. It should be clear that attempts to integrate all flash-lag phenomena within a single overarching conceptual scheme have been fraught with problems. However, though it is fair to say that the majority of publications on the flash-lag effect at least attempt to weigh in on the debate regarding its cause, it is not always the principal focus. While the nature of such a pervasive perceptual illusion is obviously of considerable interest, it is worth noting that a subsection of the literature reports experiments that make use of the flash-lag effect in order to examine other perceptual effects. The section to follow will review this approach.

1.2 Using flash-lag to address other questions

1.2.1 Dissociating retinal and perceived positions

Perhaps the most prominent example of using the flash-lag effect to probe an issue unrelated to mislocalisation came from Nijhawan (1997), who used it to demonstrate that colour channels are integrated centrally in the cortex. Specifically, this study

showed that a combination of superimposed coloured light is perceptually decomposed into its constituent colours if one component is in motion and the other is flashed. Nijhawan (1997) had observers view a green bar of light tracing a circular path around fixation, while a smaller red line was flashed on top of it as it reached a certain location. The green bar's path was either uncovered so briefly that it appeared static (at the same moment and position that the flashed red line was presented), or else the bar was visible for its full trajectory. Under normal circumstances, superimposing red and green light produces a sensation of yellow, however, as has already been established, a moving stimulus is perceived to be spatially separated from a flash presented in the same location (e.g., Nijhawan, 1994). The question was, then, whether retinal collocation, but perceptual separation would lead to the flash appearing yellow, as with static stimuli, or red, suggesting that it had been cortically decomposed via input from motion processing. To test this, a red-green comparison line was presented on the opposite side of fixation from the flash, comprising of the same red component, as well as an adjustable green component. Subjects had to alter the green component until the red-green mixture appeared to match the colour of the flashed line. It was found that when the moving green bar was presented only briefly (so that it appeared static), the green component of the comparison line was set much higher than when the full trajectory of the green bar was exposed. That is, the flashed line appeared reddish in the extended exposure (i.e., full motion) condition, and yellowish in the brief exposure (i.e., static) condition, despite the retinal stimulation at the time of the flash being identical. Further experiments shored up this finding by showing that the effect was specifically attributable to the perceived displacement of the stimuli, and that the visible persistence of the green bar in the brief exposure condition did not bias the flashed line's colour towards green. Fundamentally it was concluded that motion signals have an input to colour processing, and therefore, that the percept of yellow must come about from the central cortical combination of separate red and green channels.

While Nijhawan (1997) offered an interpretation of his colour decomposition finding in terms of a visual prediction mechanism that underpins the flash-lag effect, this was not the main focus of the study. Indeed, while the observed decomposition of yellow may be explained by way of a cortical process of motion extrapolation, it is not a prediction explicitly drawn from the visual prediction theory. Rather, the flash-lag effect was simply used here to reliably dissociate retinal location from perceived location in order

to get at the separate issue of how combinations of coloured light are processed. This leads us onto an analogous example of the use of flash-lag to distinguish between retinal and perceptual positioning, but in a rather far removed field of vision science.

Khurana and colleagues made use of the flash-lag effect to investigate the processes underlying facial identification (Khurana, Carter, Watanabe, & Nijhawan, 2006). It had been shown previously that when the bottom half of one face and the top half of another are fused into a facial ‘chimera’, recognition of the constituent faces is impaired, compared to when the two halves are misaligned (Young, Hellawell, & Hay, 1987). The conclusion drawn from this *composite face effect* was that facial identification is based on automatic processes that examine the configuration of facial features. Essentially, the suggestion is that one cannot help but initially see a chimera as a new identity, which interferes with the ability to identify the component faces. Khurana et al. (2006) questioned whether retinal or perceptual alignment of the face halves was key to the composite face effect, and made use of the flash-lag effect to dissociate the two. They performed three experiments in which the top half of a face flashed in synchrony with the appearance of the aligned bottom half, which then moved to the right for 280ms before disappearing (i.e., a flash-initiated cycle). The faces could either be chimeras, in which the two halves were from different famous people, or non-chimeras, in which the two halves were from the same famous person. The first experiment revealed that when the bottom half moved following the disappearance of the flashed top half, identification reaction times were shorter than when the bottom half remained static (for the same 280ms used in the motion condition). This was only the case for chimeras, which in general took longer to identify than non-chimeras. The second experiment used the same chimeras and non-chimeras to verify that subjects genuinely perceived a misalignment between the face-halves when they were physically aligned. This was done by measuring the point of subjective equality with a method of constant stimuli, in which the flashed face-half was presented at various offsets from the starting point of the moving face half, and subjects had to judge whether one was left or right of the other. The third experiment used the exact same stimuli as the second, except that subjects were tasked with identifying as quickly as possible the flashed face half. Crucially, a peak in reaction times was observed that corresponded with each subject’s point of subjective alignment, as indicated by the results of the preceding experiment. Thus, the first experiment showed that retinal alignment and perceptual misalignment

disrupts the composite face effect, while the second and third experiments showed that perceptual alignment but retinal misalignment reinstated it. It was made clear, therefore, that the composite face effect is based more upon perceptual than retinal alignment of two halves of a facial chimera.

Khurana et al. (2006) acknowledge that, like Nijhawan (1997), their study was not aimed at uncovering the causes of the flash-lag effect, but instead capitalises on it to address an issue in face perception. Nijhawan (1997) and Khurana et al. (2006) may represent the only adoptions of flash-lag for disentangling retinal and perceived positions, but a related mislocalisation, the flash-drag effect, has been put to analogous use elsewhere.

The *flash-drag effect* describes the phenomenon of a brief flash being perceptually mislocalised in the direction of motion of a nearby moving stimulus (Whitney & Cavanagh, 2000a). For a diagram see Figure 1.2 further on. Kosovicheva et al. (2012) used this illusion to repeatedly shift the perceived (but not retinal) position of a briefly presented adapting grating. Earlier work had found that presenting a tilted grating to one part of the visual field biased the perception of subsequently viewed gratings in the opposite direction (*tilt aftereffect*; Gibson & Radner, 1937). Neurophysiological evidence also suggested that this effect resulted from the adaptation of orientation-selective cells in V1 (e.g., Maffei, Fiorentini, & Bisti, 1973; Movshon & Lennie, 1979). By using the flash-drag effect to shift the perceived position of the adapting stimulus, Kosovicheva et al. (2012) were able to show that the tilt-aftereffect was strongest when the test grating was presented in the retinal location of the adaptor. However, the effect was also greater in the perceptually shifted position of the adapting grating, than it was in the ‘anti-perceived’ position, in the opposite direction. By dissociating the retinal and perceived positions of the adapting stimulus with flash-drag, Kosovicheva et al. (2012) provided evidence that motion signals are able to bias retinotopic mapping in V1.

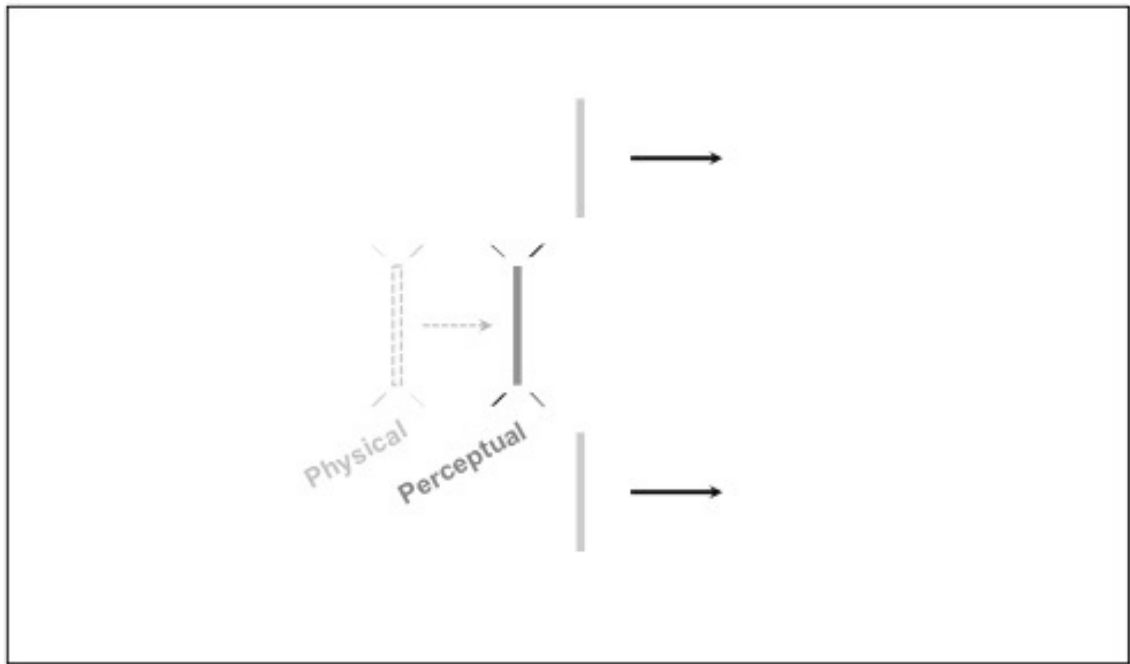


Figure 1.2. The flash-drag effect: Flashes in the vicinity of moving stimuli are dragged in the direction of motion.

This series of experiments, then, is analogous to those outlined in the preceding paragraphs: the aim was not to uncover the nature of flash-drag, but to make use of it to gain insights about other processes by distinguishing between retinal and perceptual positioning. The section following departs from this, reviewing some of the research in which variations in the size of the flash-lag effect have been used, and could be used, to examine a wide range of issues.

1.2.2 Variations in flash-lag magnitude

Vroomen and de Gelder (2004) used the flash-lag paradigm to study temporal ventriloquism, a crossmodal phenomenon in which sounds bias the perceived timing of visual stimuli. Previous work had shown, for example, that the perceived rate of a flickering light is biased towards the rate of a concurrently fluttering sound (Gebhard & Mowbray, 1959), and that a series of auditory clicks before or after a flash make the flash appear to occur earlier or later, respectively (Fendrich & Corballis, 2001). It was noted, however, that all prior work on temporal ventriloquism had made use of rhythmic sequences of auditory stimuli, and never isolated auditory and visual stimuli (Vroomen & de Gelder, 2004). Vroomen and de Gelder (2004) thus performed an initial experiment in which a sound burst sometimes accompanied the flash in a standard visual flash-lag display. It was found that when the sound was presented, the flash-lag effect was smaller and the psychometric curve was steeper. This was interpreted as an enhancement of visual processing due to a perceptual sharpening of the temporal boundaries of the flash due to the concurrent sound burst. This explains why the perceived displacement of the moving and flashed stimuli was smaller, and the categorisation function of the flash was less variable. Comparable to the aforementioned finding of Fendrich and Corballis (2001), a second experiment by Vroomen and de Gelder (2004) also showed that if a sound burst was presented before or after the flash, the flash-lag effect was diminished or enhanced, respectively. A follow-up study with event-related potentials again used this adaptation of flash-lag to probe the time course of temporal ventriloquism in the brain (Stekelenburg & Vroomen, 2005). It is important to note here that these studies were different from those in the preceding section inasmuch that flash-lag was not used to separate physical and perceptual positions. Instead, differences in the size of the flash-lag effect under different conditions (e.g., with and without sounds) were studied in order to make inferences about a distinct phenomenon (i.e., temporal ventriloquism). The two studies that follow share this characteristic, though they diverge in that they base their use of the effect upon particular interpretations of its cause.

Recall earlier the attentional allocation explanation of the flash-lag effect. It was proposed that the time taken to shift attention from the moving to the flashed object in

order to compare their positions resulted in a misalignment due to the continued motion of the moving stimulus (Baldo & Klein, 1995). While later studies disputed that attention is at the heart of the effect (Khurana & Nijhawan, 1995; Khurana et al., 2000), other evidence implied that it can at least modulate it (Baldo et al., 2002; Chappell et al., 2006; Namba & Baldo, 2004; Sarich et al., 2007). Shioiri and colleagues exploited this to investigate whether the flash-lag effect could actually be used as a measure of spatial attention (Shioiri, Yamamoto, Oshida, Matsubara, & Yaguchi, 2010). In their first experiment the authors showed that when there are multiple moving objects, one of which is cued as the flash-lag target, the flash-lag effect is diminished, consistent with the aforementioned role of attention. Additionally, their second experiment revealed that the larger flash-lag effect seen in faster moving stimuli (which they argue require more attentional resources to track) was relatively diminished when the target was cued. These results were taken as confirmation that focusing attention on the target reduces the flash-lag effect, and the authors subscribed to the idea that attention affects, but does not cause, the misalignment. In their third experiment, the authors demonstrated that when a location near to the real target stimulus is cued, a reduction of the flash-lag effect is also observed. It was highlighted that this is consistent with previous findings showing that attention is spread over a region around an attentionally-tracked moving object (Matsubara, Shioiri, & Yaguchi, 2007). Finally, Shioiri et al. (2010) argue that the consistency of the results across their experiments suggest that the flash-lag effect could be an effective measure of spatial attention. Alternative measures, for instance, might require eye-tracking procedures, or more difficult psychophysical tasks such as detecting the perceptual threshold of a probe. These authors therefore suggest that, with a suitably grounded understanding of how it is modulated by certain effects (in this case, attention), flash-lag can be used as a measure of those effects in other contexts.

This broad approach was also taken by Khan and Timney (2007) in a study of the effects of alcohol on neural latencies. In one of their experiments it is shown that drinking fruit juice mixed with alcohol leads to greater flash-lags than drinking an equivalent volume of fruit juice alone. They claim that since flash-lag is caused by differential latencies for the moving and flashed objects, the enhanced flash-lag effect after drinking alcohol must reflect a general slowing of neural processing speed. Not unlike Shioiri et al. (2010), Khan and Timney (2007) make use of an interpretation of the flash-lag effect's underlying mechanism in order to address another question. While

Shioiri et al. (2010) asked whether the flash-lag effect could be used to measure visual attention, Khan and Timney (2007) are interested in whether alcohol affects perceptual latency. However, this is perhaps a good time to begin discussing the limits of using flash-lag as a tool for other research questions, since the justification of Khan and Timney's (2007) claim is flawed and requires unpacking.

To begin, if one assumes that differential latencies are the sole cause of the flash-lag effect (which is unlikely – see further on), Khan and Timney (2007) give no justification for their prediction that a general elevation of neural latency should result in a greater misalignment. The differential latencies account has at its heart the claim that moving stimuli are processed faster than flashed stimuli, so that the flash is only seen after the moving stimulus has shifted forwards (e.g., Purushothaman et al., 1998; Whitney & Murakami, 1998). So, if as they say, “alcohol acts to increase neuronal latency for both the flash and the moving stimulus” (Khan & Timney, 2007, p. 1825), it follows that there should be no impact on the size of the flash-lag effect unless the latencies for the moving and flashed stimuli are affected to different extents. For their results to support their argument Khan and Timney (2007) would have had to justify why alcohol might be expected to slow the neural processing of the flash more than the moving stimulus.

Second, the idea that differential latencies are the root cause of the perceptual misalignment between moving and flashed stimuli is not as widely accepted as the authors imply. In the treatment given earlier to the differential latencies account it was highlighted that, like attention, differences in processing latency might contribute to, but do not cause the flash-lag effect (Arnold et al., 2003, 2009; Arrighi et al., 2005). Other research suggests that the latencies for moving and flashed stimuli are either the same (Eagleman & Sejnowski, 2000b), or different, but in the opposite direction to that predicted by the differential latency account (Nijhawan et al., 2004; Raiguel et al., 1989). It should be clear, then, that processing latency differences might not be able to explain the discrepancy between effects observed after having, and having not, consumed alcohol. Indeed, other contending explanations of the flash-lag effect could also account for the difference. For example, in light of the preceding discussion of Shioiri et al. (2010), it could be that alcohol enhances the flash-lag effect because it increases the time taken to shift attention from the moving to the flashed stimulus.

While Shioiri et al. (2010) provided evidence that flash-lag was affected by attention in their stimuli, this was not the case for Khan and Timney (2007).

Despite the flaws of this particular study, it nevertheless serves to demonstrate how variations in the size of the flash-lag effect can be used to address other issues in perception. As mentioned, Khan and Timney (2007) imply that the differential latency account of flash-lag is broadly accepted, though it should be clear now that this is not the case. Khan and Timney's (2007) approach, however, should be commended in that it highlights that if a consensus is reached about the cause of the flash-lag effect, the deeper level of insight would enhance its potential for applications elsewhere. So, for example, if it were true that differential latencies are at the root of the illusory displacement, inferences could be made about the latencies of different stimuli by examining how flash-lag is modulated when they are presented as moving and flashed objects.

A specific pair of findings in the literature hints at a further, more speculative use of flash-lag. These results bear upon the nature of the flash-lag effect, but it will be argued here that they point to a further, unrelated application of the illusion. Specifically, the idea posited is that differences in the size of the flash-lag effect could be used to compare cognitively based spatial associations between things. In justification of this, let us consider first the work of Noguchi and Kakigi (2008), who performed experiments including a crucial condition in which half of a Japanese Kanji character moved sideways, while the other half was flashed close to alignment with it. It was found that this condition produced smaller flash-lag effects than simply presenting moving and flashed bars or a pseudo Kanji character. Furthermore, an additional experiment showed that non-Japanese English speakers, with no knowledge of Kanji characters revealed no such reduction for the same Kanji stimuli. However, when viewing real and pseudo versions of an alphabetical character, English speakers produced results comparable to the Japanese speakers with Kanji characters; that is, a recognisable character resulted in a smaller flash-lag effect. The consistency of the findings across experiments, and an earlier response in the brain to Kanji characters in Japanese speakers (indicated by magnetoencephalography), is suggestive of a higher cognitive influence on the flash-lag effect (Noguchi & Kakigi, 2008). The conclusion

was that prior experience in other contexts of spatial associations between the moving and flashed stimuli can reduce the flash-lag effect.

A second finding that implies flash-lag is reduced by cognitive associations between the moving and flashed stimuli was reported in the Khurana et al. (2006) paper mentioned earlier. Recall that these researchers presented combinations of face halves from the same famous person (i.e., a non-chimera) and different famous people (i.e., a chimera), with the top half flashing briefly as the bottom half began moving. The primary issue under investigation was not the nature of flash-lag, but instead whether the composite face effect depended on retinal or perceptual alignment of face halves. In their second experiment they verified that the flash-lag effect was perceived when using their facial chimera and non-chimera stimuli. While both stimulus types produced flash-lags, it was also shown that non-chimeras produced significantly smaller flash-lags than chimeras. That is, when the two halves were from the same, recognisable person, the flash-lag effect was diminished. This result is in accord with Noguchi and Kakigi (2008), in that the misalignment between the moving and flashed stimuli is reduced when they recognisably belong to the same overall object, or Gestalt. Performing the same experiment with unfamiliar faces might of course strengthen this finding. If the difference between chimeras and non-chimeras was relatively diminished or eliminated, it would suggest that mere surface level consistencies between facial features cannot explain the reduction of the flash-lag effect in facial chimeras. Especially in light of Noguchi and Kakigi (2008), however, the possibility must be considered that cognitive processes interact with spatial perception to reduce the flash-lag effect in things that are associated at a higher level. For instance, this could be in terms of either an effect of priming, whereby the moving stimulus primes the registration of the flashed stimulus (Khurana et al., 2006; Khurana, 2008), or because prior knowledge of things makes them appear more like they do in more familiar contexts (Noguchi & Kakigi, 2008). Further experiments could reveal whether experimentally induced associations (e.g., learned in the lab) between unfamiliar shapes, symbols, or images have a similar potency to reduce the flash-lag effect. If this literature were built upon, the size of the flash-lag effect could even be used as a tool to measure the strength of spatial associations, not unlike the suggestion of Shioiri et al. (2010) that it be used to measure attention. So, in this way flash-lag shows potential as a tool for assessing learning outcomes as they pertain to spatial associations. For instance, to draw closely from the

Noguchi and Kakigi (2008) study, the extent of children's learning of characters could be measured by assessing changes in flash-lag magnitude when half is in motion and half is flashed.

In the previous section, two examples were highlighted of flash-lag's use for distinguishing between the contributions of retinal and perceptual positioning to unrelated phenomena, and a single example was given of a comparable use of the flash-drag effect. The current section, on the other hand, has reviewed literature reporting either uses of flash-lag magnitude to measure parameters unrelated to the nature of the effect, or else point towards its application in other capacities. Variations in the size of the illusion have been made use of to study temporal ventriloquism, attention, and the effects of alcohol on perceptual latencies. It has also been conjectured that flash-lag might, with further empirical grounding, be exploitable in measuring the level of spatial association between pairs of stimuli. The section to follow will give an overview of the research reported in the body of the thesis, and give commentary on how it takes up the mantle of using the flash-lag effect, and particularly its magnitude, to probe miscellaneous issues.

1.3 A synthetic overview of the research reported herein

1.3.1 A common approach to answering different questions

The three papers that make up the body of this thesis report programmes of research that are, on the surface, very different from each other, though they all leverage flash-lag to elucidate disparate issues in spatiotemporal perception. This section will provide a short summary of each paper in conjunction with a synthetic overview, bringing the topics together in light of research outlined in the preceding section. As will become clear, a tenet common to all of the papers herein is that they examine differences in flash-lag magnitude between opposing directions of motion. This approach is used to make

predictions and draw conclusions about the parallels between perception and action (Paper I), the effect of threat on visual perception (Paper II), and the way in which we perceive abruptly disappearing stimuli (Paper III).

1.3.2 A common methodology

Every experiment reported in the current papers makes use of a psychophysical method of constant stimuli to present the stimuli at various physical offsets from each other. Subjects are required to make binary choice judgments about where one stimulus appears in relation to another, and the physical offset that elicits 50% of each response is estimated by fitting a psychometric curve. This is taken to refer to the relative physical offset that yields perceptual alignment. This approach is widely used to measure the flash-lag effect (e.g., Eagleman & Sejnowski, 2000a; Kanai, Sheth, & Shimojo, 2004; Khurana et al., 2006; Sheth et al., 2000; Shi & Nijhawan, 2008). In Paper I, two experiments are reported that measure the flash-drag effect, which is also often estimated with a similar method of constant stimuli (e.g., Durant & Johnston, 2004; Fukiage, Whitney, & Murakami, 2011; Shi & Nijhawan, 2008; Whitney & Cavanagh, 2000a). Finally, in Paper III, two experiments are presented in which the forward displacement of a changing object's endpoint is measured in relation to a continuously visible, rather than flashed, reference stimulus. This approach was most directly inspired by very similar work by Whitaker and colleagues, who also used a comparable method of constant stimuli (Whitaker, McGraw, & Pearson, 1999).

It should be highlighted that the binary choice approach to measuring perceptual biases can be problematic in certain circumstances. Importantly, Morgan and colleagues have recently argued that, unlike two-alternative forced choice discrimination tasks, binary choice leaves open the possibility that decisional criteria change between conditions, rather than perception itself (Morgan, Melmoth, & Solomon, 2013). For instance, cognitive effects might make a subject slightly more likely to give a certain response in one condition more than the other. When it is suspected that this might be an issue at play, it is discussed in the corresponding section.

1.3.3 A summary of Paper I: ‘Motor’ versions of visuospatial illusions reveal shared perceptual space of vision and action

Paper I uncovers similarities and differences between the visual and motor versions of the flash-lag effect. A great deal of literature argues that perception and action systems are not fundamentally distinct from one another. For instance, mechanisms of action production affect how motion is perceived visually (e.g., Viviani & Stucchi, 1989, 1992; Viviani, 2002), and viewing a behaviour can affect action production (e.g., Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000). Similarly, several classes of neuron exhibit both motor and perceptual properties (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Murata et al., 1997). A paper from Nijhawan and Kirschfeld (2003) has also shown that the flash-lag effect occurs when the moving stimulus is not visual, but rather the motor/kinaesthetic representation of one's body. This result was taken to further indicate that there is a deep intertwining of perception and action systems in the brain.

Paper I starts with two experiments that build on Nijhawan and Kirschfeld's (2003) finding of a ‘motor’ flash-lag effect, with an examination of whether it displays a difference in magnitude when motion is either towards or away from the fovea. It has been shown elsewhere that this occurs in visual flash-lag, with foveopetal motion (i.e., towards fixation) leading to a larger forward displacement of the moving stimulus (Shi & Nijhawan, 2008). If the motor and visual flash-lag effects exhibited the same motion direction based anisotropy it would suggest that both are based on the same underlying systems. The subject gripped a handle in their right hand and moved it from one end of a rail to the other in complete darkness while fixating directly ahead. An LED was flashed at some offset from their handle, and they judged whether it had come from ahead of or behind the handle. The position at which the handle triggered it was varied between trials, and was always while the subject's hand was to the right of their midsagittal plane.

It was found that during motion towards fixation, there was a strong flash-lag effect, such that a flash aligned with the handle was perceived to lag considerably behind the position of the hand. However, during motion away from fixation there was a flash-*lead*

effect, with an aligned flash being perceived ahead of the hand. Velocity differences between motion directions were ruled out as a determining factor in the perceptual anisotropy. However, it was noted that in Experiment 1a, the distance travelled by the hand before hitting the first possible trigger location differed between foveopetal and foveofugal motion directions. In Experiment 1b this parameter was equalised between directions and the same results were obtained.

Experiment 2a looks at whether this anisotropy is the result of a differential bias of the perceived position of the flash caused by the unseen motion of the arm. In vision, for instance, it has been shown that foveofugal motion in the right visual field can lead to a flash-lead effect, due to a small forward displacement of the moving stimulus and a large forward displacement of the flash (Shi & Nijhawan, 2008). Here a very similar set up to Experiments 1a and 1b was used, except that a reference bar was visible throughout each trial, somewhere above the flash. The task was to judge the location of the flash relative to the bar, rather than relative to the moving handle. It was found that during foveopetal motion (i.e., leftwards arm movement), a flash physically aligned with the reference bar was perceived approximately 4mm to its left. During foveofugal motion, on the other hand, an aligned flash was perceived accurately. The difference between conditions represents the first demonstration of a ‘motor’ flash-drag effect, in which one’s unseen arm movement biases the perceived position of a nearby visual stimulus. A follow-up experiment (Experiment 2b) removed the reference bar and used fixation as the reference stimulus. Movement directions were no longer explicitly foveopetal or foveofugal, and it was found that there was a rightwards bias (1.65mm) of the flash during rightwards (i.e., backhand) arm movement, but no bias during leftwards arm movement. This experiment therefore showed another motor flash-drag effect, though it appeared somewhat differently to that in Experiment 2a. It was argued that in Experiment 2a, a general foveopetal bias of briefly presented visual stimuli was added to by motor flash-drag during foveopetal motion, and cancelled out by it during foveofugal motion. The results of Experiment 2b are explained in terms of backhand arm movement being more associable with foveofugal than foveopetal visual motion. Since foveofugal visual motion produces a larger flash-drag effect (Shi & Nijhawan, 2008), it is suggested that this might be evidence of parallels between the visual and motor flash-drag effects.

In light of the motor flash-drag effects seen in Experiments 2a and 2b, the results of Experiments 1a and 1b can be re-examined. While the flash position is clearly biased by the motion of the hand, it is not to an extent that would be able to explain the foveopetal flash-lag and foveofugal flash-lead seen in the initial experiments. It is suggested, therefore that Experiments 1a and 1b revealed a differential bias of hand position more than of flash position. Finally, it is proposed that more research is required to uncover the nature of the motor flash-lag/lead anisotropy, but that its overall character is still consistent with its reflection of common mechanisms in perception and action.

Paper I expands on the perception-action literature by investigating ‘motor’ versions of two well-known perceptual illusions. Of particular interest in these experiments is the difference in flash-lag and flash-drag magnitude between opposing motion directions. On the whole, it is shown that the motor flash-lag and flash-drag effects display parallels with their visual counterparts, albeit with some caveats. This demonstrates how the size of the flash-lag and flash-drag effects can be measured across different modalities to infer similarities and differences between those modalities. In light of this one might, for example, devote further effort to examining the extent of the parallels between the visual and auditory flash-lag effects in a similar way. If analogous stimulus variations in the visual and auditory flash-lag effects produced analogous results, it would strengthen the suggestion that the effect is truly cross modal (Alais & Burr, 2003).

1.3.4 A summary of Paper II: Threat enhances the flash-lag effect

Paper II looks at how threat can (and cannot) influence visual perception. This issue has become especially pertinent in the context of numerous studies claiming that the process of vision is ‘paternalistic’ (for a review, see Firestone, 2013). In general, the suggestion is that we perceive things not necessarily how they are in reality, but in ways that lead us to err on the side of caution when selecting a behavioural response. This position has stemmed from a multitude of findings. For example, hills look steeper when one is wearing a heavy backpack (Bhalla & Proffitt, 1999), or when one is lacking in either

calories (Schnall, Zadra, & Proffitt, 2010) or psychosocial resources (Schnall, Harber, Stefanucci, & Proffitt, 2008). A counter position has emerged, however, suggesting that many of these apparently perceptual effects may actually reflect higher cognitive biases on processes of judgment and memory, for example (e.g., Durgin et al., 2009; Durgin, Klein, Spiegel, Strawser, & Williams, 2012; Firestone & Scholl, 2014; Firestone, 2013). It has been shown, for instance, that when a satisfactory explanation is given for the backpack worn by subjects judging how steep a hill is, the tendency to report the hill as steeper disappears (Durgin et al., 2009). The implication is, then, that subjects without a cover story guess at the experiment's hypothesis, and provide responses in accordance with it. Other cognitive processes, such as memory, have also been shown to influence similar findings (e.g., Cooper, Sterling, Bacon, & Bridgeman, 2012).

A part of the paternalistic vision literature that has received less of this type of critical attention has proposed that threat can bias visuospatial perception, such that we see threatening objects as either closer (Cole, Balci, & Dunning, 2013), larger (van Ulzen, Semin, Oudejans, & Beek, 2008), or faster (Riskind, Kelley, Harman, Moore, & Gaines, 1992; Riskind, Moore, & Bowley, 1995; Vagnoni, Lourenco, & Longo, 2012; Witt & Sugovic, 2013), than non-threatening objects. It is argued that, for the most part, this literature potentially suffers from the same cognitive confounds as the research on, for instance, hill gradients. An adapted version of the flash-lag effect – an unambiguously perceptual measure of relative positioning – is offered as an appropriate test of whether threat can indeed bias visuospatial perception.

In Experiment 1, subjects high or low in spider phobia viewed an image of a spider or a butterfly looming or receding on one side of the display. During this animation, the same image was flashed on the other side of the screen at one of several size offsets from the animated image, and subjects had to judge which image appeared larger at the time of the flash. It was predicted that if threatening objects are perceived as closer or larger, then the high-phobia group should display both a greater looming flash-lag and a smaller receding flash-lag for spiders than they do for butterflies, and that this anisotropy should be greater than it is in the low-phobia subjects. Regarding the claim that threatening objects are perceived to move faster, previous studies (e.g., Witt & Sugovic, 2013) only tested motion towards the subject. The only prediction to be tested here, then, is that the high-phobia group should produce a larger looming effect in

spiders than in butterflies, and that this difference should be greater than it is in the low-phobia group, since flash-lag scales up with speed (Nijhawan, 1994).

The results of Experiment 1 showed that there was no difference in the flash-lag effect between phobia groups for either direction of motion, or with either animal image. While this is inconsistent with the paternalistic vision stance, since it suggests that perception is not affected by threat, several possible issues with the study are identified. Overall, it is found that the receding spider produced a smaller flash-lag than the receding butterfly. It could be, therefore, that everyone found the spider more threatening than the butterfly, and that an enhanced effect during looming motion was not observed due to a ceiling effect. Furthermore, the moving (target) and flashed (comparison) images were the same, something which has been suggested as a factor that may eliminate a perceptual bias (Firestone & Scholl, 2014). Experiment 2 attempted to address these points.

Each trial in Experiment 2 uses one of two spider images (more- and less scary) that linearly translate upwards or downwards across the display, while two lines (constant separation) are flashed simultaneously above and below it. The flash-lag effect is measured by varying the physical position of the spider between the lines and asking subjects to judge which line appeared closer to the spider at the time of the flash. Crucially, in one condition the display is oriented normally (i.e., vertically), and in the other it is oriented horizontally, so that motion up or down the screen corresponds to either towards or away from the subject. Again, subjects were either high or low in spider phobia. The principal finding from this experiment is that while the more- and less scary spider images produce similar flash-lag effects in the low-phobia subjects, the more scary spider results in a considerably enhanced flash-lag effect in the high-phobia group. It did not matter whether the motion was towards or away from the subject, but flash-lag was greater overall in those who found the moving stimulus more threatening.

It is argued that these results provide support for the broad claim of paternalistic vision that threat can bias visual perception, but that they contradict the specific claim that threatening stimuli are perceived closer to us. For this to be the case one would have expected to see an effect of display orientation, which did not manifest.

This paper, like the previous one, makes predictions about how the size of the flash-lag effect should vary between motion directions if certain mechanisms are at play. In the previous paper the directions of motion were (mostly) of one's hand relative to fixation, while in this paper the directions of motion are of stimuli towards or away from the body. Unlike with motor flash-lag in Paper I, however, Paper II shows that the direction of motion has little effect on the flash-lag effect, but that other manipulations (i.e., how threatening the stimulus is, per se) have a considerable impact. The findings from Paper II are ultimately discussed in terms of several of the perspectives put forward to explain the flash-lag effect, though the data do not explicitly arbitrate between the divergent viewpoints.

1.3.5 A summary of Paper III: Additive and subtractive effects of gamma movement on the forward displacement of size-changing stimuli

Paper III demonstrates that when a size-changing stimulus abruptly disappears, its size at offset is more shifted forwards after contraction than it is after expansion. Whitaker et al. (1999) previously showed that expanding or contracting stimuli that suddenly disappear are perceived to be larger or smaller, respectively, than a continuously visible static stimulus visible for the same period of time. These authors, however, did not report a difference in the size of the effect between expanding and contracting motion. Informal observations suggest that contracting motion results in a greater effect.

In Experiment 1, a vertical line expanded or contracted for some time before disappearing in synchrony with a flashed line on the opposing side of fixation. Subjects judged which line appeared longer at the time of the flash. While flash-lag does not normally manifest under such flash-terminated circumstances (e.g., Nijhawan, 1992), the size of the flash was perceived to lag behind the size-at-offset of the dynamic stimulus. It is argued, though, that this could well be the result of stimulus eccentricity (see Kanai et al., 2004), rather than something particular to expanding or contracting motion. More interesting is that the flash-lag effect was larger for contracting than

expanding lines. It is suggested that this might be the result of gamma contraction – the rapid apparent contraction of abruptly disappearing stimuli (e.g., Bartley, 1941; Kenkel, 1913). More specifically, the idea is that the forward displacement of contracting stimuli is added to by gamma movement at offset, while the forward displacement of an expanding stimulus is subtracted from.

Rather than using a flashed reference, Whitaker et al. (1999) used a comparison stimulus that remained visible throughout the presentation of the dynamic stimulus, and did not report a forward displacement advantage of contracting motion. Experiment 2 adopted this procedure in order to test whether the result in Experiment 1 came about from using flashed references. The experiment was thus identical to Experiment 1, except that instead of the reference line being flashed, it was visible throughout the same time period that the dynamic line was presented. Again, it was found that the size of the dynamic stimulus was displaced forwards at offset, and that the effect was greater for contracting than expanding lines.

It was then reasoned that, if gamma movement were occurring in Experiment 2 when the dynamic stimulus suddenly disappeared, it should likewise have been occurring in the reference line. At the moment of comparison, then, this would have relatively diminished apparent size of both stimuli, and so augmented the forward displacement of expanding stimuli, and reduced it in contracting stimuli. Experiment 3 examined this possibility by having the reference line remain on screen for some time after the disappearance of the dynamic line. Consistent with the posited effect of gamma movement, Experiment 3 (compared to Experiment 2) produced a more pronounced forward displacement for contracting lines and a smaller shift for expanding lines.

To examine further the possibility of gamma movement's involvement in the forward displacement anisotropy observed thus far, Experiment 4a presented the same stimuli as Experiment 1, except that only the very top and bottom portions of each line were shown. The dynamic stimulus was thus a pair of small squares that moved vertically towards or away from each other. Subjects judged whether the moving or flashed pair of squares was more widely spaced. The idea was that since gamma contraction only occurs in stimuli that are perceived as coherent objects, squares moving towards or away from each other should produce less of an anisotropy than a coherent line that

contracts or expands. Experiment 4a also tested whether the motion of the ends of the lines relative to fixation might have produced the greater forward displacement for contracting stimuli. Consistent with predictions, the results showed that the expanding and contracting lines were not shifted forwards to different extents.

Experiment 4b, however, took these stimuli a step further, and presented only one square from each stimulus, that either moved towards or away from the display's horizontal meridian. Here it was shown that the anisotropy reappeared, and re-established the possibility that the motion direction of the ends of the lines relative to fixation contributed to the effects observed in Experiments 1-3. It is argued, however, that while the anisotropy in Experiment 4b may occur due to a flash-terminated flash-lag advantage for foveopetal motion (e.g., Kanai et al., 2004), it is unlikely to be able to explain the anisotropy seen in Experiments 1-3, since Experiment 4a showed no such difference.

To better establish whether motion direction relative to the fovea produces the greater forward displacement of abruptly disappearing contracting stimuli, Experiment 5 uses a full-cycle flash-lag procedure, in which the dynamic stimulus continues after the flash. It has been shown previously with linearly translating stimuli, that full-cycle flash-lag results in a relatively enhanced foveopetal effect (Shi & Nijhawan, 2008). However, if gamma contraction is the principal factor in the anisotropy seen in Experiments 1-3, the difference between conditions should not manifest, since the dynamic stimulus does not disappear at the moment of comparison, and cannot, therefore, be subjected to gamma movement. This is indeed what is shown in Experiment 5, with no difference between the forward displacements of contracting and expanding lines.

It is discussed that contracting stimuli are in the process of transitioning towards a natural endpoint, of 'zero' size, while expanding stimuli do not have an implicit endpoint. When either stimulus disappears, gamma contraction makes them appear to rapidly (but not instantaneously) attain 'zero' size. It is claimed, then, that the forward displacement of abruptly disappearing contracting stimuli is greater than that of expanding stimuli because it effectively fast-forwards its transit to its inferred endpoint. In formerly expanding stimuli, on the other hand, this process has to work against the underlying forward displacement, and thereby reduces it.

Finally, a novel interpretation of gamma movement is offered that invokes our lack of experience with the phenomenon of sudden, instantaneous disappearance, both with distal objects and their retinal images. Since objects and their images tend to become less visible over a period of time before going entirely out of view, it is argued that our visual systems prefer to interpret abrupt disappearance as rapid contraction (as when an object rapidly recedes), given that this is more likely to reflect the true state of things.

This paper makes use of the flash-lag effect to gain insight into how we perceive stimuli that abruptly disappear. Experiments 2 and 3 are not strictly flash-lag studies (since they do not employ flashes), but the forward shift effects they produce are similarly useful for uncovering the mechanisms at play. As in the preceding papers, the focus is on the magnitude differences in effects that can be observed between different directions of motion. The paper begins with the observation that motion direction (contraction versus expansion) has an impact on the size of forward displacements, and proceeds to whittle down the possible underlying cause of the anisotropy.

1.4 Discussion

The body of this thesis is made up of three papers, each devoted to a distinct topic in perception, but tied together by their use of flash-lag (and some related mislocalisations) in order to draw inferences about separate issues. Before moving on to discuss this in more detail, however, it should be noted the three papers can be integrated under a further high-level conclusion. In short, the flash-lag effect represents an attempt by the visual system to discern the most likely, or most behaviourally useful set of environmental circumstances. In Paper I, this is evidenced by the greater effect for foveopetal, than foveofugal arm movement, which is argued to be a more behaviourally significant type of limb motion. In Paper II, flash-lag is shown to be larger for scary objects – permitting the threatened observer more time to select a response to their changing positions. Finally, in Paper III, flash-lag findings are used to back the claim that disappearing stimuli are seen to rapidly contract because prior experience with stimuli that go out of sight implies they are more likely to have done so gradually,

rather than instantaneously. Whatever the system that underlies flash-lag, the present findings suggest that it is an active, adaptive mechanism, allowing the observer of a moving object a more useful and actionable percept. On this basis, however, a single theory of flash-lag is still not favoured over the alternatives.

Let us take a step back from this line of thought, though, and return to the main thrust of the thesis – that is, the utility of flash-lag. Recall that Paper I looks at the similarities and differences between the visual and motor versions of the flash-lag and flash-drag effects in order to establish whether they have a common cause. The second paper investigates the effect of threat on visuospatial perception, by examining differences in the magnitude of the flash-lag effect for scary and less scary stimuli that move towards or away from the observer. In Paper III, flash-lag magnitude differences between expanding and contracting stimuli that suddenly vanish are taken to reflect the processes underlying how we perceive abruptly disappearing stimuli. Alongside previous research that takes a similar approach to using the illusion, it is hoped that attention will be drawn to flash-lag's wide-ranging potential as a tool in psychophysics.

Highlighted earlier were two main ways in which the flash-lag effect can be put to use in perception research. Firstly, the misalignment itself permits a distinction between retinal and perceptual positioning. This has been used, for example, to demonstrate that colour can be perceptually decomposed via motion signals (Nijhawan, 1997), and that for the composite face effect to occur, face halves need only be aligned perceptually, and not necessarily on the retina (Khurana et al., 2006). Secondly, flash-lag can be used in the way adopted in the current papers, by examining how the size of the effect varies between experimental conditions. This approach has previously yielded insights about the processes underlying temporal ventriloquism (Stekelenburg & Vroomen, 2005; Vroomen & de Gelder, 2004), the speed of neural processing following alcohol consumption (Khan & Timney, 2007), and the potential for flash-lag to be used as a measure of attention (Shioiri et al., 2010). Setting the current studies apart from previous research in this vein, however, is that they relied on comparisons of the size of the misalignment between different directions of motion, that is, directional anisotropies in the flash-lag effect. The ideas that guided each avenue of research enabled predictions to be derived about how opposing directions of motion might produce different flash-lag magnitudes. Previously, flash-lag anisotropies have only been used to

inform about the cause of the misalignment itself (e.g., Kanai et al., 2004; Shi & Nijhawan, 2008).

Focusing on directional anisotropies in the effect should be seen, however, as only one approach to the size of the flash-lag effect across conditions. For example, in Paper II it is notably demonstrated that the magnitude of the flash-lag effect can vary between populations. While predictions are made about how flash-lag should change between directions of motion relative to the observer, it is found that the effect's size depends more on how threatening the observer finds the stimulus. When the observer considers the moving object more threatening, (i.e., when high-phobia subjects viewed the more scary spider), the flash-lag effect is relatively enhanced, regardless of motion direction. It should be noted that this is comparable to the research by Noguchi and Kakigi (2008), who found flash-lag differences in specific meaningful stimuli (moving and flashed components of Kanji characters) dependent on the observer's experience, or interpretation of the stimulus (i.e., whether they were a Japanese or non-Japanese speaker). Not only does the potential for flash-lag in investigating the perceptual effects of cognition considerably widen the scope of its use, this approach also highlights how between-group differences can be observed.

The real-time, perceptual nature of flash-lag endows it with much potential. At the moment that the flash is perceived, there are two stimuli, with an unambiguous separation between them that participants easily make a perceptual judgment about (e.g., Khurana et al., 2006). This attribute is central to the use of flash-lag in Paper II, in which potential biases in judgment and responding are teased apart from perception itself. As a counter example, it is helpful to consider how another forward displacement phenomenon does not share the same real-time characteristics of flash-lag, and is thus less useful in the contexts outlined above. Representational momentum is evident when several successive views of a stimulus are shown as it is moved in some consistent direction, and observers judge whether a final view is the same as or different to the penultimate view (for reviews, see Hubbard, 1995, 2005). Observers tend only to give a "same" response when the final view is progressed further along the implied trajectory than the penultimate view. While it has been argued that flash-lag and representational momentum reflect the same underlying systems (e.g., Hubbard, 2013), it should be noted that the methods of their measurement are rather different. In flash-lag, people

make a judgment about two stimuli perceived simultaneously, while in representational momentum, subjects must compare a currently perceived stimulus with a remembered stimulus. One cannot claim, therefore, that variations in the magnitude of representational momentum reflect perception, more than they do cognition. Flash-lag, on the other hand, provides a convenient perceptual snapshot of the misalignment of two simultaneously presented objects. Differences in the size of the effect are thus more likely to be perceptual in nature.

For investigating issues unrelated to mislocalisation, researchers may also consider other real-time, perceptual forward displacements, such as the motion-induced position shift (e.g., De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). In this illusion, adjacent windows containing stimulus fields translating in opposite directions appear shifted in the direction of the motion they respectively contain. While this forward shift effect is just as ‘perceptual’ as flash-lag, in that the target and comparison stimuli are simultaneously visible, the requirement for two windows containing moving surfaces limit the scope of applications. Flash-lag is more versatile in this respect, since observers need only be presented with a moving object and a flashed object, with few other constraints on the stimuli.

Before concluding, however, it is worth noting that caution should be taken when adopting flash-lag for one’s particular application. The results of Paper III suggest that flash-lag can be linearly added to and subtracted from by some effects (e.g., gamma movement), but Paper II highlights that some factors (e.g., threat), can interact with the processes underlying flash-lag itself. If one plans to use flash-lag to address another issue, it is certainly worthy of consideration that the effect of interest may or may not be independent of the mechanisms behind the flash-lag effect. Furthermore, as outlined earlier with the example of Khan and Timney (2007), discretion is required when basing one’s use of flash-lag on a contentious interpretation of its cause. These authors relied entirely on the differential latencies account of flash-lag in the interpretation of their results, though this is not widely accepted as an explanation of the effect. Shioiri et al. (2010) also predicated their use of the illusion on a particular account (i.e., attentional allocation), but backed up their arguments with data suggesting that it was indeed an important factor. The lesson here is that the disputed source of the flash-lag effect means that using it on the basis of a theory as to its cause requires special justification.

1.5 Conclusions

This overview chapter began by outlining the prominent theoretical positions in competition with each other to explain the nature of the flash-lag effect. Following on, a review was given of a separate literature, presenting numerous examples of flash-lag's use by researchers in addressing separate issues not directly related to perceptual mislocalisation. This led into a summary and synthetic overview of the papers compiled to form the body of the thesis, including discussion of the factors that draw them together.

The cause of the flash-lag effect is hotly debated, though a particular vein of research, contributed to by this thesis, has recognised that the effect's contentious origins need not hinder its use in alternate fields. Flash-lag is robust, versatile, cross modal, and unequivocally perceptual, and thus lends itself to a breadth of possible applications. Two ways of using flash-lag for other purposes have been drawn attention to. First, there is the potential to distinguish between retinal and perceptual alignment of stimuli, and second, predictions and conclusions can be made about variations in the size of the effect between conditions. The current papers report research that falls under the second of these categories, with the more specific characteristic that they all probe for differences in the size of the effect between different directions of motion.

The debate regarding the nature of flash-lag is undoubtedly important, though will likely not produce a commonly accepted explanation in the near future. It is argued here that, in spite of this, the potential for the effect to be used in other capacities should not be overlooked. However, as was highlighted earlier in a review of work by Khan and Timney (2007), further narrowing the scope of explanations for flash-lag will greatly enhance its possible benefits to researchers.

Paper I: ‘Motor’ versions of visuospatial illusions reveal shared perceptual space of vision and action

2.1 Abstract

It has been argued by many researchers that perception and action are intimately intertwined. A review of the literature is followed by a series of experiments that support this general position by demonstrating ‘motor’ analogues of two well-known visual illusions. It has been shown previously that the position of one’s unseen moving limb is perceived to lead the position of a collocated flash (motor flash-lag effect; Nijhawan & Kirschfeld, 2003), and separately, that visual flash-lag is larger for foveopetal than for foveofugal motion (Shi & Nijhawan, 2008). The first two experiments show that the motion direction based anisotropy in vision is similarly evident in the motor domain, but that the smaller effect in foveofugal motion actually becomes a flash-lead effect when the moving stimulus is one’s unseen hand. Additionally, it is demonstrated for the first time that limb movement in the dark biases the perceived position of nearby flashes in the direction of motion: a motor equivalent of the visual flash-drag effect (Whitney & Cavanagh, 2000a). The findings overall are claimed to represent common mechanisms in perception and action. It is ultimately suggested that the primacy of earlier-developing motor systems may engender analogous biases in the later-developing visual system through processes of associative learning.

2.2 Introduction: The common ground between perception and action

In this section a broad outline will be given of some of the commonalities between perception and action systems. Psychological perspectives, principally informed by behavioural measures will be covered first, followed by neurophysiological evidence that also suggests a weakening of the theoretical distinction.

Intuitively we feel that our sensations are distinct from our actions. It is not novel to suggest, however, that the historical separation between sensory and motor processes is too rigid to reflect the reality of the brain. Representative of this position is Sperry (1952), who highlights that

[a]mong the salamanders and lower fishes, where thought processes are presumably negligible, the bulk of the nervous apparatus is clearly concerned with the management of motor activity... From the fishes to man there is apparent only a gradual refinement and elaboration of brain mechanisms with nowhere any radical alteration of the fundamental operating principles. (p. 297)

Here, the notion is that, compared to more primitive vertebrates, human brains simply have a greater capacity for cognitive processing in the mediating stage between afference and efference, but that a stark divide remains absent. The following section will review how this general perspective has gained momentum in the intervening years, and how a venerable literature has grown around it.

2.2.1 Psychological perspectives

Numerous experiments have demonstrated either the motor system exerting an effect on perception, or of perception affecting motor processes, which taken together expose the underlying parallels of these two branches of the nervous system. Outlines of the literature from these two viewpoints will be considered before moving on to cover the

contributions of two influential psychological theories: the theory of event coding, and the motor theory of speech perception.

A profitable area of research has concerned how the ways in which the brain controls movement also affect how motion is perceived. Take, for example, how limb velocity varies when tracing shapes on a two-dimensional plane. Under these circumstances it has been shown that instantaneous velocity depends in a lawful fashion upon curvature, such that it is higher at less curved, than at more curved parts of the trajectory - something that has come to be known as the *two-thirds power law* (Flach, Knoblich, & Prinz, 2004; Schütz-Bosbach & Prinz, 2007; Viviani & Schneider, 1991; Viviani, 2002). This aspect of motor control is difficult to violate in one's own movement (Viviani & Mounoud, 1990; cf. Beets, Rösler, & Fiehler, 2010), and is thought to directly reflect updating processes in populations of motor cortical neurons (Schwartz, 1994; Viviani, 2002). Crucially, the two-thirds power law has also been demonstrated to bias visual perception in a number of ways. In an influential experiment, Viviani and Stucchi (1989) showed subjects a moving dot tracing an ellipse with a principal axis that could be varied in extremity. The task was to decide which axis was longer. When the dot's velocity profile was in accordance with the two-thirds power law for either a vertical or horizontal ellipse, subjects' discrimination thresholds were biased in that direction. So, for example, if the trajectory of the dot described a perfect circle, but its velocity profile described an ellipse with a vertical principal axis, subjects would be more likely to say that it was a vertically oriented ellipse. In a separate study, the same authors asked subjects to vary the velocity of a moving dot tracing an ellipse so that it appeared constant throughout its trajectory (Viviani & Stucchi, 1992). It was found that only if the velocity profile obeyed the two-thirds power law was it judged as uniform, despite this being an objectively inaccurate estimate. The generalisability of the two-thirds power law, out of motor processes, and into perceptual processes, reveals how limits upon systems of movement production can also constrain how motion is perceived. Indeed, there is also evidence that people are equally, and highly, sensitive to deviations from the two-thirds power law in displays comprising just a dot trace, or also including a point-light display of a whole-body human, or of just an arm appearing to draw the trace (Bidet-Ildei, Orliaguet, Sokolov, & Pavlova, 2006). The insensitivity to biological form implies that the effect of motor constraints upon perception extend

beyond biological motion, and into movement in general. This point will be returned to in the discussion.

Another line of research has looked at how the manipulation of motor systems through training or adaptation affects visual perception. Staying briefly with the two-thirds power law, it initially appeared that one could not retrain the motor system to violate the rule (Viviani & Mounoud, 1990; Viviani, 2002), though a more recent finding has shown that this is not the case. Subjects were given passive motor training in velocity profiles that disobeyed the two-thirds power law, and it was found that this made them more sensitive to that particular velocity profile in an ensuing visual discrimination task (Beets et al., 2010). A similar experiment showed that when subjects were trained on a cyclical arm movement task, subsequent duration estimations were enhanced for a similar movement presented visually (Hecht, Vogt, & Prinz, 2001). These experiments relied on motor training, but shorter-term motor adaptation effects have also been shown to exert an effect on vision. For instance, Volcic and colleagues started by noting that there are systematic inaccuracies in depth perception that are not present at a certain distance from the body corresponding approximately to the length of one's arm (Volcic, Fantoni, Caudek, Assad, & Domini, 2013). After performing an adaptation task in which subjects' arms were made to seem longer, however, the region of accurate visual depth perception became recalibrated to the 'new' arm length. Similarly (though returning to motion, rather than depth perception), another study showed that adapting to a constant lateral force during reaching movements made people more accurate at interception movements, but only when the target moved in a direction consistent with the adapting force field (Brown, Wilson, Goodale, & Gribble, 2007). The authors claimed that motor adaptation produces a predictive model for motor systems that is also made use of by visual perception. These findings all represent examples of vision following the lead of motor systems in a fluid, changeable manner, so that when the motor processes change, so too do the visual processes. Consistent with the claim that perception follows action in an *ad hoc* way, Knoblich and Flach (2001) further showed that people are more capable of predicting the outcomes of their own behaviour, viewed on video, than they are the outcomes of other people's actions. This implies that inherent familiarity with one's own motor system enhances visual perception of it in action.

Thus far the focus has been on behavioural and psychophysical evidence for action systems calibrating visual perception. However, particular effort has also been applied to the complementary perspective of how perception affects action, and more specifically, how viewing the behaviour of conspecifics influences behavioural execution. For example, it has been shown that viewing a given action automatically facilitates subsequent performance of that action (e.g., Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Castiello, Lusher, Mari, Edwards, & Humphreys, 2002; Edwards, Humphreys, & Castiello, 2003; Knoblich & Flach, 2001; Vogt, Taylor, & Hopkins, 2003; Wohlschläger & Bekkering, 2002). Brass et al. (2000), for example, found that when people are tasked with performing a particular finger movement in response to a short video clip, reaction times are shorter to videos of the same, rather than different finger movements, and to finger movements in general, rather than to symbolic cues. Similar findings have also been reported for whole-hand prehension actions, and further show that viewing human hands has more of an effect than viewing robot hands (Castiello et al., 2002; Edwards et al., 2003). The implication of this is that viewing an action automatically primes the motor systems involved in performing a similar action, suggesting a fundamental connection between action perception and production. Consistent with this, interference effects are also evident when the *observed* and *produced* behaviours are incompatible (for a review, see Blakemore & Frith, 2005). This was found in the aforementioned Brass et al., (2000) study when a task-irrelevant finger movement was incongruent with the to-be-performed finger movement. Another characteristic example comes from Kilner and colleagues, who had their subjects make repeated vertical or horizontal sinusoidal movements of their extended arm while viewing someone else perform a similar movement along either the same or the perpendicular axis (Kilner, Paulignan, & Blakemore, 2003). Motion capture data revealed more variance in the subjects' arm movements when observing movement along the incongruent, versus the congruent axis. Taken together, these findings show that perceiving the actions of a conspecific can facilitate or impede the observer's behaviour, depending on whether they are trying to perform a similar or dissimilar action. Why should this be though? This question brings us on to two separate theories that account for the unity of perception and action in their own ways.

2.2.1.1 Theory of event coding

Proposed by Prinz (1997), the theory of event coding has at its heart the common-coding principle: the claim that perceptions and planned actions are represented in the same cognitive domain. It is said that at more peripheral levels of the nervous system, afferent sensory codes (from receptors) and efferent motor codes (to muscles) might well be distinct, but that they overlap at a central, higher level, “between (late) perception and (early) action” (Hommel, Müsseler, Aschersleben, & Prinz, 2001, p. 849). This is in contrast with the more orthodox assumption that sensory and motor systems are coded independently and require an intermediary process of translation in order to interact (Hommel et al., 2001).

A further theoretical tenet is that actions are planned on the basis of the perceptual effects they are aimed at producing (the action-effect principle; Prinz, 1997). The idea is that perceiving and acting are both ways of “internally representing external events (or, more precisely, interactions between these events and the perceiver/actor)” (Hommel et al., 2001, p. 860). Put differently, an action is simply a way of producing a perceptual effect in the world. In this manner it is proposed that external *events* are coded for, and that the only distinction between codes for action and codes for perception are that the former are used to supervise the motor system in producing the desired perceptual result. Importantly, it is thought that the sensory outcomes aimed for in a planned action are not the relatively proximal feedback one gets from, say, an arm movement, but are instead higher-level, more distal effects. An action plan to turn on a light, for example, will not be oriented towards achieving visual and proprioceptive feedback of operating the light switch itself, but will instead be focused on achieving the action’s end goal – the perceived illumination of the room.

Often experiments are cited as consistent with the theory when they demonstrate an interaction between features (e.g., the spatial location) of a stimulus and a required response, as these are thought to represent the use of the same event code (Prinz, 1997). A prominent example comes from the spatial stimulus-response compatibility effect, noted by Fitts and Deininger (1954). In short, when asked to respond to a stimulus, subjects show shorter reaction times when stimulus and response are spatially

compatible. Simon, Hinrichs, and Craft (1970), for instance, had subjects rest each of their hands on one of two buttons out in front of them. Speeded left or right button-presses were required on the basis of high or low auditory tones (relationship counterbalanced across subjects) presented monaurally. Even though subjects were told to ignore which side the tone came from, reaction times were shorter when the required response was on the same side as the tone presented. This compatibility effect suggested to Prinz (1997) that action was facilitated when it required use of the same, already-active, event code that incorporated the side of space as one of its features. In the same study, it was shown that when subjects' hands were crossed, the pattern of results remained constant, rather than reversing along with the arm positions (Simon et al., 1970). That the effect followed the side of space, rather than the subject's arm position, leant further supported the idea that actions were coded for in terms of their distal, external effects. The action-effect principle found further support from a variation of this experiment by Hommel (1993). Here the button presses also operated one of two lights positioned above each loudspeaker. In a crucial condition, the left-hand button switched on the right-hand light, and vice versa. Under these circumstances, it was found that when subjects were instructed to press the button indicated by the tone, the aforementioned compatibility effect was present, but when they were asked to produce the right- or left-hand light, the results reversed, and they were now quicker to respond with the contralateral hand. This was strong support for the action-effect principle, as it seemed that the compatibility effect varied with the distal effects of actions, rather than with their proximal, body-centred features.

Implicitly, the theory of event coding emphasises the part played by perception in action, inasmuch as it claims that the perceptual effects of actions are the principal concern of codes-for-action. However, to make this observation is perhaps to do the theory of event coding a disservice, since really its core tenet is that there is no fundamental distinction between perception and action planning. We move now to another theory, which is not necessarily at odds with the aforementioned, but that clearly accentuates the role of action systems in perception over the reverse relationship.

2.2.1.2 Motor theory of speech perception

According to the motor theory of speech perception, we do not perceive speech by translating acoustic features into phonemes, but rather we rely on our mechanisms of speech production to decode the speaker's own intended phonetic gestures (Galantucci, Fowler, & Turvey, 2006; Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; Liberman & Mattingly, 1985, 1989).

Liberman and colleagues began with an interest in how speech is understood given the various difficulties of deriving phonetic information directly from an acoustic signal in natural speech (Liberman et al., 1967). For instance, it is highlighted that we can understand speech at rates far exceeding the temporal resolving capacity of our auditory apparatus. Indeed, attempts to construct reading machines that translate print into sequences of arbitrary sounds were unsuccessful due to subjects' inability to decipher the sounds at useful speeds, even after considerable practice (Galantucci et al., 2006; Liberman et al., 1967). It was also noted that while invariant acoustic cues for perceived phonemes are elusive, the articulatory gestures of the vocal tract, measured by electromyogram, are noticeably consistent across utterances of a phoneme (Liberman et al., 1967). Put differently, when acoustics point to one phonetic outcome, and articulatory gestures to another, perception follows the latter (Galantucci et al., 2006).

The motor theory of speech perception therefore proposes that mechanisms of speech production might also underlie its perception, by decoding the intended phonetic gestures of the speaker from the auditory signal (Liberman et al., 1967; Liberman & Mattingly, 1985). It is posited that in the brain, intended phonetic gestures are represented by the relatively unchanging motor commands that are used to produce the individual vocal tract movements associated with a particular gesture (Liberman & Mattingly, 1985). Phonemes are constructed from one or more of these units of articulation. Additionally, the tendency of multiple phonetic gestures to overlap in time is thought to allow the auditory system more time to resolve the sound produced by each articulatory event.

It follows, then, that phonetic perception is not strictly auditory, as it works on the basis of gestures rather than acoustics (Mattingly & Liberman, 1988). It is said that speech is perceived through a process of ‘generative detection’, in which the gestures required to produce a speech signal are reconstructed internally (Mattingly & Liberman, 1988). In this way it is thought that speech is recognised as such (by both speaker and listener), by virtue of the fact that it can be reproduced. So, in the case of the reading machines mentioned earlier, normal speech perception was not approximated because it was impossible to reconstruct the artificial articulatory events.

In essence, the motor theory of speech perception puts forth the claim that in terms of speech, perception and action are interwoven, or in Liberman’s (1967) words, “there is only one process, with appropriate linkages between sensory and motor components [of the nervous system]” (p. 452). This was later elaborated on with the assertion that a special phonetic module had evolved to empower both speech production and perception in unison (Liberman & Mattingly, 1985). Liberman and colleagues thus claim that their account satisfies a theoretical requirement for parity between speaker and listener, because perceived and produced speech events are represented in the same, commensurate fashion (Liberman & Whalen, 2000; Mattingly & Liberman, 1988).

In line with the evidence outlined earlier that perception of a behaviour can facilitate its subsequent production, the motor theory of speech perception has been supported by the finding that one can verbalise a syllable faster upon hearing that same syllable, rather than a tone (Fowler, Brown, Sabadini, & Weihing, 2003; Porter & Castellanos, 1980; Porter & Lubker, 1980). Neurophysiological findings have also been congruous. For instance, when speech is perceived, transcranial magnetic stimulation (TMS) of the tongue (Fadiga, Craighero, Buccino, & Rizzolatti, 2002) and lip (Watkins, Strafella, & Paus, 2003) regions of the motor cortex produces stronger motor evoked potentials (MEPs) in the corresponding musculature. More recently, functional magnetic resonance imaging (fMRI) has also been used to show that areas involved in the production of specific phonemes are likewise in use during their perception (Pulvermüller et al., 2006; Wilson, Saygin, Sereno, & Iacoboni, 2004). Further discussion of the relevance of the discovery of mirror neurons to the motor theory of speech perception will be given further on.

It is interesting to note here the parallels between the motor theory of speech perception and the theory of event coding outlined earlier. Fundamentally, they are aligned in their advocacy of a common-coding approach to perception and action– both claiming that the traditionally distinct processes in fact rely on a common psychological resource. However, they come at the issue from different perspectives. The motor theory of speech perception emphasises the role of action-in-perception, while the theory of event coding is an account of the part played by perception-in-action, though this should be seen as simply a difference in empirical starting points. An important difference, however, is that the motor theory of speech perception claims that both perception and action are permitted by recourse to motor commands, while the theory of event coding suggests that it is only at a higher-cognitive level, divorced from the low-level specifics of motor commands, that the two can interact (Galantucci, Fowler, & Turvey, 2001).

2.2.2 Neurophysiological perspectives

This section will consider several classes of neuron that might be considered to bridge the perception-action divide. First addressed will be mirror neurons, which respond both to perception and performance of actions. This will be followed by briefer outlines of the properties of canonical neurons, which respond when an object is either fixated or manipulated, and visuotactile neurons, which fire during action execution and also during visual and somatosensory stimulation. The relevance of these neurophysiological findings will also be linked back to the aforementioned psychological theories.

2.2.2.1 Mirror neurons

Mirror neurons that discharge during both the performance and observation of an action, were initially observed in area F5 of the monkey ventral premotor cortex (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). It was found that the spike rate of a ‘grasping mirror neuron’, for example, would dramatically increase when the monkey watched the experimenter taking a piece of food in his hand, and also when the monkey

grasped the food itself, and would cease activity when the action was completed (Gallese et al., 1996). It is worth noting that area F5 is traditionally considered to be a predominantly ‘motor’ oriented area, with a functional emphasis on orchestrating movement, so it was of great interest that cells there also responded to visual input, and particularly in such a specific way (Gentilucci et al., 1988; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997).

Three major classes of mirror neuron were identified in those early studies (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996). Some cells (~30%) were termed ‘strictly congruent’, as they only responded to observed and executed actions that were very similar to each other, such as to a particular type of precision grip, and not to other types of grip. ‘Broadly congruent’ neurons showed less discriminatory selectivity, so that they would discharge in response to grasping in general, for example, rather than to a precision grip only. Neurons of this class might otherwise have been very particular about either their visual or motor tuning, but in these cases were more broadly selective for the other modality. ‘Broadly congruent’ cells made up the majority of the F5 population (~60%). Finally, if a cell reacted to observed and executed actions that were distinct, but perhaps associated or complementary, it was labelled as a ‘logically-related’ mirror neuron. There therefore appears to be a population of mirror neurons with diverse and specialised selectivities, which would allow them to support sophisticated computational functions (see further on).

Some mirror neurons in area F5 are furthermore responsive to auditory stimuli that signify the performance of particular actions (Keysers et al., 2003; Kohler et al., 2002). Kohler et al. (2002) found that neurons that responded, for example, to the sight and sound of a peanut being broken by the experimenter, also responded when the monkey itself broke the peanut. This replicates the initial findings of visuomotor matching properties of mirror neurons (e.g., Gallese et al., 1996). Importantly, a further condition demonstrated a similar sensitivity to the sound of the breaking peanut alone. Taken with the original findings of mirror neuron properties, this illustrates that action execution and perceptual input in general (i.e., not simply vision) can stimulate mirror neuron populations.

Cells with ‘mirror’ properties are also prominent in the inferior parietal lobule (IPL; Bonini et al., 2010; Fogassi et al., 2005). The IPL is connected to F5 via the superior temporal sulcus – in which some neurons are selective for action observation, but not execution (Perrett et al., 1989; Rizzolatti, Fogassi, & Gallese, 2001). This circuit has come to be recognised as the classic, and perhaps predominant, functional mirror neuron system (Cook, Bird, Catmur, Press, & Heyes, 2014; Rizzolatti et al., 2001), though the presence of neurons with mirror-like properties has also been demonstrated in other areas of the monkey brain, such as the dorsal premotor and primary motor cortices (for a review, see Casile, 2013).

A weight of evidence has concurrently accumulated to suggest that humans too have mirror neurons (for reviews, see Molenberghs, Cunnington, & Mattingley, 2012; Rizzolatti et al., 2001). An early example applied TMS to the motor cortex and found increased MEPs in hand muscles while the subjects viewed hand grasping actions (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). The implication here is that activity in the relevant motor neurons is facilitated by the passive observation of actions. Indeed, much of the evidence covered earlier showing behavioural facilitation and interference effects when viewing similar or different actions also cites a role for mirror neurons (e.g., Brass et al., 2000; Castiello et al., 2002; Kilner et al., 2003). Such findings surely compel some reflection on the use of the word ‘passive’, since it seems that simple action observation may be less passive than intuitively assumed. A more recent fMRI study by Kilner and colleagues required that human subjects perform and observe the same and different actions one after another (Kilner, Neal, Weiskopf, Friston, & Frith, 2009). When the same action was observed twice or performed twice, adaptation effects were found in the inferior frontal gyrus (considered the human homologue of the monkey’s area F5), so that repetition of the stimulus resulted in a weaker response. Importantly, this was also the case when subjects observed an action and then performed it, and vice versa, suggesting that the region is substantially composed of neurons with mirror-like properties. A similar methodology also revealed consistent findings in the human IPL (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008). Evidence of mirror neurons in humans has almost exclusively been from indirect, non-invasive measures, though recently human single-cell recordings have also yielded supportive results (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010).

Before addressing interpretations of the function of mirror neurons, it is worth noting that, at the very least, these cells represent a bridging of perceptual and motor systems. This fronto-parietal network codes for actions, both perceived and performed. Consideration will now be given to the function they may serve.

2.2.2.1.1 Mirror neuron functions

Regarding the computational function that mirror neurons may play, the principle account suggests that they aid in the understanding of actions by conspecifics, and was posited by those who originally discovered the cells (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996). In short, the suggestion is that when an action is visually perceived, mirror neurons allow an internal simulation of the observed action in the neural substrate of the perceiver's own motor system. It is argued that such a mechanism would permit observers a much more thoroughgoing comprehension of others' behaviour than could be gained from a purely visual analysis of action (Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001). From this perspective, it might be said that actions of conspecifics are not remotely perceived like other events. Instead, they are perceived intimately and familiarly, with one's own motor systems privately resonating in conformity. As Rizzolatti and Craighero (2004) suggest,

[e]ach time an individual sees an action done by another individual, neurons that represent that action are activated in the observer's premotor cortex. This automatically induced, motor representation of the observed action corresponds to that which is spontaneously generated during active action and whose outcome is known to the acting individual. Thus, the mirror system transforms visual information into knowledge. (p. 172)

The conspicuous parallels between the action understanding theory of mirror neuron function and the motor theory of speech perception have not gone unnoticed (e.g., Galantucci et al., 2006; Gallese et al., 1996; Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004). Recall that, according to the latter, speech perception is not simply the apprehension and cognitive analysis of acoustic information, but a process of generative detection of the intended phonetic gestures of the speaker (Lieberman & Mattingly, 1985; Mattingly & Liberman, 1988). In the motor theory of speech perception, then, speech is perceived by recruiting the listener's own speech production

system, much as in the action understanding account of mirror neurons, one's motor system internally simulates observed actions in order to better comprehend them. The discovery of mirror neurons has also been invoked to support the theory of event coding on the basis of the suggestion that the class of cells demonstrates shared representations (i.e., common coding) between perception and action (Hommel et al., 2001). However, the notion of resonant motor systems connecting sender and receiver proposed by the action understanding theory of mirror neurons certainly seems more readily applicable to the motor theory of speech perception (Rizzolatti & Arbib, 1998).

2.2.2.3 Canonical neurons

Some cells that share similar anatomical loci with mirror neurons also show some comparable visuomotor matching properties. 'Canonical' neurons, for example, respond when a particular object is fixated on, as well when that object is manipulated (Murata et al., 1997; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Sakata, Taira, Murata, & Mine, 1995; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990). These cells were originally noted in the monkey anterior intraparietal sulcus, and were found to respond to visual fixation of, say, a lever, as well as to the action of pulling the lever, with or without vision (Murata et al., 2000; Sakata et al., 1995; Taira et al., 1990).

Subsequently, canonical neurons were also discovered in monkey area F5 (Murata et al., 1997), the same region in which mirror neurons were first found. Neuroimaging in humans has further suggested that we also possess canonical neurons in a similar frontoparietal circuit (Grèzes, Armony, Rowe, & Passingham, 2003).

Both mirror and canonical cells have very similar motor properties (e.g., some firing during precision grip, others during whole hand prehension) but the difference is in their visual selectivity (Fadiga, Fogassi, Gallese, & Rizzolatti, 2000). Canonical neurons respond to the visual presentation of objects, while mirror neurons respond to the observation of actions. The finding that some canonical neurons are additionally sensitive to the spatial orientation of their preferred object has led researchers to suggest that perhaps they are involved in the visual guidance of hand movements for object manipulation (Chao & Martin, 2000; Murata et al., 2000; Taira et al., 1990).

Fundamentally though, it is sufficiently interesting to note that perception of objects

draws upon motor systems, as if in preparation for potential action, or perhaps even for some deeper level of ‘motor perception’ (Fadiga et al., 2000). This idea is not dissimilar to the aforementioned action understanding theory of mirror neuron function, in which the actions of others are internally reproduced in the observer’s motor system to enable a stronger understanding. Canonical neuron properties are also consistent with the theory of event coding (Hommel et al., 2001), in which it is suggested that perceptions and planned actions are co-represented by the same cognitive resource. Cells that are selective for both the manipulation and perception of an object could certainly be seen to embody this principle of common-coding.

2.2.2.4 Visuotactile neurons

We have seen that both mirror neurons and canonical neurons are present in area F5 of the monkey ventral premotor cortex. Just posterior of F5, in area F4, another class of neuron with sensorimotor properties is also of interest. The cells in this region are commonly thought to be focused on coding for the movement of proximal body parts, such as the head or arms (Gentilucci et al., 1988; Rizzolatti et al., 1997). In this latter respect they can be distinguished from F5 neurons, which tend to be active during the movement of distal body parts such as the hands and fingers (Gentilucci et al., 1988). It has also been demonstrated, however, that many of the F4 neurons also discharge in response to both visual and tactile sensory stimulation (Gentilucci et al., 1988; Graziano, Hu, & Gross, 1997b; Graziano, Yap, & Gross, 1994). Interestingly, the visual receptive fields appear to be anchored to the tactile receptive fields, extending out into the close vicinity, and moving with the body part, rather than eye position (Graziano et al., 1997b, 1994). So, when an object is brought close to a neuron’s tactile receptive field on the monkey’s face or arm, for instance, the cell will begin firing in response to the visual stimulus, and will cease firing as it is moved away. This was found to be the case irrespective of eye position (Graziano, Hu, & Gross, 1997a). Furthermore, it was shown that if the lights went out and the object was quietly removed from the monkey’s peripersonal space, the cell would continue to fire until the lights were switched back on and fresh visual input could verify that it was no longer in the receptive field (Graziano et al., 1997a).

One interpretation is that these neurons underpin the visual guidance of actions towards objects, for which they would no doubt be useful (Gentilucci et al., 1988; Graziano & Gross, 1998; Graziano et al., 1997a, 1997b, 1994). Alternatively, Rizzolatti and coworkers (Rizzolatti et al., 1997) suggested that perhaps the region is responsible for representing the positions of things in motor terms, that is, in terms of how one might go about interacting with them. This is comparable to the way in which canonical neurons represent objects with reference to how they can be manipulated. Again, like canonical neurons, this is consistent with positions outlined earlier that assert the role of action systems in perceptual processes.

Similarly bimodal cells with body-part-anchored visual and tactile receptive fields have also been recorded in the ventral intraparietal area of the monkey brain (Avillac, Denève, Olivier, Pouget, & Duhamel, 2005; Colby, Duhamel, & Goldberg, 1993; Duhamel, Colby, & Goldberg, 1998). Interestingly, it has further been shown that, at least in this parietal area, the neurons exhibit mirror-like properties (Ishida, Nakajima, Inase, & Murata, 2009). Like those described above, the cells discharge both when an object touches a certain body part and when an object is moved close to that body part, but also when an object is moved close to the corresponding part of a conspecific's body. Inspired by the action understanding theory of mirror neurons, the inference made is that we use the representations of ourselves to understand the bodies of others. Presumably, the interpretation of Rizzolatti et al. (1997) would be that our own motor systems are utilised in understanding the peripersonal space of conspecifics, as if we are anticipating their potential actions.

2.2.3 Summary of perception-action unity

An outline has been given of some of the major theoretical positions and fields of research that support a weakening of the distinction between perception and action. We saw that principles of action production, such as the two-thirds power law, also affect visual perception. It was then highlighted that motor training and adaptation are able to modulate these sorts of perceptual effects. Evidence from a different perspective was then discussed, showing that observing behaviour could facilitate or impede behaviour

performance. The rationale and principal forms of evidence behind the influential theory of event coding and the motor theory of speech perception were given treatment to highlight the ways in which perception and action could be coupled. Finally, the properties and functions of mirror, canonical, and visuotactile neurons were addressed, since they demonstrate a concrete neurophysiological underpinning that helps explain much of the behavioural data. We turn now to another angle of attack on the unity of perception and action that has received little attention and that will be the focus of the current experiments.

2.2.4 Motor counterparts of perceptual illusions

Leading on from the literature just reviewed, the motivation behind this approach is the possibility that perceptual illusions could also manifest in a ‘motor’ domain, if the two aspects of the nervous system really are as connected as claimed. Take, for example, the flash-lag effect – an illusion in which a flash appears to lag behind an instantaneously collocated moving object (MacKay, 1958; Nijhawan, 1994). It has been shown that the effect is modulated by the observer’s control of both the moving (Ichikawa & Masakura, 2006, 2010; Scocchia, Actis Grosso, De’Sperati, Stucchi, & Baud-Bovy, 2009) and the flashed (López-Moliner & Linares, 2006) stimuli, and that motor or vestibular motion signals alone (in the absence of retinal motion) can also produce the displacement (Cai, Jacobson, Baloh, Schlag-Rey, & Schlag, 2000; Schlag, Cai, Dorfman, Mohempour, & Schlag-Rey, 2000). While these findings imply that motor involvement can modulate the visual illusion, an experiment by Nijhawan and Kirschfeld (2003) did away with a moving *visual* stimulus altogether. In complete darkness subjects held a 53cm long rod out in front of them and repeatedly rotated their wrist side-to-side to produce a sinusoidal motion of the rod’s end. During this movement a flash was sometimes presented at some lateral offset from the end of the rod and subjects had to judge whether it was ahead, behind, or centred on the rod itself. Only when the flash was 7-9cm ahead did subjects report that it was actually aligned. This shows that the flash-lag effect occurs when the moving stimulus is not visual, but is instead the unseen, felt position of an extension of the body in motion. The conclusion was that analogous internal forward models in the motor (e.g., Miall &

Wolpert, 1996) and visual (Nijhawan & Kirschfeld, 2003; Nijhawan, 2008) systems produce the motor and visual flash-lag effects, respectively. This idea is consistent with the wealth of literature outlined earlier suggesting that perception and action share close functional ties. For example, the finding of both a motor and a visual flash-lag effect could be accounted for by the theory of event coding's assertion that perceptual and motor events are coded for in the same representational space. The claim would be that we see similar forward displacements of moving objects in vision and action because the same processes underpin them. The motor theory of speech perception, and the action understanding theory of mirror neuron function might claim in their own terms that we observe similar displacements in perception and action because action systems are recruited in perception. Such a suggestion would be consistent with the findings of motor principles guiding visual perception (e.g., two-thirds power law; Viviani, 2002).

There has however yet to be a follow-up to Nijhawan and Kirschfeld's (2003) basic finding. The first two experiments in the current investigation will therefore attempt to replicate and extend Nijhawan and Kirschfeld's (2003) finding by examining whether the motor flash-lag effect displays a motion direction based anisotropy comparable to that in visual flash-lag. Specifically, it has been shown that the visual flash-lag effect is larger for motion towards the fovea (foveopetal; FP) than for motion away (foveofugal; FF) (Kanai et al., 2004; Mateeff & Hohnsbein, 1988; Shi & Nijhawan, 2008). Revealing such a parallel between the well-studied visual effect and the under-studied motor effect would shore up the suggestion that they reflect analogous mechanisms in the motor and sensory pathways.

Related to flash-lag is another motion-related spatial mislocalisation, commonly termed the flash-drag effect (e.g., Eagleman & Sejnowski, 2007; Shi & Nijhawan, 2008). This illusory displacement was initially discovered by Whitney and Cavanagh (2000), who had subjects judge the direction of misalignment of horizontal lines flashed on opposing sides of a rotating radial grating. When physically aligned, the flashed lines were perceived as if dragged in the direction of motion of the nearest edge of the grating, such that one line appeared above the other. Later research has expanded on this finding to suggest more generally that the positions of stationary flashes are biased in the direction of nearby motion (for a review, see Whitney, 2002). There has not, however, been an investigation of whether one's unseen body movement is similarly able to drag

the perceived positions of nearby flashes. The second two experiments probe this issue, by looking at whether arm motion in the dark biases the perceived positions of flashed lights relative to continuously visible reference stimuli. Demonstrating a motor flash-drag effect would be further evidence that visual and motor domains share a representational space.

2.3 Experiment 1a

2.3.1 Methods

2.3.1.1 Pilot observations

Two informal pilot studies suggested that there exists an anisotropic motor flash-lag effect. In one, an LED was attached to the end of a rod (approximately 400mm long), which the experimenter held at one end and passed back and forth through a vertical infrared beam to trigger a 1ms flash. When movement was towards a fixation point (approximately 200mm left of the trigger beam), the flash was perceived to lag the felt position of the rod. When movement was away from the beam this was also the case, but to a smaller extent. In a similar method, the experimenter pinched the LED between the thumb and forefinger of his right hand and moved his arm back and forth through the beam. Here there was the compelling sense that the flash came from somewhere behind where it was actually known to be. This was the case for both foveopetal and foveofugal motion, though again the effect was larger in the former. This is consistent with the anisotropy found in the visual flash-lag effect (Kanai et al., 2004; Mateeff & Hohnsbein, 1988; Shi & Nijhawan, 2008).

Pilot experiments were also performed with naïve subjects. In these, subjects gripped a handle attached to a horizontal rail and moved it side-to-side beneath a row of static light sources, one of which flashed as the handle passed the midpoint of the row. There seemed to be a general tendency towards foveopetal flash-lag effects and foveofugal

flash-*lead* effects, though there was also a great deal of inconsistency between subjects. It was hypothesised that the consistent perceptual effects observed across subjects by Nijhawan and Kirschfeld (2003) may have been due to every subject having a very clear notion that the source of the flash was in motion along with the handheld rod. In the pilot studies mentioned above, however, this may not have been the case. It was thus decided that in the main experiments all subjects would be deceived into believing that the source of the flash in each trial was in motion with their hand.

2.3.1.2 Subjects

Eight naïve subjects (4 male, 1 left-handed) with normal or corrected-to-normal vision participated in exchange for money or course credits.

2.3.1.3 Apparatus

Handle, slide rail, and false flash array. Subjects sat at a desk with their head immobilised by a chin rest and used their right thumb and forefinger to grip a handle (12.5mm in diameter × 23mm long) in front of them, angled up and pointing towards the level of their eyes. The base of the handle was attached to a vertical rod, which was in turn attached to a ball-bearing slide rail mounted on the desk. The handle itself was thus freely movable in the frontoparallel plane, from 450mm to the right to 150mm to the left of one's midsagittal plane (600mm extent-of-travel). Attached to the top of the handle, approximately 400mm from subjects' eyes, was a horizontal row of sixty-one 2mm diameter spots positioned at 5mm intervals, the central of which was directly above the handle. Nine of the spots, randomly distributed over the full length of the array, could be flashed (white light; 1ms) in sequence with repeated presses of a button by the experimenter (see Procedure).

Fixation, real flash, and half-silvered mirror. Directly in front of subjects was a 2mm red fixation spot, reflected in a half-silvered mirror mounted between them and the false flash array. Also reflected in the mirror was a 2mm spot that could be flashed (white light; 1ms) 150mm (20.43°) to the right of fixation. Both fixation and flash were

projected in the same optical plane as the row of spots on the false flash array. The brightness of the flash was adjusted to approximate the brightness of the flashes from the false array. Thus, when the light spot was flashed and seen in the mirror, its image was superimposed over the false flash array and thus appeared to have come from one of the 61 false flash spots. The real flash and central spot on the false flash array were aligned with each other when the slide rail reached the halfway point of its extent-of-travel. The fixation and flash light sources were suspended above the mirror and concealed from view by a screen.

Trigger positioning and velocity measurement. Three infrared trigger switches were attached to a motorised linear positioner mounted on the desk, oriented parallel to the slide rail. The positioning of these switches relative to each other was fixed. When a pin (yoked to the subjects' handle) passed through the 1st then 3rd of the switches, a computerised timer was started then stopped, respectively. Halfway between the 1st and 3rd switches, the 2nd switch was used to trigger the light spot flash reflected in the half-silvered mirror. The timing switches allowed the subjects' arm velocities at the time of the flash to be monitored on a trial-by-trial basis. Having these switches attached to the linear positioner meant that they could be repositioned between trials, so that the subjects' handle could trigger the flash before reaching, when in alignment with, or after passing the flash. The experiment was controlled using custom Matlab scripts running with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). See Figure 2.1 for a diagram of the experiment.

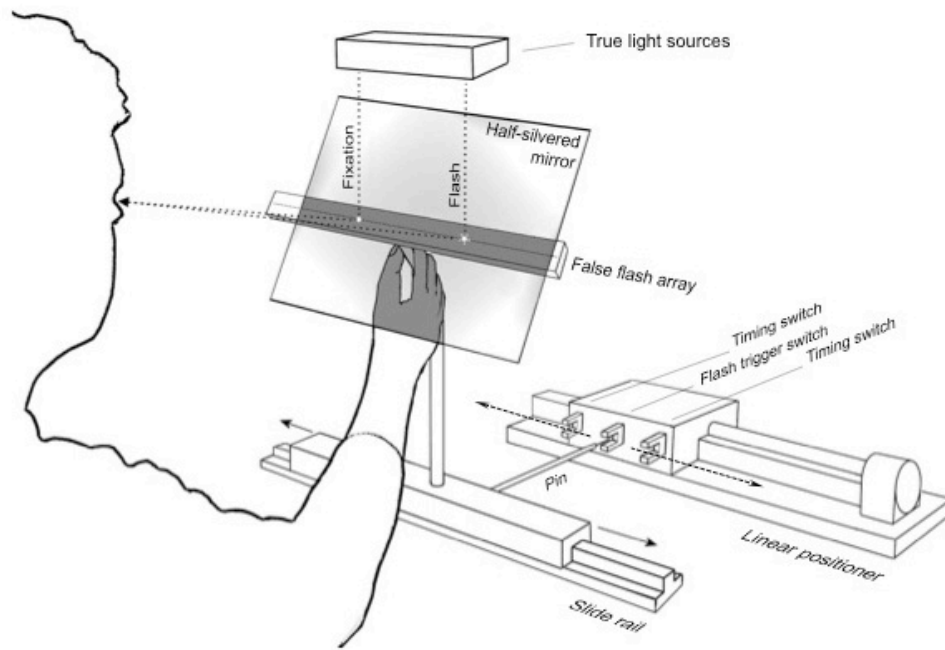


Figure 2.1. Experiment 1a: Diagram of experimental set-up.

2.3.1.4 Procedure

Instructions. With the room lights on, subjects were given a chance to pinch the handle and move it from one end of the rail to the other. If the subject appeared to be moving the rail particularly fast or slow the experimenter demonstrated an approximate ideal velocity, which they were asked to maintain as consistently as possible throughout the experiment. Their attention was then drawn to the row of spots on the false flash array and they were told that a random one of the spots would flash during each trial while they were moving the handle, and that they would have to say aloud whether they thought the flash had come from ahead of or behind the handle (binary choice). So, when moving leftwards, for example, a “flash-ahead” response would mean that they thought the flash had come from one of the spots to the left of their handle. The experimenter then showed the subject several of the spots on the false flash array flashing one at a time. After this point the false flash array was discreetly turned off, and all subsequent flash presentations came from the fixed flash source suspended above the half-silvered mirror. This meant that during the experiment the flash was always at the same retinal eccentricity, so that the changing distance between the

fixation point and the flash between trials could not be used as a cue for responding. Subjects were made to believe that the source of the flash was in motion with their arm so that their task was more clearly defined. That is, rather than having subjects judge where a static flash was (attached to the desk, represented in allocentric coordinates) in comparison to their limb (in egocentric coordinates), subjects had to judge whether the flash came from ahead of or behind the middle of an array. Finally, subjects were told that they would hear whirring mechanical noises during the experiment (i.e., from the motorised linear positioner) and that they should ignore them as best as possible.

Experiment. The fixation point was visible throughout the experiment. Before the room was made completely dark it was ensured that subjects were in the correct position and holding the handle properly. The lights were switched off and a computerised voice told the subject to move the handle to either the left or right end of the rail. Once in position, the linear positioner moved the trigger switch to one of 7 locations, so that the handle would trigger the flash when it reached one of 7 physical offsets from alignment. For the FP condition this meant that the flash was triggered while the handle was -160mm, -120mm, -80mm, -40mm, 0mm, 40mm, and 80mm from physical alignment. For the FF condition, the flash was triggered when the handle reached -80mm, -40mm, 0mm, 40mm, 80mm, 120mm, or 160mm from the flash. The difference in handle offsets between motion directions was in anticipation of a flash-lag effect in FP motion and a flash-lead effect in FF motion, as indicated by pilot experiments. Once the trigger was in position, the computerised voice asked subjects to “move right”, or to “move left”, depending on the condition. A single smooth arm motion brought the handle from one end of the rail to the other, and the flash was presented when the trigger was hit somewhere in the middle of the handle’s trajectory. Upon reaching the rail’s end-of-travel, the computerised voice said “respond”, prompting the subject to speak aloud whether they thought the flash had come from a source on the false flash array ahead of or behind the handle. The experimenter entered this response by pressing one of two keys on a computer keyboard, at which point the linear positioner moved the switch platform to a random position at a velocity that was varied between trials. This was a decoy movement to prevent subjects from being able to respond on the basis of the sound of the motor. Subjects were then told to “reset” the handle position by moving it back to the original starting point. Upon completing this

motion, another decoy movement of the trigger was made before it was moved into its intended position for the next trial. At this point the next trial began.

In sessions lasting approximately 1 hour, subjects performed 14 training trials (2 motion directions \times 7 handle offsets \times 1 repetition of each handle offset), followed by 280 experimental trials (2 motion directions \times 7 handle offsets \times 20 repetitions of each handle offset) in 4 blocks, between which the room was illuminated for at least 2 minutes and the direction of arm motion was alternated. Block order was counterbalanced across subjects. Within each block the order of trials was randomised. After the final trial of each block, excluding the final block, the computerised voice asked subjects to “hold position,” so that when they let go of the handle it would be in the correct position when the time came to begin the next block of trials. At the end of the experiment the method of deception was explained and subjects were questioned about whether they suspected the true source of the flashes; none did.

Data analysis. Subjects’ responses from each motion direction were fit with a cumulative normal function (as implemented by the Palamedes toolbox for Matlab; Prins & Kingdom, 2009). Points of subjective equality (PSEs) and confidence intervals were estimated by means of a bootstrap procedure with 2000 iterations. PSEs referred to the extent of offset of the handle from the flash that received approximately 50% ‘flash-ahead’ and 50% ‘flash-behind’ responses. A flash-lag effect, for example, would be evidenced by a positive PSE value, meaning that the flash had to be physically ahead of the hand in order to be perceived as aligned. Conversely, a flash-lead would appear as a negative PSE value. All PSEs are in millimetres (mm), and all velocities are in metres per second (m/s). Figure 2.2 shows the psychometric curves from a representative subject.

2.3.2 Results

PSEs. A paired-samples t-test revealed that the mean FP PSE ($M = 45.34\text{mm}$, $SD = 27.09$) was significantly different from the mean FF PSE, ($M = -50.25\text{mm}$, $SD = 20.35$), $t(7) = 6.16$, $p < .001$, $d = 2.183$. This indicates that physically aligned flashes during FP

motion were more likely to have received a “flash-behind” response than physically aligned flashes during FF motion. One-sample t-tests furthermore showed that the mean FP PSE was greater than zero, $t(7) = 4.73$, $p = .002$, $d = 3.578$, indicating a flash-lag effect, and the mean FF PSE was less than zero, $t(7) = 6.98$, $p < .001$, $d = 5.279$, indicating a flash-lead effect. The data from the left-handed subject were similar to those from the right-handed subjects. The mean PSEs across subjects are plotted in Figure 2.3.

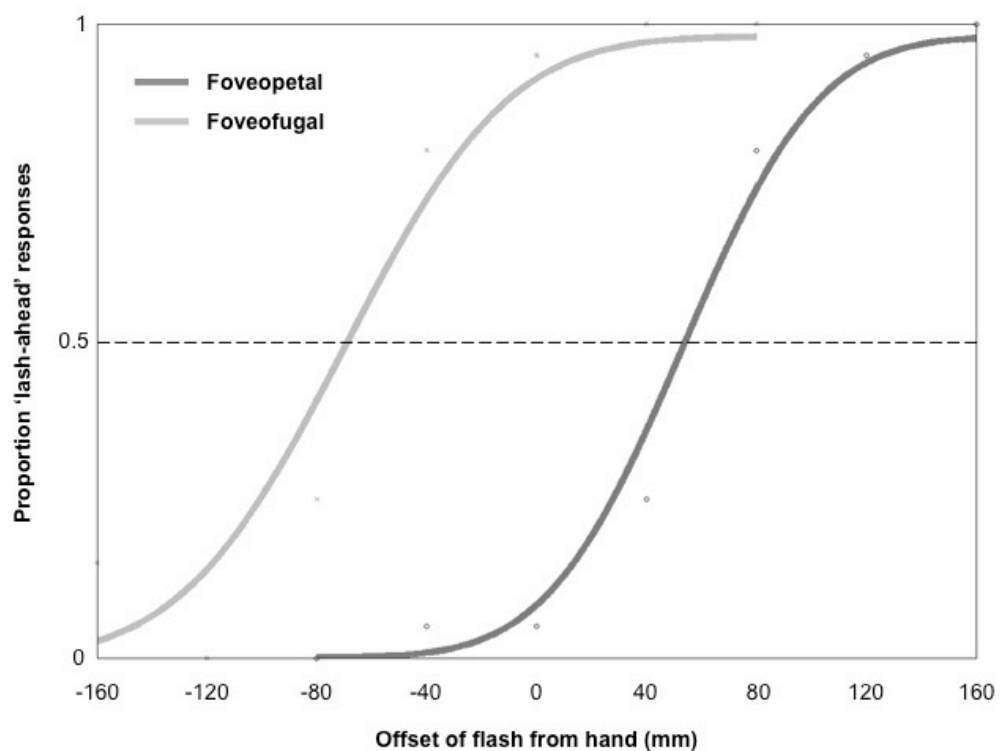


Figure 2.2. Experiment 1a: Psychometric curves from a representative subject. Negative offsets represent flash positions behind the hand.

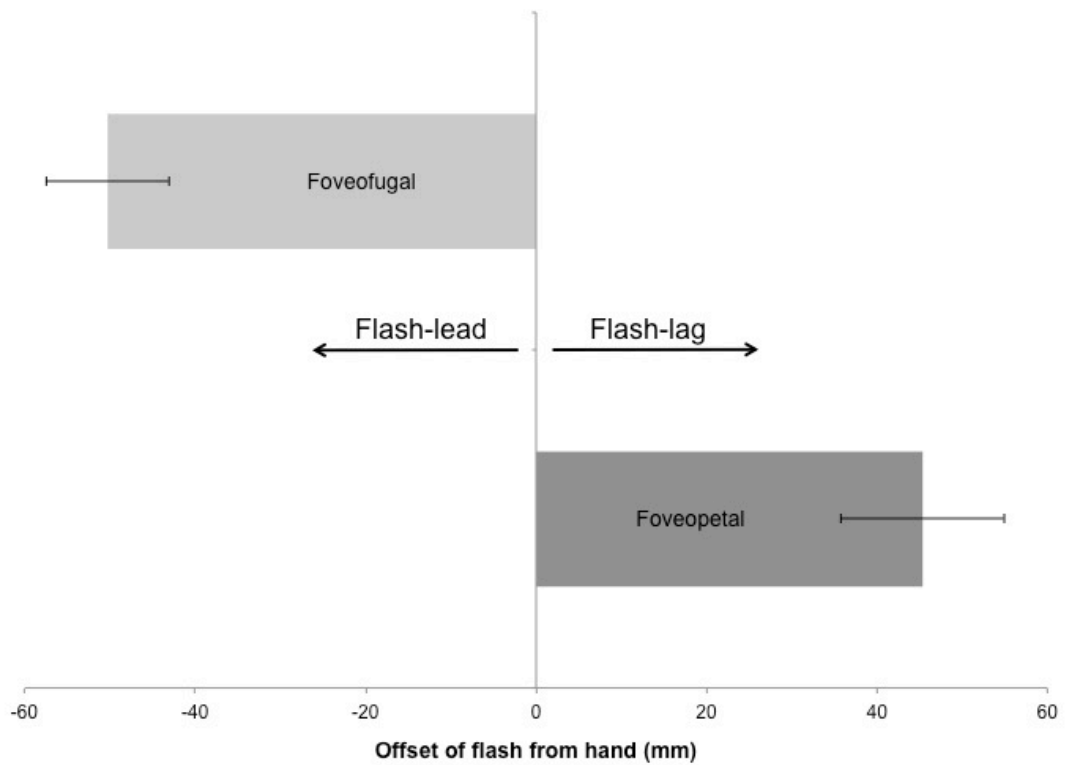


Figure 2.3. Experiment 1a: Mean points of subjective equality for foveopetal and foveofugal motion. Error bars indicate ± 1 standard error.

Velocity at the time of the flash. Subjects tended to move at higher velocity during FP motion trials ($M = 0.61\text{m/s}$, $SD = 0.11$) than during FF motion trials ($M = 0.55\text{m/s}$, $SD = 0.06$), $t(7) = 2.66$, $p = .033$, $d = 1.428$. However, there was no correlation ($r = -.348$, $p = .399$) between the velocity anisotropy and the PSE anisotropy, indicating that difference in velocity between directions did not explain the PSE difference between directions.

2.3.3 Discussion

These findings show that, when moving one's arm towards fixation in total darkness, an aligned flash appears to lag behind the felt position of the hand. The data also show that

during motion away from fixation, an aligned flash is not only less likely to receive a “flash-behind” response, but actually tends to be perceived ahead of the hand.

Besides being more likely to give “flash-behind” responses during FP motion, subjects’ arm movements also tended to be faster in that direction. While the visual flash-lag effect increases with velocity (Krekelberg & Lappe, 1999; Lee, Khuu, Li, & Hayes, 2008; Nijhawan, 1994; Wojtach, Sung, Truong, & Purves, 2008), differences in velocity are unlikely to explain the difference in perceptual effects observed herein, since the velocity anisotropy did not correlate with the perceptual anisotropy across subjects. Furthermore, to argue that velocity differences are responsible for the perceptual anisotropy, one would have to assume that arm movement velocity above or below a certain threshold leads to a flash-lag or flash-lead effect, respectively. This has not been observed in visual flash-lag, and it is unlikely that subjects would have consistently moved their arm above this threshold velocity in one direction, and below it in the other.

It cannot be ruled out, though, that differences in the layout of the trigger positions between movement directions lead to the difference in perceptual anisotropy. Consider that the earliest encountered trigger position for FP motion was 140mm from the start-of-travel, compared to 220mm in FF motion. So, while the physically aligned trigger position was at the halfway point of motion in both directions, the overall spread of trigger positions over the full trajectory was inconsistent between motion conditions. Another experiment was therefore performed to investigate whether centring the array of trigger positions (rather than the aligned trigger position) on the halfway point of arm motion produced the same results.

2.4 Experiment 1b

2.4.1 Methods

2.4.1.1 Subjects

A further 8 naïve subjects (5 male, 3 left-handed) with normal or corrected-to-normal vision participated in exchange for money or course credits.

2.4.1.2 Apparatus and Procedure

This experiment was identical to Experiment 1a, except that the rail's left-most end-of-travel was brought in 80mm further to the right, so that the full extent of travel was 520mm rather than 600mm in Experiment 1a. This meant that the distance to the first trigger position was identical (140mm) in both directions of motion but that the physically aligned trigger position was reached after 300mm in the FP condition, compared to 220mm in the FF direction. Post-experiment questioning revealed that no subjects suspected the true source of the flash.

2.4.2 Results

PSEs. A paired-samples t-test again showed that the mean FP PSE ($M = 93.89\text{mm}$, $SD = 77$) was significantly different from the mean FF PSE, ($M = -68.39\text{mm}$, $SD = 68.74$), $t(7) = 4.39$, $p = .003$, $d = 1.556$. Two one-sample t-tests were used to compare the PSE in each direction with zero. These showed that, as before, the FP PSE was greater than zero, $t(7) = 3.45$, $p = .011$, $d = 2.607$, and the FF PSE was less than zero, $t(7) = 2.81$, $p = .026$, $d = 2.127$. The data from the left- and right-handed subjects were similar. Mean PSEs are plotted for each direction of motion in Figure 2.4 below.

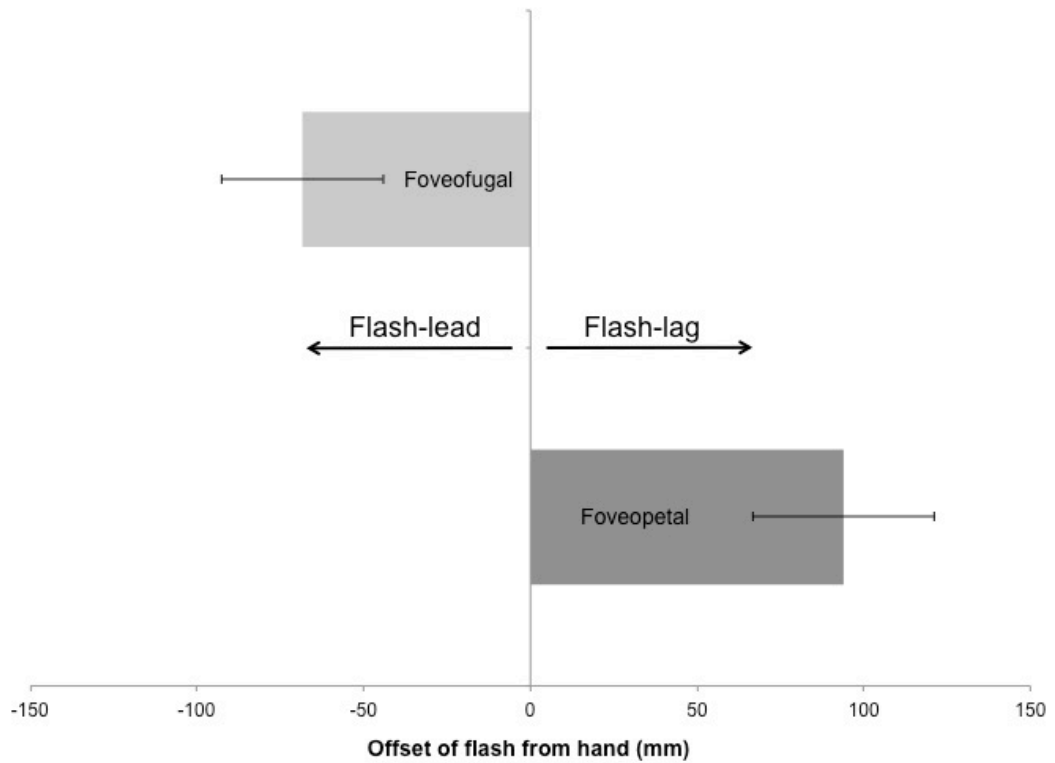


Figure 2.4. Experiment 1b: Mean points of subjective equality for foveopetal and foveofugal motion. Error bars indicate ± 1 standard error.

Velocity at the time of the flash. Also as before, subjects tended to move the handle faster during FP motion ($M = 0.57\text{m/s}$, $SD = 0.14$) than they did during FF motion ($M = 0.54\text{m/s}$, $SD = 0.11$), $t(7) = 2.51$, $p = .041$, $d = 1.477$, but there was no correlation ($r = -.349$, $p = .396$) between the velocity anisotropy and the PSE anisotropy.

2.4.3 Discussion

Experiment 1b produced the same overall findings as Experiment 1a, despite centring the array of trigger positions on the halfway point of arm motion. This suggests that the FP flash-lag effect and the FF flash-lead effect found in Experiment 1a are not due to differences in the layout of the trigger positions between motion directions.

An examination of the individual data from Experiments 1a and 1b (see Figure 2.5) suggests that there was a trend for those who produced a large FP flash-lag effect to also produce a large FF flash-lead effect. However, this was not borne out as a significant negative correlation between the PSEs in each direction, $r = -.156, p = .563$.

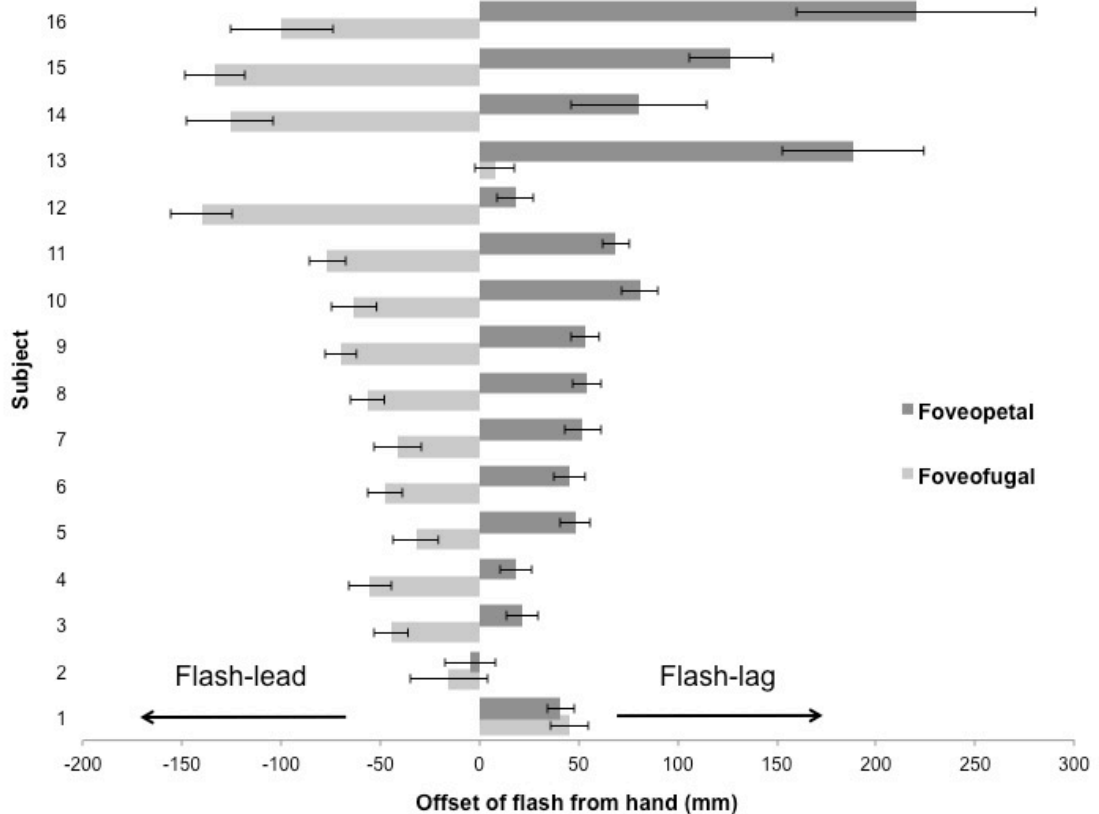


Figure 2.5. PSEs for foveopetal and foveofugal motion from each individual in Experiments 1a and 1b in ascending order of anisotropy magnitude. Error bars indicate ± 1 standard error.

These experiments reveal that when unseen hand movement is towards the fovea, a collocated flash is perceived to lag behind the felt position of one's hand. This replicates Nijhawan and Kirschfeld's (2003) basic finding of a motor flash-lag effect, though it should be noted that in their experiment the flash occurred when the motor stimulus (a handheld rod) was aligned with fixation, so motion at the time of the flash was neither foveopetal nor foveofugal. It has been shown herein that when motion is away from fixation, the perception is rather of the flash leading the hand's position. It was

mentioned earlier that the visual flash-lag effect occurs regardless of movement direction relative to the fovea, but that it is larger when motion is towards, rather than away from fixation (Kanai et al., 2004; Mateeff & Hohnsbein, 1988; Shi & Nijhawan, 2008). The direction, or sign, of the anisotropy is therefore the same between visual and motor domains, though some more in depth examination is required (see further on). Finding a foveopetal flash-lag and a foveofugal flash-lead in almost every subject suggests that making subjects believe that the flashes were in motion with their hand resulted in more consistent between-subject data than was found in the aforementioned pilot studies.

Visual flash-lead effects have been reported under certain circumstances (for a review, see Hubbard, 2014), such as when the luminance of the flash is increased (Purushothaman et al., 1998), when the contrast between moving and flashed stimuli is decreased (Arnold et al., 2009), or when the appearance of the flash is precued (Hommuk, Bachmann, & Oja, 2008). However, only a finding from Shi and Nijhawan (2008) helps elucidate why there might be a flash-lag effect in one motion direction and a flash-lead effect in the other. In an experiment analogous to the motor versions reported above, these authors presented bars that translated towards or away from fixation in either the right or left visual field. Large flash-lags were found in both visual fields during foveopetal motion, though a small flash-lag, and a flash-lead were found during foveofugal motion in the left and right visual fields, respectively. Considering that the experiments reported herein were using the right visual field exclusively, it stands out that this combination of motion direction and visual field might hold the key to understanding the present anisotropic effects. That is, a foveofugal flash-lead may not be peculiar to motor flash-lag. Shi and Nijhawan (2008) performed further experiments and demonstrated that their flash-lead was the result of a small forward displacement of the moving object coupled with a large forward displacement of the flash (i.e., a large flash-drag effect, in which the position of the flash is shifted in the direction of nearby motion), that actually shifted the perceived position of the flash past that of the moving stimulus. Compared to foveopetal movement, it was shown that motion in a foveofugal direction (regardless of visual field) is associated with both a reduced flash-lag, and an enhanced flash-drag. The same study also found that, when motion is towards fixation, the perceived position of the flash is actually repulsed, rather than dragged. On this view, a flash-drag in the FF condition and a flash-repulsion in the FP condition

contributed to – but did not fully account for – the visual flash-lag anisotropy. If similar but more pronounced effects are present when the position of an unseen arm in motion is probed with a visible flash, this could account for the difference between the FP and FF conditions observed herein. Most notably, a strong flash-drag might explain why the flash was perceived to lead the position of the hand during foveofugal motion. This leads to the further question of whether the hand or the flash is biased to a greater extent. Take, for example, that in both directions of motion the percept tends to be of the flash being to the right of (i.e., more foveofugal than) the hand. Is this because the flash is repulsed during foveopetal motion and dragged during foveofugal motion, while hand position is relatively stable? Or, might the flash position remain stable, while the hand position is biased further along its trajectory in foveopetal motion, and less far in foveofugal motion? These questions will be examined in more detail in the next experiments, which look at whether flash-drag effects occur when the moving stimulus is one's unseen limb.

2.5 Experiment 2a

2.5.1 Methods

This experiment was an attempt to produce a flash-drag version of Experiments 1a and 1b, in much the same way that flash-drag adaptations of visual flash-lag experiments have been performed (e.g., Shi & Nijhawan, 2008). The aim was thus to measure whether there exists a motor flash-drag effect when the flash is presented at a comparable eccentricity to that at which it appeared in the former experiments.

2.5.1.1 Subjects

Twelve subjects (4 male, 2 left-handed) with normal or corrected-to-normal vision participated in exchange for payment or course credits.

2.5.1.2 Apparatus

The handle, false flash array, half-silvered mirror, central fixation point, and computerised voice remained unchanged from the preceding experiments. The slide rail's extent-of-travel was 600mm, as it had been in Experiment 1a. This time, however, the trigger switch and timing switches were fixed in position, such that the flash was always triggered when the subject reached the halfway point of arm motion. Instead of just one true flash, there was a row of true flash light sources spaced at 8mm intervals, again mounted above the half-silvered mirror and superimposed over the false flash array spots. During leftwards (FP) movement, the horizontal offsets of the flash from the reference line could be 24mm, 16mm, or 8mm to the right, physically aligned, or 8mm or 16mm to the left. During rightwards (FF) movement the offsets were 24mm, 16mm, or 8mm to the left, physically aligned, or 8mm or 16mm to the right. Also above the half-silvered mirror was a vertical reference line (1mm × 25mm; white light), visible in the same plane of depth as the flashes, with its lowest point 25mm (3.55°) above the central flash. This allowed a flash to be presented at a particular horizontal offset from the reference line. To prevent subjects using the changing position of the flash relative to fixation to inform their judgments, the row of true flashes and the reference line were yoked together and their position was randomly jittered between 3 locations to the right of fixation (150mm ± 15mm; equating to 20.43° ± 2.13°). See Figure 2.6 for a schematic diagram of the experimental set up. The experiment was controlled with custom Matlab scripts running with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

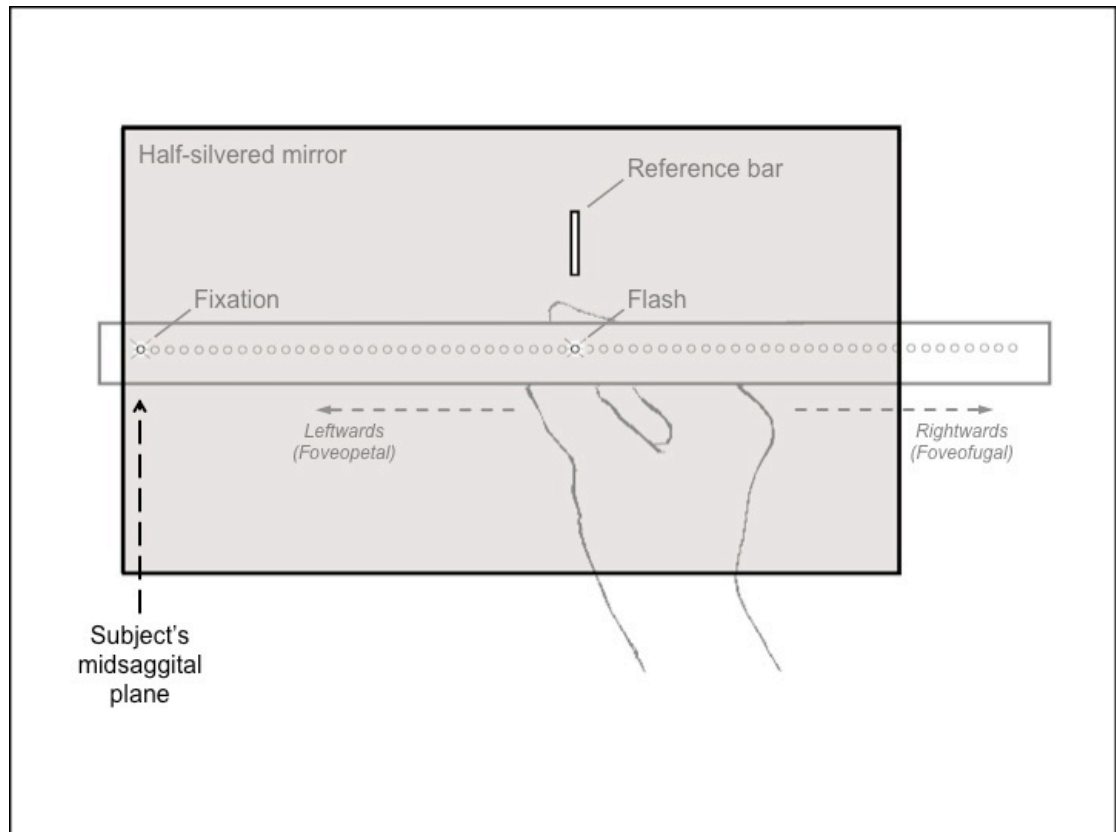


Figure 2.6. Experiment 2a: Schematic diagram of apparatus and stimuli.

2.5.1.3 Procedure

Instructions. As in the previous experiments, subjects gripped the handle between the forefinger and thumb of their right hand and were given a chance to familiarise themselves with the full extent of the slide rail's travel (600mm). An approximate ideal movement velocity was demonstrated. The same method was used to imply to subjects that during the experiment the flashes would be coming from the false flash array attached to the top of the handle. Subjects were then told that they would fixate their eyes straight ahead while they moved the handle from one end of the rail to the other, during which a flash would appear from the false flash array. Their task was to judge (verbally) whether the flash had been to the left or right of the reference line (binary choice). The same computerised voice was used to give verbal instructions throughout the experiment.

Experiment. The fixation point was visible throughout. With the lights switched off, the computerised voice requested that subjects move their arm either to the right or left end of the rail, depending on whether the first block would consist of leftwards (FP) or rightwards (FF) trials, respectively. Before each trial began, the reference line and row of true flashes were moved into a decoy position, before being moved to the intended position, so that the sound of the linear positioner did not reliably indicate to where they had moved. Once in position, the reference line was illuminated and the computerised voice said either “move left” or “move right,” depending on the condition. When the handle reached the halfway point of motion, one of the true flashes was presented (1ms). As in the previous experiments, arm velocity at the time of the flash was measured using the time taken to pass between two switches (120mm apart) either side of the flash trigger. Upon reaching the end-of-travel the computer voice asked the subject to “respond,” to which the subject said either “left” or “right.” In response, the experimenter pressed one of two keys on a computer keyboard accordingly. At this point the reference line was switched off, and was moved along with the flashes to another decoy position. The computerised voice then said “reset,” which was the signal for the subject to move their handle back to the start. After resetting the handle position, the reference line and true flashes were moved to another decoy location, and then to the intended location for the following trial. At this time the reference line was illuminated again and the next trial was in progress.

After 12 training trials (2 motion directions \times 6 flash offsets \times 1 repetition of each flash offset), subjects performed 288 experimental trials (2 motion directions \times 6 flash offsets \times 3 reference positions \times 8 repetitions of each flash offset) in sessions lasting approximately 1 hour. The same block design (counterbalanced across subjects) was used as in previous experiments, with the same procedure of illuminating the room during each break. Trials were randomised within each block. When shown the true flashes at the end of the experiment all subjects indicated that they had believed the flashes they saw had come from the false flash array.

Data analysis. The same procedure of fitting psychometric curves to each subject’s data was used to generate PSEs and confidence intervals. Each PSE corresponded to the horizontal offset of the flash from the reference line that would be expected to receive 50% “flash-left” and 50% “flash-right” responses. A positive value would mean that the

flash had to be to the right of the reference bar in order to be perceived as aligned with it, while negative values mean that the flash had to be to the left. A flash-drag would therefore be indicated by a positive value in the leftwards condition, and by a negative value in the rightwards motion. All PSEs are in millimetres (mm), and all velocities are in metres per second (m/s). Psychometric curves from a representative subject are plotted in Figure 2.7.

2.5.2 Results

PSEs. A paired-samples t-test revealed that leftwards PSEs ($M = 3.98\text{mm}$, $SD = 4.45$) were significantly to the right of rightwards PSEs ($M = -0.26\text{mm}$, $SD = 4.39$), $t(11) = 5.16$, $p < .001$, $d = 1.493$. Additionally, one-sample t-tests showed that the mean leftwards PSE was significantly to the right of physical alignment, $t(11) = 3.1$, $p = .01$, $d = 1.87$, but that the mean rightwards PSE was not significantly different from alignment, $t(11) = .21$, $p = .84$, $d = 0.12$. There was furthermore a significant paired-samples correlation, $r = .793$, $p = .002$, indicating that those who produced large leftward biases during leftwards motion, also tended to produce relatively large leftward biases during rightwards motion. Mean PSEs for each direction of motion are plotted in Figure 2.8.

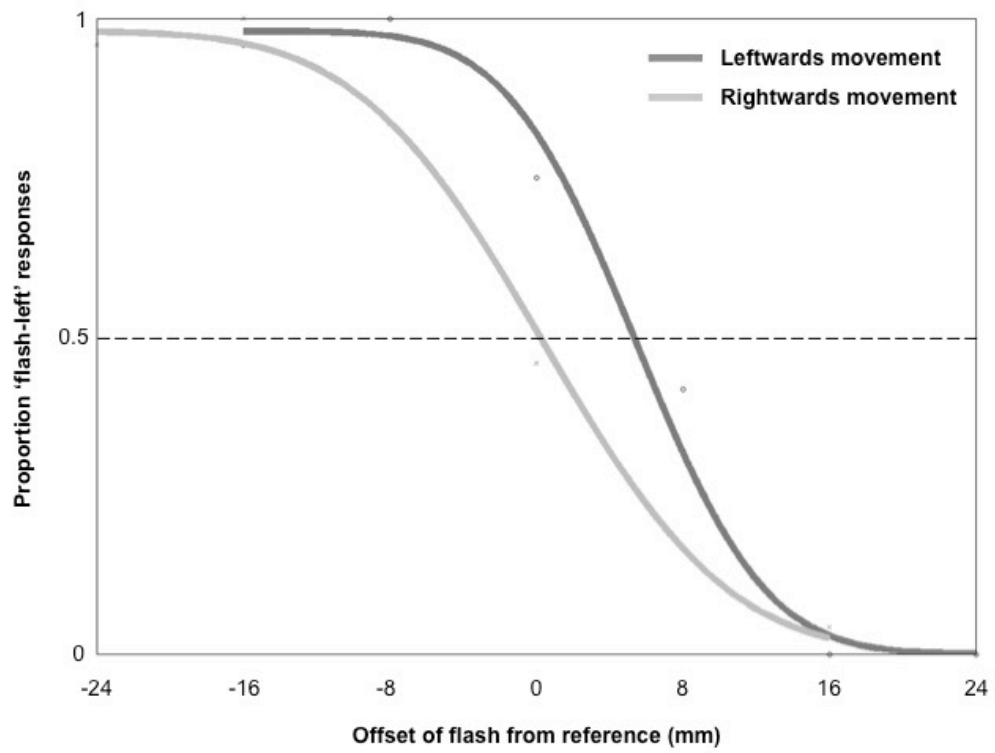


Figure 2.7. Experiment 2a: Psychometric curves from a representative subject. Negative offsets represent flash positions to the left of the reference.

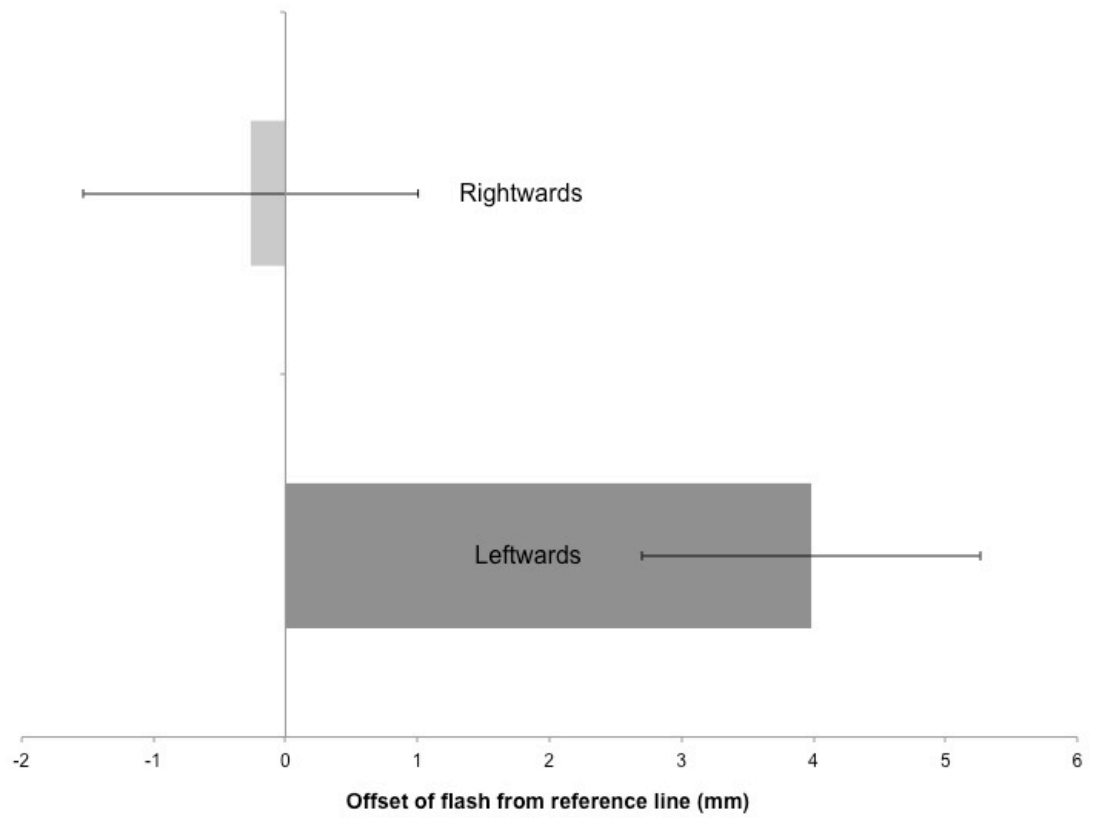


Figure 2.8. Experiment 2a: Mean PSEs for leftwards and rightwards motion. A positive value means that the flash had to be to the right of the reference line in order to be perceived as aligned. Error bars indicate ± 1 standard error.

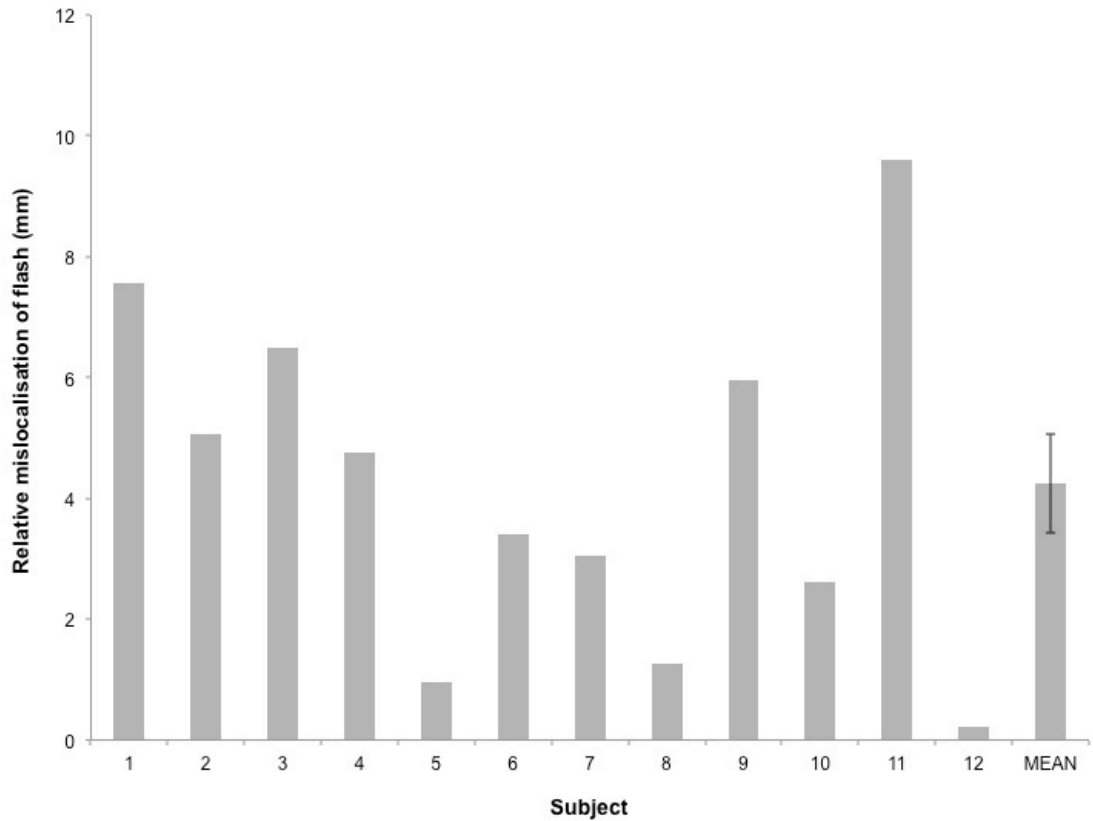


Figure 2.9. Experiment 2a: PSE anisotropy scores (i.e., the difference between leftwards and rightwards PSEs) for each individual, and the mean anisotropy. A positive anisotropy score means that the leftwards PSE was right of the rightwards PSE (i.e., a relative flash-drag). Error bar indicates ± 1 standard error.

Velocities. A paired-samples t-test shows that mean velocity was not different between motion directions, $t(11) = 2.07$, $p = .063$, $d = 0.603$, nor was PSE anisotropy correlated with velocity anisotropy between directions, $r = .031$, $p = .925$. This indicates that velocity did not have a major impact on the perceptual task.

2.5.3 Discussion

These data show that the perceived position of a flash presented in the visual periphery is biased by the direction of nearby unseen hand movement. During leftwards (FP)

motion, the flash had to be an average of 4mm right of physical alignment with a continuously visible reference line in order to be perceived as aligned. During rightwards (FF) movement, however, the flash was not significantly biased away from physical alignment. An examination of Figure 2.9 demonstrates that, for every subject, the difference between the perceived positions of the flashes in each direction was consistent with a direction-dependent flash mislocalisation. Put differently, an aligned flash during leftwards motion was perceived to the left of an aligned flash during rightwards motion. This represents the first demonstration of a motor flash-drag effect. While modest, the effect during leftwards movement is highly robust, and equal to approximately twice the width of the flash itself, or 0.57° of visual angle.

However, it is worth considering whether this bias reflects a change in perception between conditions, or simply a change in how subjects respond. It has been posited that measuring illusions with binary choice tasks such as that adopted here means that the possibility of shifts in decisional criterion masquerading as shifts in perception is not ruled out (Morgan et al., 2013). In terms of the present experiment, it might be, for example, that when moving one's hand leftwards, or immediately after having heard the instruction to "move left", subjects were more likely to give a "left" response, due to cognitive biases. Given that the stimuli were presented peripherally, where spatial uncertainty is greater (Kanai et al., 2004), one might also have expected the potential influence of cognitive factors to be high. This possibility is addressed in the following experiment, in which stimuli are presented closer to fixation.

Why, though, should leftwards movement produce a drag effect and rightwards movement no effect at all? There is evidence that visual stimuli are often biased towards fixation (foveal attraction; Eggert, Ditterich, & Straube, 2001; Mateeff & Gourevich, 1983; Nieman, Sheth, & Shimojo, 2010; O'Regan, 1984; Osaka, 1977), and it has been shown in particular that the perceived positions of brief flashes are biased towards fixation in comparison to continuously visible stimuli (e.g., Mateeff & Gourevich, 1983). In light of this, it could be that in the current experiment there was a general tendency to perceive the flash closer to fixation than the continuously visible reference line, which was enhanced by leftwards (FP) arm movement and nulled by rightwards (FF) arm movement. In support of this, subjects who demonstrated a large leftwards bias during leftwards motion were also likely to show a relatively large leftwards bias

during rightwards motion. This is consistent with the possibility that there are individual differences in the extent of the foveal attraction of flashes. The possibility is thus raised that the motor flash-drag effect observed during leftwards movement was augmented by foveal attraction, making it greater than it might otherwise be. The next experiment tests this possibility by having subjects judge the position of the flash relative to a central fixation point, rather than to a reference line in the periphery.

2.6 Experiment 2b

2.6.1 Methods

2.6.1.1 Subjects

Ten subjects (5 male, 1 left-handed) with normal or corrected-to-normal vision participated in exchange for money or course credits.

2.6.1.2 Apparatus

The handle, false flash array, half-silvered mirror, and computerised voice remained unchanged from the last experiments. A row of 5 true flashes was mounted above the half-silvered mirror (as the true flashes had been in previous experiments) and its image was superimposed over the row of light spots on the false flash array – itself projected through the mirror. The true flashes did not change position during the experiment. The face of the false flash array was approximately 318mm from subjects' eyes. The fixation point was also reflected in the half-silvered mirror, though it was now visible 35mm (6.29°) above the central true flash. The fixation point was projected in the same plane of depth as the flashes. The horizontal offsets of the 5 true flashes from fixation were 6mm or 3mm to the left, physically aligned, or 3mm or 6mm to the right. The slide rail was restricted to 400mm extent-of-travel, so that the subjects' handle could be

moved 200mm to either side of fixation. The flash trigger switch and timing switches were mounted on the motorised linear positioner (as in experiments 1a and 1b), and their position was jittered between 3 locations, allowing the flash to be presented at the moment the handle reached fixation, or 30mm before or after reaching it. This meant that the amount of handle motion required to trigger the flash was unpredictable. Figure 2.10 shows a schematic diagram of the experimental set up.

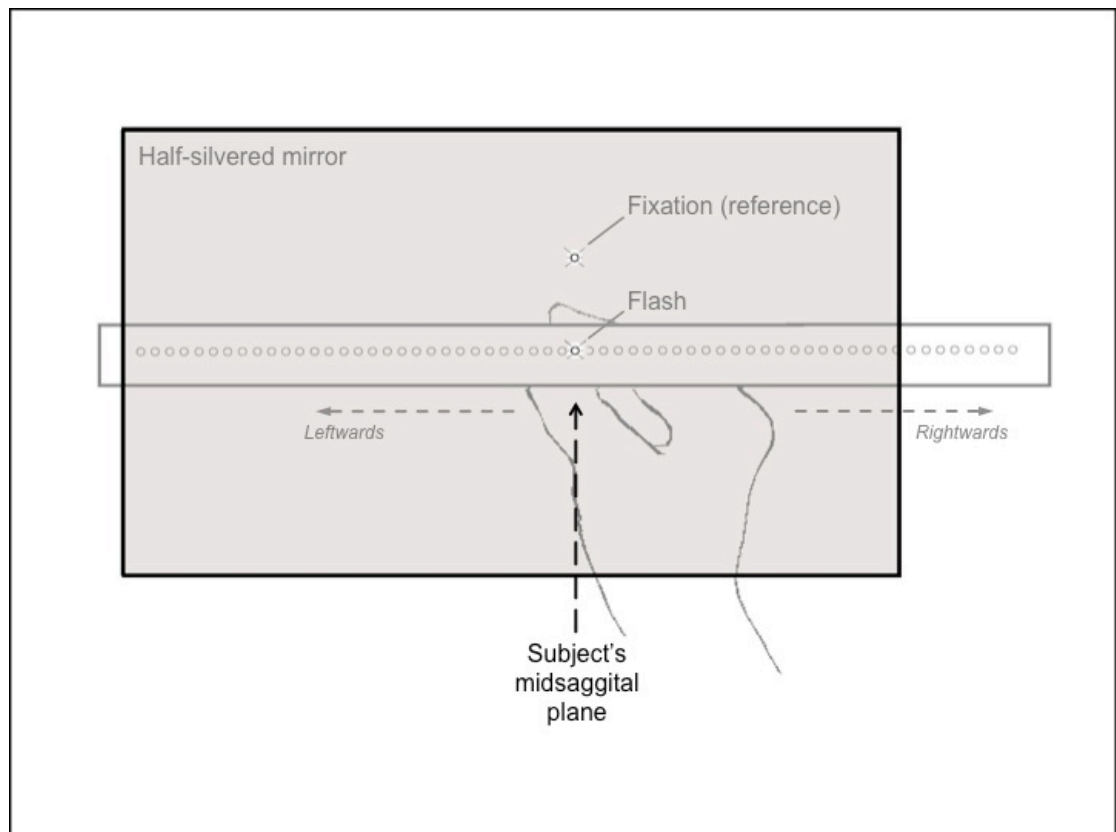


Figure 2.10. Experiment 2b: Schematic diagram of apparatus and stimuli.

2.6.1.3 Procedure

Instructions. The instructions procedure from Experiment 2a was used again, except that now subjects were tasked with judging whether the flash had appeared to the left or right of fixation (binary choice).

Experiment. As in previous experiments, the fixation point was visible throughout. The same instructions from the computerised voice were used to ensure than the subject's handle was in the correct starting position. Once the linear positioner had moved the triggers into a position (preceded by a decoy movement), the command was given to “move left” or to “move right.” Subjects moved their hand from one end of the rail to the other, during which one of the 5 true flashes was presented at a given offset from fixation. Upon reaching the end-of-travel, the “respond” command was given, at which time subjects verbalised whether they thought the flash had been to the left or right of fixation. The experimenter entered the response before a decoy movement of the triggers was made, and then the command to “reset” was given. After reaching the starting position, another decoy movement was made, followed by a movement of the triggers into the assigned position for the next trial.

Subjects performed 10 training trials (2 motion directions \times 5 flash offsets \times 1 repetition of each flash offset), followed by 240 experimental trials (2 motion directions \times 5 flash offsets \times 3 trigger positions \times 8 repetitions of each flash offset) in sessions lasting approximately 1 hour. The same counterbalanced alternated block design was used, with the same procedure of illuminating the room during breaks. All subjects indicated at the end of the experiment that the deception method had worked. The fitting of psychometric functions was identical to the procedure used in Experiment 2a, although now PSEs referred to biases relative to fixation, rather than to a peripheral reference.

2.6.2 Results

PSEs. A paired-samples t-test again showed that the mean leftwards PSE ($M = -0.15\text{mm}$, $SD = 0.59$) was significantly right of the mean rightwards PSE ($M = -1.65\text{mm}$, $SD = 1.01$), $t(9) = 5.93$, $p < .001$, $d = 2.113$. One-sample t-tests showed that while the mean leftwards PSE did not differ significantly from alignment, $t(9) = .81$, $p = .437$, $d = 0.543$, the mean rightwards PSE was significantly biased to the left, $t(9) = 5.2$, $p = .001$, $d = 3.47$. The paired-samples correlation did not reach significance, $r = .606$, $p = .063$. See Figure 2.11 for the mean PSEs plotted for each direction of motion.

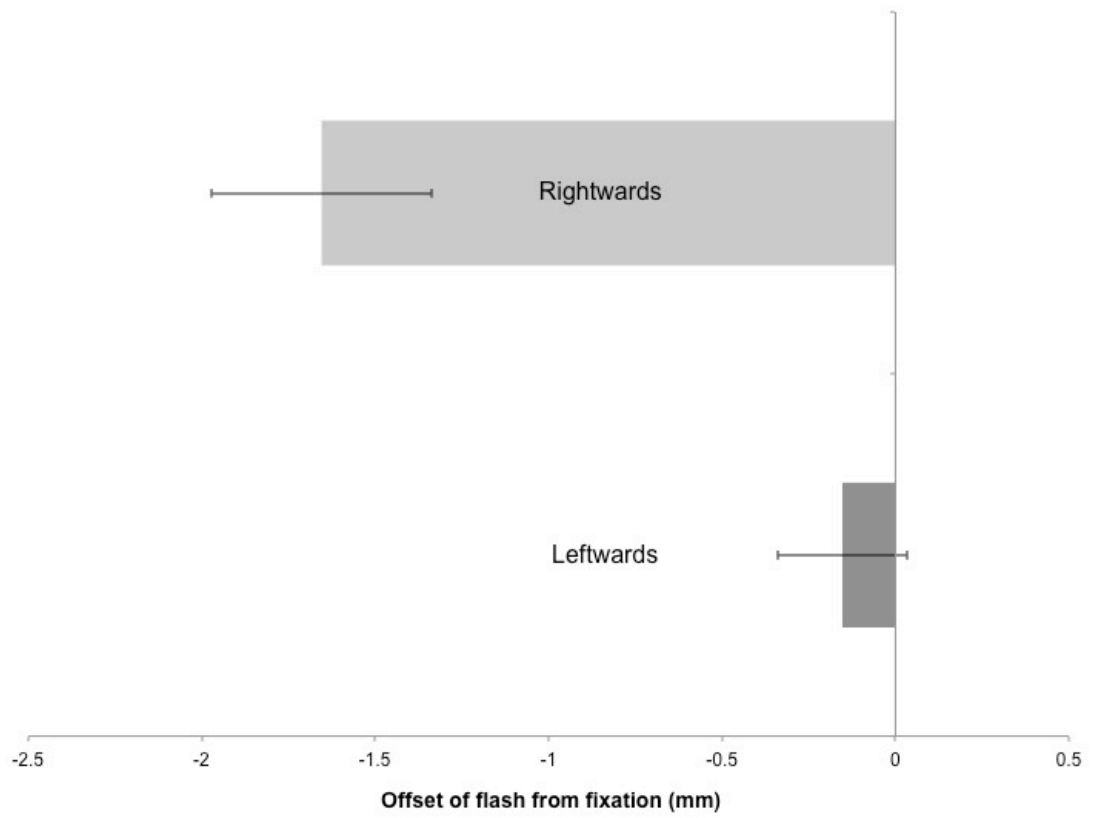


Figure 2.11. Experiment 2b: Mean PSEs for leftwards and rightwards motion. A negative value means that the flash had to be to the left of fixation in order to be perceived as aligned. Error bars indicate ± 1 standard error.

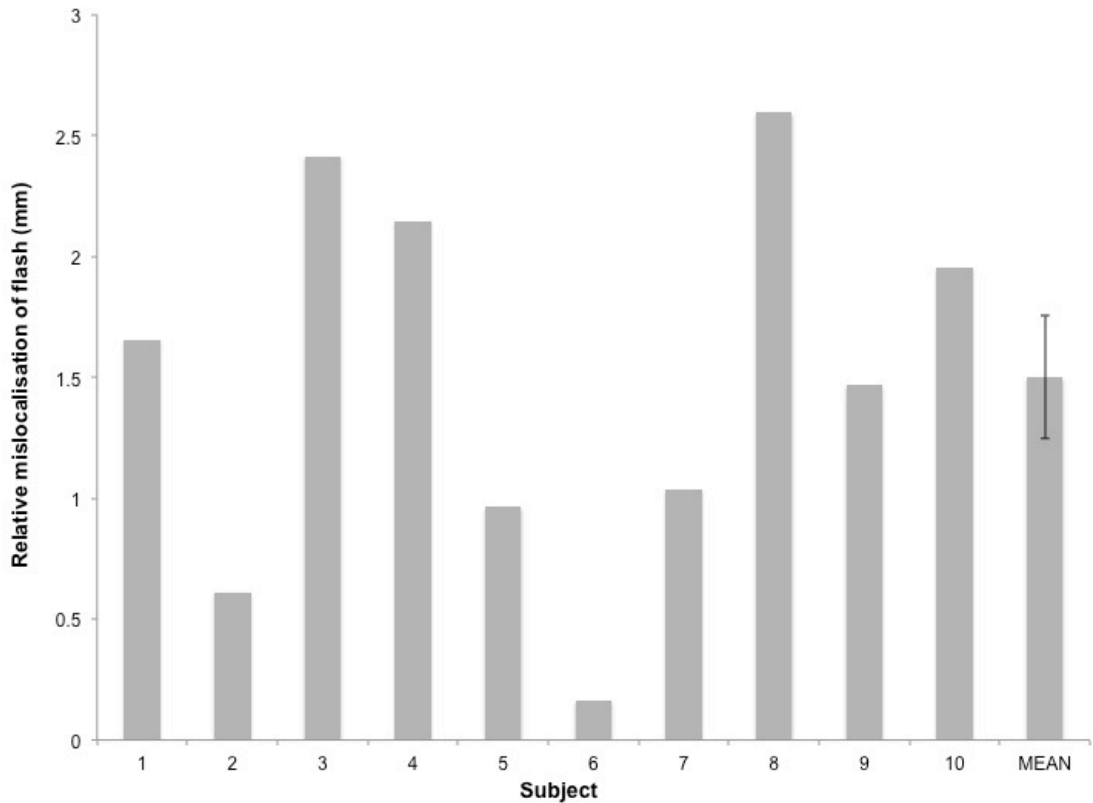


Figure 2.12. Experiment 2b: PSE anisotropies (i.e., the difference between leftwards and rightwards PSEs) for each individual, and the mean anisotropy. A positive anisotropy score means that the leftwards PSE was right of the rightwards PSE (i.e., a relative flash-drag). Error bar indicates ± 1 standard error.

Velocities. A paired-samples *t*-test shows that subjects moved the handle faster during leftwards motion ($M = 0.69\text{m/s}$, $SD = 0.11$) than during rightwards motion ($M = 0.62\text{m/s}$, $SD = 0.11$), $t(9) = 4.91$, $p = .001$, $d = 1.552$. There was however no correlation between PSE anisotropy and velocity anisotropy, $r = .311$, $p = .382$, suggesting that directional differences in velocity did not explain the PSE differences.

2.6.3 Discussion

These findings replicate those of Experiment 2a, inasmuch as rightwards PSEs are left of leftwards PSEs (see Figure 2.12) – indicating a general motor flash-drag effect. Unlike the previous experiment, however, rightwards motion produced a significant flash-drag, while leftwards motion did not. This particular facet of the results is in fact the opposite of what was found previously, when the flash was judged with reference to a continuously visible line in the periphery, and will be revisited shortly. The shift during rightwards motion in this experiment was smaller than that found during leftwards motion in Experiment 2a ($\sim 0.57^\circ$), though still corresponds to approximately 0.3° of visual angle. That an unseen arm movement can bias the position of a flash in relatively central vision to this extent is especially interesting given that people are normally extremely accurate at judging the relative alignment of two visual stimuli (Westheimer, 1987, 2009). In light of this it seems unlikely that a shift in decisional criterion (see Morgan et al., 2013) could explain the result. This also lends weight to the suggestion that the bias observed in Experiment 2a was genuinely perceptual in nature, and not due to a change in criterion.

We turn now to considering why an effect was found in rightwards motion, but not in leftwards motion. In discussing Experiment 2a it was argued that foveal attraction of the flash might enhance a flash-drag effect during leftwards motion (which was towards fixation), though cancel it out during rightwards motion (which was away from fixation). In Experiment 2b, neither motion direction was explicitly foveal or foveofugal. The same distance was travelled leading up to, and after passing fixation, and the flash was triggered when the hand was either about to reach, aligned with, or having just passed fixation. The flashes appeared at small offsets from fixation, and all offsets were used an equal number of times during both directions of arm movement. It could be therefore that some horizontal foveal attraction of the flash reduced the flash-drag effect, but it is unclear why it should be to different extents in each motion direction. An argument from the perspective of foveal attraction thus fails to clarify why rightwards motion should produce an effect that leftwards motion does not. The findings on visual flash-drag though might help to shed some light on the situation. Attention was brought earlier to the findings of Shi and Nijhawan (2008), who showed

that the visual flash-drag effect was larger during foveofugal motion than it was during foveopetal motion. Now, consider that in everyday life, unless one is adopting a slightly awkward posture (e.g., if their arm crossing to the opposite side of their midsagittal plane), the right hand tends to stimulate the right visual field more often than the left visual field, and vice versa for the left hand. A backhand movement of either hand away from the body will therefore produce foveofugal visual feedback more often than it will foveopetal visual feedback. So, it could be that in the present experiment, backhand (rightwards) movement produced a flash-drag effect because of the fundamental interaction, or similarity, between visual and motor systems. That is to say, even when backhand movement is not clearly foveopetal or foveofugal in nature, perhaps the close association of foveofugal visual motion with backhand arm movement means that the two types of motion are similarly potent at yielding flash-drag effects. The relatively small flash-drag that is evident in visual foveopetal motion (Shi & Nijhawan, 2008), might also therefore translate to a small motor flash-drag for forehand (leftwards) arm movement. While we saw that this class of motion resulted in a strong flash-drag in Experiment 2a, it was argued that it was probably supplemented by foveal attraction. In the current experiment, however, this reasoning would imply that a flash-drag in either direction would have to work against foveal attraction. A weak foveopetal, or forehand, motor flash-drag effect might therefore have been nulled by a stronger tendency to see the flash closer to fixation.

On the basis of the findings of Experiments 2a and 2b it is argued that the flash-drag effect occurs in the motor domain, as well as in vision, though some other potential explanations must also be addressed. For a start, it cannot be ruled out that the flash mislocalisation observed here occurred because subjects attempted to pursue with their eyes the felt position of their hand, and that this eye movement itself was responsible for the perceived shift of the flash. This would simply reassert previous findings that flashes presented during smooth pursuit are mislocalised in the direction of eye movement (Ward, 1976). However, for smooth pursuit eye movements to produce the effects observed, subjects would have had to have been doing this only during leftward arm movements in Experiment 2a, and only during rightwards arm movements in Experiment 2b – an unlikely set of circumstances. It is thus proposed that smooth pursuit eye movements are probably not at the heart of the motor flash-drag effect observed herein.

An issue that compels caution in interpreting the size of the present motor flash-drag effects concerns the use of a continuously visible reference stimulus for judging the relative position of the flash. Visual flash-drag is most often probed by measuring the perceived offset of two simultaneously presented flashes – each nearby to one of two stimuli moving in opposite directions (e.g., Durant & Johnston, 2004; Eagleman & Sejnowski, 2007; Fukiage, Whitney, & Murakami, 2011; Watanabe, Nijhawan, & Shimojo, 2002; Whitney & Cavanagh, 2000). The perceived distance between the two flashes when they are physically aligned is taken as a measurement of the sum of two flash-drag effects – one in each direction (Whitney & Cavanagh, 2000a). Another method, upon which the current approach was based, has been to present a continuously visible stimulus, which the position of the flash must be judged with reference to in the presence of motion (e.g., Shi & Nijhawan, 2008). This method has its drawbacks though, since it has been shown that the positions of brief visual stimuli are often biased towards continuously visible nearby landmarks (Sheth & Shimojo, 2001). The implication, then, is that the flash-drag effects observed in the current experiments may actually represent underestimations, due to the use of continuously visible reference stimuli that could limit the dragging effect of arm motion. An alternative method, analogous to the majority of the visual flash-drag literature, would have been to have subjects move their arms in opposite directions and present simultaneous flashes near to each of them. The offset of the flashes (divided by 2) would have demonstrated a flash-lag effect uncontaminated by the presence of visual landmarks. Unpublished observations with such a method, however, indicate effects of a similar size to those shown herein, of less than 5mm (approximately 0.6°) in each direction (Nijhawan, 2004). This suggests, therefore, that the presence of a continuously visible reference probably did not greatly impact the size of the motor flash-drag effect as measured in Experiments 2a and 2b.

A separate possibility is that the perceptual system attempts to reconcile the position of the flash with the felt position of the hand, by shifting the former closer to the latter, as if the flash is treated as a brief glimpse of the hand's position. This would be a form of multisensory integration not unlike the well-known ventriloquist effect, in which the location of an auditory stimulus is biased towards a visual stimulus that appears to be associated with it (Howard & Templeton, 1966). Other multisensory illusions also show

that vision can ‘capture’ the location of touch (Botvinick & Cohen, 1998; Pavani, Spence, & Driver, 2000) and proprioception (Holmes, Crozier, & Spence, 2004; Holmes & Spence, 2005), so that tactile and proprioceptive judgments are spatially biased towards, for instance, a fake hand, or a mirror image of the subject’s opposing hand. It has been shown too that proprioceptive information is more reliable during active versus passive movements (Chokron, Colliot, Atzeni, Bartolomeo, & Ohlmann, 2004; van Beers, Wolpert, & Haggard, 2002), and that visual input is less reliable when a solitary stimulus is viewed in total darkness, compared to when the whole visual field is illuminated (Mon-Williams, Wann, Jenkinson, & Rushton, 1997; Plooy, Tresilian, Mon-Williams, & Wann, 1998). Taken together with the assertion that sensory inputs are integrated in an optimal fashion given the reliability of current input (e.g., van Beers et al., 2002), the present experiments seem ideal candidates to display the proprioceptive capture of vision, given that they all involved active arm movements and minimal visual stimuli. To reiterate, then, the question here is whether the flash-drag effects found herein represent attempts by the brain to integrate an impoverished visual stimulus, with a relatively compelling kinaesthetic and proprioceptive sense of the arm in motion. In addressing this issue let us reconsider the findings of Experiments 1a and 1b, in which it was shown that the flash was perceived to lag the position of the foveopetally moving hand by about 45mm, and lead the position of the foveofugally moving hand by around 50mm. The displacements of the hand are therefore approximately an order of magnitude greater than the largest displacements of the flash. It seems unlikely, therefore, that motor flash-drag effects contribute in any major way to the motor flash-lag and flash-lead effects (something that will be revisited in more detail later). So, if we take the foveofugal flash-lead effect to represent a shift in the position of the hand, rather than of the flash, it suggests that one’s hand is perceived less far along its trajectory than it really is when moving away from fixation. If this was also the case during Experiment 2a, (which used comparable stimuli to Experiments 1a and 1b, but in a flash-drag configuration), and if the flash positions were biased towards the perceived location of the hand, we would have expected to see the flash shifted left, towards the hand during rightwards motion. This was however not the case. Flashes in this condition were not significantly shifted away from the reference line. This finding implies that capture of the flash position by the hand was not responsible for the motor flash-drag effects.

A final finding that should be addressed is that of Watanabe, Sato, and Shimojo (2003), who demonstrated that flash-drag can occur when the moving stimuli have been occluded at the time of the flash. In their experiment a flash-drag was observed when two white circles translated vertically in opposite directions and flashes were presented over each of their trajectories when they were close to horizontal alignment. This effect persisted even when the central portions of the circles' trajectories (but not the flashes themselves) were seemingly occluded by a black rectangle. That is to say, when the flashes were presented after the circles had completely disappeared (apparently behind the occluder), a flash-drag effect, though diminished, was still present. The conclusion was that visual objects in motion are tracked even when out of view by relatively high-level mechanisms able to influence the processes behind the flash-drag effect. In support of this general idea, it has been shown that visual flash-drag can occur with illusory motion (Watanabe et al., 2002) and apparent motion (Shim & Cavanagh, 2004; Whitney, 2006) stimuli. The possibility therefore, is that the present motor flash-drag effects were the result of inferred visual motion, or perhaps mental imagery of the hand. While the aforementioned experiments all differed from the current study in that they involved explicitly visual motion percepts, cognitive processes cannot be ruled out as an explanation for the motor flash-drag effect. However, as we shall see further on, a more promising, lower-level account presents itself in the intertwined nature of perceptual and motor systems.

2.6.3.1 Motor flash-lag and lead in light of motor flash-drag

Let us return briefly to consider the findings from Experiments 1a and 1b, in light of the flash-drag effects observed in Experiments 2a and 2b. In discussing the dual finding of a flash-lag in foveopetal arm motion, and a flash-lead in foveofugal arm motion, the possibility was raised that the flash may have been repulsed in the former, and dragged beyond the hand in the latter, analogous to vision (Shi & Nijhawan, 2008). Essentially, it was not clear whether the hand or flash position was biased differently depending on the direction of motion, or whether it was a combination of both. Indeed, it has now been argued that while the position of the flash is generally dragged in the direction of motion, the size of the effect is too small (by approximately an order of magnitude) to

account for the difference of the perceived position of the hand relative to the flash observed between foveopetal and foveofugal flash-lag. It seems, therefore, that the findings of Experiments 1a and 1b reflect a motion direction based anisotropy of perceived hand position. During unseen arm movement towards fixation, the motor flash-lag effect is observed to approximately the same extent as was originally reported by Nijhawan and Kirschfeld (2003). However, when the arm is moving away from fixation, and a flash is presented in alignment, the percept is in the opposite direction, such that the hand lags the position of the flash.

Before attempting to explain the difference between the foveopetal and foveofugal effects, it is worth returning briefly to a possible interpretation of motor flash-lag in general. Since the latency of proprioceptive information is lower than that of vision (Stein, Wallace, & Meredith, 1995), one's hand might be perceived ahead of a brief visual stimulus because its representation arrives earlier in perception. A reduced latency for moving objects compared to flashes has been put forward to explain the flash-lag effect in general (Purushothaman et al., 1998; Whitney, Murakami, et al., 2000; Whitney & Murakami, 1998), though it is doubtful whether it can account for the variety of phenomena observed (Alais & Burr, 2003; Arnold et al., 2009; Krekelberg & Lappe, 2001; Nijhawan et al., 2004; Nijhawan, 2002; Sheth et al., 2000). In addition to these issues with the approach, the current finding of a flash-lead effect in FF motion is entirely at odds with a differential latency account. In spite of the faster processing of proprioceptive information, a limb moving away from fixation was perceived to lag behind a visible flash.

What, then, might cause hand position to be biased further along its trajectory in foveopetal motion, and less far along its trajectory in foveofugal motion? One explanation might be that, irrespective of motion direction, the hand is biased towards fixation more so than the flash. Indeed, in both directions of motion, subjects perceived their hand to be closer to fixation than an aligned flash. While it was discussed earlier that visual stimuli are often foveally attracted, the particular issue here is whether an invisible limb is biased in the same way, but to a larger extent than a visible flash. It has been highlighted elsewhere that if a foveofugally moving stimulus is foveally attracted more so than a flash, it might produce what appears to be a flash-lead effect (differential foveal attraction; Kanai et al., 2004). This leads to a question: are we really seeing the

flash *lead* the position of the hand in the FF conditions, or is it just that subjects perceive their hand closer to fixation than the flash, irrespective of motion direction? The apparent tendency for people with a large foveopetal flash-lag to also produce a relatively large foveofugal flash-lead, though not significant, would support this interpretation. However, if a static force (Nieman et al., 2010) such as differential foveal attraction were strong enough to produce a bias of the magnitude observed, one would have expected it to cancel out the motor flash-lag effect reported by Nijhawan and Kirschfeld (2003), though their experiment used similar velocities and produced a flash-lag effect comparable to that observed in the present foveopetal motion condition. This last point warrants further attention. Consider that if the limb were especially biased towards fixation by foveal attraction, foveopetal motion (as in the present experiment) should produce a larger effect than motion that is neither towards nor away from fixation (as in Nijhawan & Kirschfeld, 2003), because the bias would drag the former far beyond the flash and the latter back towards the flash. The differential foveal attraction hypothesis is therefore difficult to reconcile with the present findings in conjunction with those of Nijhawan and Kirschfeld (2003). Finally on this matter, it is conceptually unclear why limb position should be foveally attracted more than a visual stimulus, given that accurately localising objects relative to one's hand is required to effectively interact with the environment. An uncorrected bias to perceive a body part closer to fixation than a visual object would likely lead to judgment errors. It is thus improbable that the anisotropy reported herein can be explained by differential foveal attraction, and that motion away from fixation really does generate a flash-lead; that is, a tendency to perceive the flash ahead of the hand, rather than simply further from fixation. It should be noted, though, that while it has been argued that a differential foveal attraction account is not without its difficulties, it explains the data rather well, and has certainly not been ruled out in the present experiments. The section that follows will present an alternative position, which may explain both the motor flash-lag/lead, as well as the flash-drag findings.

Before moving on, however, another possibility is worth considering. As outlined above, it has been observed that the perceived position of one's moving hand relative to a flash is different depending on the direction of motion of the hand relative to fixation. It could be though that this anisotropic effect depends on a 'reference point' other than fixation. For example, it might be that the direction of hand motion relative to the

direction in which one's head or body is facing determines whether the hand is perceived more or less far along its trajectory. In the current experiments the subjects' eyes, head, and body all faced in the same direction, so this has not been tested. This point will require further research, and is returned to later on (see Section 2.7.2).

2.7 General Discussion

In the introduction, literature was outlined that emphasised the close association between perception and action systems. It will be argued herein that the motor flash-lag/lead findings of Experiments 1a and 1b, and the motor flash-drag findings of Experiment 2a and 2b, derive from such a relationship.

Nijhawan and Kirschfeld (2003) interpreted the motor flash-lag effect in terms of the operation of forward models, a prevalent concept in the motor control literature (e.g., Miall & Wolpert, 1996). The idea extends from the broader concept of internal models, which posits that the nervous system internally simulates the workings of the musculoskeletal system to solve various computational problems (Kawato, Furukawa, & Suzuki, 1987). More specifically, forward models are thought to take as input the motor system's current state and a given motor command in order to predict a future state (Jordan & Rumelhart, 1992). It has been suggested that a function of such a prediction could be to reduce the system's reliance on delayed proprioceptive feedback, which would otherwise result in control instability (Miall & Wolpert, 1996). This idea is notably comparable to the suggestion that the future states of visual stimuli are predicted in order to compensate for the transmission delays between retinal activity and perception (e.g., Nijhawan, 1994, 1997, 2002, 2008).

Several avenues of research provide behavioural evidence for prediction in arm motor control. In a virtual pole-balancing task, for instance, Mehta and Schaal (2002) showed that when the visual display was momentarily blanked-out, performance was consistent with subjects having access to an internal estimate of the pole's current state, based on a prediction. Load-sliding tasks show that grip force is regulated in anticipation of

changes in load force (Flanagan & Wing, 1997), and that the inertial anisotropy of the arm is appropriately predicted when planning the movement of an object (Flanagan & Lolley, 2001). Another strand of research reveals that adjustments of the legs are made prior to, rather than in response to, postural disturbances arising from arm movements (Leonard, Gritsenko, Ouckama, & Stapley, 2011). However, Nijhawan and Kirschfeld's (2003) claim that the motor flash-lag effect is a manifestation of forward models finds most direct support from comparable studies examining estimates of unseen hand position. It has been demonstrated, for example, that when tasked with foveating the felt position of their hand after an invisible arm movement, subjects consistently overestimate the distance it has travelled (Wolpert, Ghahramani, & Jordan, 1995). Similarly, saccades towards the hand's instantaneously felt position during movements in the dark are towards the location it will occupy in 150ms, rather than to where it is currently (Ariff, Donchin, Nanayakkara, & Shadmehr, 2002). Like Nijhawan and Kirschfeld's (2003) study, these last two papers suggest that perceptual judgments of arm position are forwardly shifted.

A flash-lead effect accompanying foveofugal arm movement is not readily explained by a motor prediction account, since the moving object is perceived to lag behind the flash. Further research is required to investigate the nature of the foveofugal flash-lead effect. It may, however, reflect the operation of very different neural systems to the foveopetal flash-lag effect. Consider the differences in motor control inherent to these opposing directions of arm motion. In everyday human behaviour, foveopetal arm motion tends to comprise forearm movement towards the midsagittal plane, with the palm of the hand facing inwards more often than outwards. This class of movement, as compared to foveofugal motion, is more likely to be used to bring the hand and fingers towards – and perhaps to interact with – an object of interest. With this in mind, it is probable that foveopetal arm movements are underpinned by more developed neural architecture, permitting, for instance, highly dextrous actions. Backhand foveofugal arm movement, on the other hand, is less commonly deployed in finely tuned, skilled interaction with objects of attention. This leads us onto the possibility that more behaviourally significant types of movement might be more likely to result in a flash-lag percept. This argument was put forth by Shi and Nijhawan (2008) to explain the difference between the larger foveopetal and smaller foveofugal flash-lag effects in vision. These authors highlighted that “a scenario where an object's image is ‘approaching the fovea’ is much

more reflective of the animal's interest in the object than the scenario where the object's image is 'moving away from the fovea'" (p. 10). That is, the need to accurately localise an object moving towards the fovea is likely to be more pressing than the need to localise an object moving away. This is similar to the conjecture outlined above that foveopetal arm movement tends to bring the hand towards a point of interest, and is thus likely to be supported by more developed neural systems. Specifically, Shi and Nijhawan (2008) invoked claims from other authors (Kanai et al., 2004; Kirschfeld & Kammer, 1999; Kirschfeld, 2006) that the visual flash-lag effect occurs due to a wave of attentional facilitation at the leading edge of a moving stimulus, and an opposing wave of inhibition at the trailing edge. However, the authors took a different tack by suggesting that the combination of attentional facilitation and inhibition works to advance the perceived position of moving stimuli to compensate for neural delays prior to perception (Shi & Nijhawan, 2008). It was proposed in particular that during foveopetal movement, there is a relative enhancement of facilitation at the leading edge of the moving stimulus, coupled with a relatively diminished wave of inhibition at the trailing edge, ultimately leading to a larger forward displacement of the perceived position. Accordingly, the authors also suggest that during foveofugal visual motion, the peak of the facilitatory wave and the trough of the inhibitory wave are less pronounced, resulting in a smaller flash-lag effect. Along these lines one might explain the motor flash-lead effect during foveofugal arm motion as the result of 'inverted' attentional waves. Perhaps when one is moving their arm in a backhand motion away from fixation there is attentional inhibition at its leading edge and facilitation at its trailing edge, producing a flash-lead effect due to a backwards displacement of the perceived limb position. A foveopetal biasing of attention not present for purely visual stimuli might explain such an effect. For example, the tendency to orient spatial attention towards fixation (Shulman, Remington, & McLean, 1979) may be stronger when there is a lack of bottom-up visual input. Additionally, or alternatively, there could be a bias to direct spatial attention towards more sensitive or utilitarian body parts, such as the foveopetally-facing palm of the hand (e.g., Reed, Betz, Garza, & Roberts, Jr., 2010). In theory, anything that serves to orient attention towards the more foveopetal side of the hand or arm could reverse the direction of the difference between the attentional waves at its leading and trailing edges, and thereby cause a backwards perceptual displacement. Given this line of reasoning, it is still possible that similar predictive mechanisms give rise to the visual and motor flash-lag/lead effects. Put differently, the

sign of the motion direction based anisotropy, which is the same between vision and action, could be more significant than the difference in surface appearance of the foveofugal effects.

The flash-drag effects observed in Experiments 2a and 2b are more intuitively accounted for under the umbrella of perception-action unity. Put simply, both visual motion and unseen arm motion are able to drag the perceived position of a stationary flash. It is argued here that this is due to a shared representational space between visual and motor systems, giving rise to analogous percepts. The original explanation of the flash-drag effect was that motion signals across the visual field are integrated when assigning positions to static stimuli (Whitney & Cavanagh, 2000a). It is suggested here that this claim need not be revised to account for motor flash-drag, except that the motion can also be action-based, rather than simply visual. Whitney and Cavanagh (2000), however, also conjectured that visual flash-drag occurred as a result of feedback from extrastriate motion areas (i.e., MT or MST) to V1. These regions are traditionally thought to take their input only from retinal stimulation, however, and there is no evidence that motor areas involved in controlling limb movement feed back to V1. It seems, then, that this circuit cannot also account for motor flash-drag. Instead, it is suggested here, that other areas with visuomotor matching properties are instrumental in producing the visual and motor versions of both the motor flash-lag/lead and flash-drag effects.

If the visual and motor versions of the motor flash-lag/lead and flash-drag effects share a representational space with their visual counterparts, then neurons responding to both vision and action at some level of the nervous system must be involved. Recall that in the introduction several prominent classes of neuron were outlined appearing to display both visual and motor functionality (i.e., mirror, canonical, and visuotactile neurons). Another potentially relevant type of neuron is found in the primary motor cortex of the rhesus monkey, and is also likely to be present in the human homologue (Port, Kruse, Lee, & Georgopoulos, 2001). These fire both during manual interception of a moving object, and when simply tracking the object visually without any accompanying muscle activity. It should be noted that these particular cells are especially relevant to the current findings because they show that processes of symbolic (i.e., non-biological) visual motion and arm motion converge onto the same neurons. Furthermore, it is not

implausible that their visual functions affect their motor functions, or vice versa. It could be, then, that these or other types of multimodal neuron are behind both the visual and motor versions of the effects, since they represent motion and position in both visual and motor terms.

2.7.1 Origins of perception-action unity

It will be useful here to consider how the multimodal functions of these types of neuron arise. Put simply, the question addressed will be whether sensorimotor connections are laid down as a result of genetics, or whether they develop within each organism's lifetime on the basis of experience. This issue has recently garnered attention with regards to the emergence of mirror neurons in the brain (Catmur, 2013; Cook et al., 2014; R. P. Cooper, Cook, Dickinson, & Heyes, 2013; Ferrari, Tramacere, Simpson, & Iriki, 2013; Heyes, 2010, 2013; Keysers & Perrett, 2004). In the introduction it was mentioned that these cells fire when performing an action, as well as when a similar behaviour is simply observed (e.g., di Pellegrino et al., 1992). The well-established 'genetic' view of mirror neurons is that the organisms possessing them were endowed with an evolutionary advantage since they had a more intimate understanding of the actions of conspecifics (e.g., Rizzolatti & Craighero, 2004). This implies that action understanding is an adaptive trait, and as a result gave rise to the neurons that subserve it. Objections to the genetic account have however been raised along the lines that mirror properties could have developed on the basis of associative learning processes quite divorced from the function they now serve (Catmur, 2013; Cook et al., 2014; R. P. Cooper et al., 2013; Heyes, 2010, 2013). In essence, it is argued that if an action is performed while that same action is observed, formerly weak connections will become stronger between visual neurons responding to the observed action and motor neurons commanding the performed action. Observation of a concurrently performed action could, for instance, occur when imitating someone else's movement, or when receiving visual feedback of one's own movement either directly or reflected in a mirror (Cook et al., 2014). The proposal is, then, that mirror neurons are the result of correlated activity between sensory and motor areas due to the co-occurrence of action observation and performance, and that their facilitation of action understanding is merely a serendipitous

side effect. Several lines of evidence support the associative hypothesis. For example, it has been highlighted that the efficiency of associative learning processes means that functioning mirror systems may even be present in young infants, and that sensorimotor training can modulate mirror functions (for a review, see Cook et al., 2014). The competing genetic and associative accounts tend to characterise the debate as an all-or-none affair (Ferrari et al., 2013; Gallese, Rochat, Cossu, & Sinigaglia, 2009), but for now it is sufficient only to establish that associative learning might help shape the properties of mirror (and similarly multimodal) neurons, without getting into the impact of genetics.

In their discussion of the possible role of ontogenetic factors (in addition to fundamental phylogeny) in the development of an action understanding system, Gallese et al. (2009) advocated that motor processes had primacy over the developing visual system (see also Gallese & Sinigaglia, 2014). The authors argue that since the motor system becomes more developed in utero than vision (e.g., Zoia et al., 2007), connectivity may already be established at birth between motor areas and “to-become-visual” areas. Their suggestion was that this would potentially allow immediate rudimentary action understanding in neonates, which could be honed through visual and motor experience. It is interesting to note that while Gallese et al. (2009) are firmly in the genetic camp of mirror neuron origins, this aspect of their thinking somewhat presages the associative learning account outlined above. The primacy of the motor processes over the visual system finds support in the findings mentioned earlier demonstrating that manipulation of motor systems has knock on effects on visual perception (e.g., Beets et al., 2010; Brown et al., 2007; Hecht et al., 2001; Volcic et al., 2013).

In light of the associative account, coupled with the motor primacy argument of (Gallese et al., 2009), an interesting possibility emerges for explaining the present findings. Herein it has been suggested that the visual flash-lag and flash-drag effects have motor analogues, though it may be more accurate to view the visual effects as derivatives of more primitive motor programs. More specifically, it could be that systematic mislocalisations inherent to the motor system in gestation translate after birth (and the onset of rich visual feedback) into analogous mislocalisations in vision through processes of associative learning. For instance, when a neonate’s eyes open and it can see its own arms moving, the forward displacement of an arm’s position induced

through motor forward models could also be used to inform the naïve visual system of the position of objects in space. In neuronal terms, multimodal cells firing on the basis of the output of the motor system might serve to calibrate the visual system to apply similar biases to visual motion in general. While Gallese et al. (2009) suggested that motor processes inform the developing visual system only in the perception of *biological* motion, others have claimed that biological motion actually forms the groundwork for motion perception in general (Viviani, 2002). Recall that the two-thirds power law describing the way that velocity varies during limb movements also constrains visual motion perception (e.g., Viviani & Schneider, 1991; Viviani & Stucchi, 1992). It was further highlighted earlier that people are sensitive to deviations from visual motion obeying the two-thirds power law even when they are unable to recognise the stimuli as biological in nature (Bidet-Ildei et al., 2006). This implies that fundamentals of the motor system are not only used in the perception of other people's behaviour, but also for motion in general. It is possible, then, that the visual flash-lag and flash-drag effects might occur (in all types of motion) in part due to analogous mislocalisations applied to the motor representation of one's moving body. This claim will of course require more evidence to support it.

2.7.2 Future directions

A number of interpretations outlined in the present paper could be tested in more detail. Of particular interest in this case is the immediately preceding argument that visuospatial illusions occur on the basis of more fundamental motor illusions. Here one could investigate whether individual differences in the magnitude of the visual flash-lag and flash-drag effects correlate with equivalent differences in the motor domain. Also along these lines, the size of the visual flash-lag and drag effects could be compared between groups of observers who have never had use of their arms, who have lost their arms later in life, and who have normal use of their arms. If the first differed from the second two groups it would support the suggestion that early visual experience of one's limbs in motion calibrates the visual system.

In Experiments 1a and 1b it was noted that differential foveal attraction might explain the apparent motion direction based anisotropy of the felt position of the hand; that is, the hand may have been foveally attracted more than the flash, regardless of its direction of motion. This possibility could be tested with a motor flash-lag-type experiment, in which static hand position (unseen in the visual periphery) is judged relative to a flash. This would reveal whether the hand is biased towards fixation more than the flash in the absence of motion.

If this crucial test revealed that differential foveal attraction could not account for the difference in felt hand position relative to a flash between motion directions, a further question remains: does the motion direction based anisotropy really occur in relation to fixation? This issue could be elucidated with experiments that disentangle foveopetal and foveofugal motion from forehand and backhand movement, and from motion that is either towards or away from the direction that the head or torso is facing.

2.8 Conclusions

The first two experiments revealed that foveopetal movement of one's arm in the dark produces a flash-lag effect, while equivalent foveofugal movement produces a flash-lead effect. The second two experiments showed that this could not be accounted for by a bias of flash position. It was argued that the visual flash-lag anisotropy and motor flash-lag anisotropy are of the same sign, and thus reflect the common underlying processes in perception and action. While the motor flash-drag effect observed in the second pair of experiments was modestly sized, it was highly robust, and was argued to represent a motor equivalent of the visual flash-drag effect. Motor illusions with visual analogues, it has been suggested, might be a result of visual systems developing on the basis of motor programs established in utero, though this claim requires further support.

Paper II: Threat enhances the flash-lag effect

3.1 Abstract

The paternalistic vision approach claims that visuospatial perception is sensitive to our behavioural requirements. One direction of research proposes that threatening objects are perceived closer, larger, and moving faster than equivalent non-threatening objects, in order to safeguard us from harm. Several researchers have contended, however, that the studies upon which these claims are based confuse perception with cognitive factors, such as memory and task demands. The effects of threat upon the magnitude of the flash-lag effect (a perceptual illusion in which moving stimuli appear ahead of flashed stimuli) are investigated in two experiments. In the first experiment, with looming and receding stimuli, no effect of threat is observed, though the second experiment, with linear translating stimuli, demonstrates larger flash-lag effects for threatening moving objects, in general support of paternalistic vision. This effect was however independent of motion direction relative to the observer, contrary to the claim that threatening objects are perceived closer. It is thus argued that threat can indeed affect basic visuospatial perception.

3.2 Introduction

3.2.1 Paternalistic vision

A growing body of research implies that our visual systems warp the perception of space to better suit our present needs. Vision, it is claimed, does not attempt to provide an accurate representation of the environment, but instead monitors our current abilities,

resources, goals, and anxieties, as well as our bodily and socio-emotional states before applying spatial biases that encourage desirable actions (for reviews, see Firestone, 2013a; Proffitt, 2006; Witt, 2011). This position is in notable contrast with the more established view that cognition is distinct from early vision and that perception – at its most basic levels – is cognitively impenetrable (e.g., Fodor, 1983; Pylyshyn, 1999, 2003). Following on from Firestone (2013a), the idea that visual perception aims to safeguard us from performing unfavourable behaviours will be termed herein the *paternalistic vision hypothesis*. This paper reports two experiments performed to test the predictions of paternalistic vision as applied to threat. The most fundamental issue addressed is whether visuospatial perception is sensitive to the threat value of a stimulus, though more specific predictions about whether threatening stimuli are perceived as closer, larger, or faster are also tested. In the following section, a spectrum of the findings used to support paternalistic vision will be outlined, before consideration is given to some of the main objections to the account. Following this, the related claim that threatening stimuli affect spatial vision will be discussed in terms of the criticisms levelled so far only at other parts of the paternalistic vision literature.

An influential experiment by Bhalla and Proffitt (1999) had subjects stand at the base of a hill and judge its incline using several measures. Some subjects wore a heavy backpack while others did not, and it was found that the encumbered subjects judged the hill to be steeper than did the subjects without a backpack. The conclusion – characteristic of much of the literature that followed – was that the backpackers would need to exert more effort to scale the hill, so their visual systems provided them with exaggerations of its gradient in order to caution against an energy-sapping ascent. Consistent with this position, subsequent experiments showed that people who were tired, unfit, elderly, or in declining health also relatively overestimated the hill's gradient (Bhalla & Proffitt, 1999). Besides incline, it has also been demonstrated that proximity estimations are biased by similar factors. For instance, in a study analogous to that just mentioned, people wearing a heavy backpack and standing in a grass field overestimated the distance to a traffic cone compared to an unencumbered group (Proffitt, Stefanucci, Banton, & Epstein, 2003). Like the Bhalla and Proffitt (1999) study, the claim was that the effort required to walk with a heavy load led to the distance appearing greater. A later study also found that subjects who had recently consumed a high glucose drink tended to underestimate the gradients of hills compared

to subjects who had drunk an artificially-sweetened drink (Schnall et al., 2010). It was proposed that the former group, loaded up on calories as they were, would have been more capable in that moment of climbing the hill, and so required less of an exaggeration of its incline. Taken together, this collection of findings implies that it is the potential physical effort required for actions, associated with caloric expenditure, that biases people's perceptual judgments. However, as we shall see, this is not the sole concern of whatever system it is that implements these apparent spatial misperceptions.

Along the same lines as the gradient estimation studies mentioned above, it has been revealed that passersby accompanied by a friend typically underestimate the slope of a hill compared to lone passersby (Schnall et al., 2008). The authors posit that having a friend nearby increases one's available psychosocial resources, making the climb seem less challenging, and so making the hill appear less steep. It has also been recently shown that magnified judgment of both distance when wearing a heavy backpack (Shea & Masicampo, 2014), and height when one's sense of self is depleted (Huynh, Stefanucci, & Aspinwall, 2014), is eliminated after performing a self-affirmation exercise. Similarly, another study showed that groups of subjects who either listened to happy music or imagined a positive life event underestimated a hill's incline in comparison to groups who either listened to sad music or imagined a negative life event, respectively (Riener, Stefanucci, Proffitt, & Clore, 2011). Previously we saw that spatial parameters are influenced by the availability of physiological resources, though these studies represent something of a departure, in that they additionally demonstrate a role for psychological resources.

Related to the effect of mood and psychosocial resources on visuospatial judgments, another stream of research has examined the impact of threat. For example, one study had subjects who were either high or low in acrophobia (fear of heights) stand on a long, two-story balcony and look down over the edge at a target at ground level (Teachman, Stefanucci, Clerkin, Cody, & Proffitt, 2008). Subjects then asked an experimenter to move towards or away from them along the balcony until they felt that the horizontal distance to the experimenter matched the vertical distance to the target. It was found that the high acrophobia group estimated themselves to be considerably higher above the ground than did the low acrophobia subjects. A follow-up study found that getting people to vividly imagine that they were falling from the balcony increased

the overestimation of the balcony's height in the high-acrophobia (but not low-acrophobia) group (Clerkin, Cody, Stefanucci, Proffitt, & Teachman, 2009). From this it seems that the more fear one feels from being on a high balcony, the further away they perceive the ground to be. This bias is consistent with the paternalistic vision hypothesis, in that it is likely to encourage threatened observers to stay away from the edge, thus avoiding potential harm.

3.2.2 Objections to paternalistic vision

From the findings reviewed thus far it is certainly tempting to conclude that vision is indeed paternalistic, and that visual space is tractable to our needs and potential actions at a given time. Others, however, have argued that, while robust and mostly replicable effects in themselves (though for failed replications, see de Grave, Brenner, & Smeets, 2011; Woods, Philbeck, & Danoff, 2009), these are not necessarily reflections of perception, but may in fact result from influences upon cognition itself – for example, in terms of task demand characteristics, or perhaps biases in memory or judgment. This section will cover several arguments that cast doubt on the perceptual nature of this class of effects, before looking at evidence in favour of alternative interpretations.

A number of theoretical contentions about why the paternalistic vision hypothesis may be unsatisfactory have been put forth, full consideration of which is beyond the scope of the current literature review (though for an in depth discussion, see Firestone, 2013a). However, as a brief example, a prominent difficulty for the paternalistic vision account is its inability to explain the lack of associated phenomenology – for instance, why we do not see hills suddenly getting steeper as we pick up heavy bags (Firestone, 2013a). Leaving this for now though, we will turn to the range of experimental evidence that renders problematic the claim that visual space itself is affected by our current needs, abilities, moods and resources.

A recent set of experiments has illustrated that one finding used to support the paternalistic view may not be the result of an effect on perception (Firestone & Scholl,

2014). The original experiment, by Stefanucci and Geuss (2009), had subjects face a doorway-like aperture made up of two vertical poles. One group held the ends of a 114cm-long, horizontally-oriented rod, while another group held their hands by their sides. After looking at the doorway, subjects turned 90° to face the experimenter, who adjusted the length of a tape measure to match the width of the aperture according to the subject's instructions. It was found that the rod-holding group produced narrower estimations of the aperture than the group without their hands held out. In line with paternalistic vision, the authors' conclusion was that holding one's arms out made the effective width of their body wider, which in turn made the doorway appear less wide because it was less passable. Firestone and Scholl's (2014) investigation focused on the visual matching task by which the estimations were made in this initial study. The reasoning behind their experiments extended from something known as the "El Greco fallacy" (Rock, 1966), and requires a brief synopsis. For some time a prevalent theory for why the famous artist, El Greco, painted elongated human forms was that he was in fact astigmatic, and therefore perceived his subjects as vertically stretched. However, it has since been asserted this could not explain the distortions in El Greco's paintings, because, if the artist faithfully committed what he saw to canvas, any perceptual elongation would be cancelled out when depicted (Anstis, 2002; Firestone & Scholl, 2014; Firestone, 2013b; Rock, 1966). Put differently, if a visual distortion occurs in the perception of an object, and if its depiction is similarly distorted, then the artist should see the original and depicted stimuli as matching; that is, the distortion should not be evident in one more than the other. This interpretation was experimentally validated by Anstis (2002). Applying the same logic as that which exposed the El Greco fallacy, Firestone and Scholl (2014) reasoned that if subjects holding a rod actually *perceive* a door to be narrower (as per Stefanucci & Geuss, 2009), then this effect should disappear if an adjustable doorway, rather than a tape measure, is also used for the visual matching task. To highlight the analogy, if the stimulus doorway is like El Greco's subject, then the matching doorway is like his canvas, and should receive an equal distortion if the originally reported effect is genuinely perceptual. It was found instead, though, that the rod-holding subjects judged the doorway to be less wide when matched both with a tape measure and with an adjustable doorway (Firestone & Scholl, 2014). Since the effect persisted when using a matching stimulus that should have in theory also been perceptually distorted, the authors concluded that apertures are not literally

seen as narrower when holding a rod that prevents easy passage. If not perception, then, what might cause these effects to manifest?

An especially fruitful direction of critique of the paternalistic vision hypothesis has been to examine the effects of task demands. The essential question here is whether subjects guess at experimental hypotheses when presented with, for instance, notably unexplained rods or backpacks. Influentially, Durgin et al. (2009) reexamined the initial finding of Bhalla and Proffitt (1999) showing that backpack-wearing subjects overestimate the slant of a hill more than backpack-free subjects. The original conclusion was that this was an effect on perception, such that carrying the extra weight actually made the hill look steeper. Durgin et al. (2009) were interested in whether the backpack group in this study may have guessed the experimenters' hypothesis and provided responses in accordance with their interpretation. That is, the authors wondered if – when given a heavy backpack and asked how steep a hill is – people are more inclined to give elevated estimates because they think that is what is meant to happen. A new version of the experiment was performed with a third group of subjects (in addition to the no-backpack and backpack groups) who wore a backpack but who were also given an elaborate explanation for its presence (Durgin et al., 2009). Subjects in this group were told that the backpack (emitting wires and electrodes that attached to their ankles, as well as making a whirring fan noise, for extra credibility) contained electromyographic equipment that would record muscle activity during the task. Subjects in both backpack groups were also questioned extensively to probe their beliefs about the backpacks and the effects they might have on their judgments. Interestingly, it was found that 12 out of 13 of the no-cover-story backpackers had indeed guessed that the backpack was meant to affect their gradient perception, compared to only 4 of 20 in the electrode group. Most importantly though, the no-cover-story backpack group provided more inflated slant ratings than either the no-backpack or cover-story groups, whose ratings did not differ from each other. In line with their suspicions, Durgin et al. (2009) here showed that when subjects were given an explanation for the burden, the relative overestimation was abolished. It is thus likely that the backpack-wearing subjects in the original Bhalla and Proffitt (1999) study interpreted a reason for the bag they were wearing and came to the conclusion that it must have been meant to affect their slope estimates. The bias they reported might therefore have been the result of implicit task demands, rather than having been an

effect on visuospatial perception. This approach was followed up and extended to demonstrate that simply asking subjects to avoid succumbing to task demand and compliance effects also eliminated the effect (Durgin et al., 2012). An analogous experiment by Firestone and Scholl (2014) further examined the finding that holding a rod horizontally leads to narrower judgments of nearby doors. Again, it was shown that when a plausible cover story was given (the rod was a balance aid), the apparently perceptual effect disappears. That manipulating task demands determines whether the biases attributed to a paternalistic visual system manifest or not indicates that expectation and compliance effects might have a greater impact on judgments than perception itself.

We have just seen that task demands can explain some important paternalistic biases, and now we come to another thread of critique that suggests some of these effects may actually stem from memory, rather than vision. It will be additionally argued that the intertwined nature of mental imagery and memory may well underpin the apparent spatial distortions. A piece of research that helped inspire the “New Look” movement in perceptual psychology in the mid-20th century will help to illustrate. Bruner and Goodman (1947) performed an experiment in which it was found that poorer children tended to overestimate the size of coins more than wealthier children. In some ways presaging the paternalistic vision account, this was taken to mean that the value of a visual stimulus was incorporated into its representation by the perceptual system. A later study, however, revealed that this effect was principally due to a difference between rich and poor children only when the judgment of coin size was made from memory, rather than when the coin itself was still visible (Carter & Schooler, 1949). It might be then that when people are left to conjure an image from memory, non-visual factors are able to exert effects that are seemingly attributable to primary visual perception. A similar approach has been taken with regards to more recent research used to bolster the paternalistic account. An initial study showed that softball batters with a high recent batting average provided larger estimates of softball size, implying to the authors that their greater batting ability made the softballs look bigger (Witt & Proffitt, 2005). This has been supported by similar findings that show well-performing golfers (Witt, Linkenauger, Bakdash, & Proffitt, 2008) and American football kickers (Witt & Dorsch, 2009) estimate golf holes and field goal posts to be larger, respectively. However, these judgments were either made without the to-be-estimated object in view,

or else after numerous shots had been made, and so it remains possible that the biases are applied in memory rather than in vision (A. D. Cooper et al., 2012). This possibility was examined in more detail in a series of experiments by Cooper et al. (2012), in which subjects judged the size of a hole after attempting to throw a marble through it, either when the hole was still visible (perceptual judgment) or after the hole had been covered up (memory judgment). By taking estimates on a trial-by-trial basis the authors showed that success at throwing increased the remembered size of the hole, but not its perceived size. Evidently, this last finding is of particular concern to the studies requiring spatial judgments once the target object is no longer visible.

In fact, memory is likely to have been confounded with perception in numerous studies that use psychophysical matching tasks to demonstrate paternalistic biases (see Cooper et al., 2012). For instance, if one reconsiders the finding that acrophobics, compared to non-acrophobics, overestimate the height of a balcony on which they are standing (Clerkin et al., 2009; Teachman et al., 2008), it could actually be that when they look away from the drop to perform their visual matching task, a bias affects their short term visual memory. The additional capacity for mental imagery to magnify this effect (Clerkin et al., 2009) could even support the role of memory, especially in light of recent arguments that visual working memory and mental imagery are intertwined cognitive processes (e.g., Albers, Kok, Toni, Dijkerman, & de Lange, 2013; Tong, 2013).

In addition to task demand effects, the equivocality of visual memory and mental imagery (Carter & Schooler, 1949) may permit additional, non-visual cognitive biases to influence subjects' judgments, which otherwise appear to all intents and purposes to reflect visual perception itself. Consider that, while there is a debate about whether visual perception is cognitively impenetrable (e.g., Fodor, 1983; Pylyshyn, 1999, 2003), mental imagery is at its core, cognitively generated, and therefore deeply susceptible to influence from higher-level processing. When bottom-up visual information is absent, such as when recalling the size of stimulus, it is likely that top-down factors, such as threat, need, and ability are able to impact fellow high-level processes of memory and mental imagery more so than visual perception supported by bottom-up, stimulus-driven input.

3.2.3 Threat and visuospatial judgments

An overview has now been given of some of the research commonly used to support the paternalistic vision hypothesis, as well as a number of experimentally validated objections to it. Earlier, the effect that threat could have on visuospatial judgments was briefly touched upon, with consideration of how acrophobics overestimate their height above the ground (Clerkin et al., 2009; Teachman et al., 2008). Now let us return to a related avenue of research that has received less attention in light of the objections raised above. This literature often focuses on the fear felt from spiders (indeed, this will be the focus of the current experiments), and we shall see that the authors tend to align their conclusions with the paternalistic vision account by claiming that visual perception itself is modulated by threat. The studies mentioned below imply that the motion (Riskind et al., 1992, 1995; Vagnoni et al., 2012; Witt & Sugovic, 2013), position (Cole et al., 2013) and size (van Ulzen et al., 2008; Vasey et al., 2012) of threatening stimuli cause perceptual biases consistent with the paternalistic vision hypothesis – that is, we see threatening objects as faster, closer and larger, presumably to facilitate responses that keep us out of danger.

In a number of studies, Riskind and colleagues claim to have demonstrated that people who fear spiders actually perceive spiders to be looming towards them more than control subjects, even when they are looking at static photographs (Riskind et al., 1992, 1995). For instance, in one experiment subjects were shown a picture of a tarantula and asked to imagine themselves in a room with it, then to draw on a plan view of the room any imagined motion trajectory of the spider (Riskind et al., 1995). With this measure it was found that high-fear subjects were more likely to envisage the spider moving towards them at speed. Another experiment showed that either while looking at photographs of spiders, or after watching videos of spiders, high-fear subjects gave greater ‘looming’ ratings than low-fear subjects (Riskind et al., 1992). These ratings were based on the answers to questionnaire items such as “how actively and energetically is the spider moving to you?”, and “how slow or fast is it moving towards you?”. On these grounds the authors of the above studies propose that high-fear subjects actually perceive spiders as moving rapidly toward them more than low-fear subjects do (Riskind et al., 1992, 1995). It should be clear, though, that these methods are far from

ideal probes of visual perception. Firstly, since perception is supposedly measured by asking direct questions about, for instance, the speed of looming motion, it would not take a great deal of reflection by the subject to infer the experimental hypothesis. This possibility is made all the greater by subjects being recruited largely on the basis of their self-reported level of spider-phobia. We saw earlier that other, even with less transparent measures, experiments into paternalistic biases were susceptible to task demands. Further problems with the conclusions of Riskind et al. (1992, 1995) arise when we consider how memory and mental imagery may have underpinned their results. In Riskind et al. (1992; experiment 3) subjects are shown videotapes of spiders crawling towards or away from the camera, before they give their ratings of 'loomingness'. Again, the problems associated with inferring perception from judgments based on memory were covered earlier. Furthermore, issues of both memory and mental imagery arise in Riskind et al. (1995), in which subjects, after looking at a photograph of a spider, had to imagine themselves in a room with it before giving their looming ratings. In conjunction with the potential task demands mentioned above it is very clear that this is not an adequate measure of perception, but rather one of imagination and memory.

A study by Vagnoni, Lourenco and Longo (2012) also examined the perception of looming of threatening visual stimuli. Here the researchers presented a range of photographs of threatening (spiders and snakes) and non-threatening (butterflies and rabbits) animals that expanded on screen for one second before disappearing. Subjects were tasked with imagining that the animal was still looming towards them and to press a button when they thought it would collide with them. Time-to-collision estimates were smaller for threatening than for non-threatening stimuli, and importantly, the degree of underestimation correlated with one's fear ratings. Echoing Riskind and colleagues, Vagnoni et al. (2012) surmised that "threatening stimuli are *perceived* as approaching more rapidly than non-threatening stimuli" (p.827, emphasis added). While certainly a possibility, it is contended here that this is not a necessary conclusion from these data. The effect observed by Vagnoni et al. (2012) could only be considered a perceptual bias, *per se*, if it was shown that the threatening stimuli were seen to have expanded further than the non-threatening stimuli before their point of disappearance. If, on the other hand, the bias is introduced after the disappearance of the looming stimulus, the subject is likely to be relying on their memory of its final appearance,

coupled with the extrapolated mental imagery of its continuing trajectory. This would not be the first time that mental imagery has affected spatiotemporal judgments of threatening stimuli in high-phobia subjects (Clerkin et al., 2009). Besides the further possibility that high-phobia subjects prefer to end trials sooner due to the discomfort felt, it could be that higher physiological arousal as a result of threat accelerates the build up of a neural accumulator, the output of which triggers the button press (Schurger, Sitt, & Dehaene, 2012). It remains to be seen, then, whether the time-to-collision underestimates reported by Vagnoni et al. (2012) are a result of perception, mental imagery, or response bias.

While still on the topic of threatening stimuli in motion, it was claimed by Witt and Sugovic (2013) that spiders are estimated to move at a higher velocity than non-threatening objects, such as a circles, ladybirds, and 'X'-shapes. The experimenters, however, only examined motion towards the observer, and not motion away, so even if the effect they uncovered is perceptual, it would be an overextension of their findings to propose that perceived velocity is affected by threat, independent of motion direction. It should also be noted that, while the researchers performed experiments with control stimuli to validate that the effect was not due to either the animacy or the overall shape of the moving stimulus, they did not measure threat. Besides an assumption that the spider was more threatening than the control stimuli, there is no guarantee that threat produced the observed effects. However, perhaps most problematic, in light of the critiques outlined earlier, is Witt and Sugovic's (2013) measure of velocity. A method of constant stimuli in which subjects judged whether the speed at which the stimulus moved towards them more closely resembled one of two reference speeds shown to them at the start of the experiment. This procedure, again, suffers from the potential effects of memory upon subjects' judgments. Comparison stimuli (i.e., the reference velocities) were not presented simultaneous with the targets for genuine perceptual judgments, but instead had to be committed to memory after being presented earlier in the session. It could therefore be that the relatively higher velocity estimates for spiders stem from them being judged to move faster than a somewhat vague recollection of the reference velocities. That is to say, subjects may selectively misremember the reference speeds according to the threatening quality of the target stimulus. Indeed, as we argued earlier, memory and mental imagery are more cognitively pliable than perception itself. It is furthermore uncertain whether the observed effect was due to spiders seemingly

moving faster, or simply being advanced in position. While velocity is little more than a variation of position over time, it has been posited that these two physical characteristics are processed independently (e.g., Smeets & Brenner, 1995). To illustrate, it could be that the apparent velocity bias is actually a tendency for threatening objects to be estimated as closer than they truly are, independent of speed. If this were the case, the final position of the spiders would have been advanced beyond that of the non-threatening stimuli, and so when questioned the observer's inference might have been that it must have moved faster in order to produce a closer percept. If it were shown that spider velocity estimates were greater than (or the same as) other stimuli it would imply that threatening stimuli really are estimated to move faster towards oneself (or in general). On the other hand, if motion away from the subject produced lower velocity estimates for threatening stimuli, it would suggest that it is an effect of estimated position, rather than speed.

Cole, Balcetis and Dunning (2013) found that people estimate threatening stimuli to be closer to them than disgusting or neutral stimuli. In their first experiment, subjects stood at some distance from a live tarantula and estimated the number of inches between them and the animal. Currently felt threat and disgust were each measured on a Likert scale, and it was demonstrated that threat, but not disgust, was negatively correlated with distance ratings. Their second experiment had separate groups of subjects watch a video of a confederate talking about their own behaviour, which was either threatening, disgusting, or neutral. The subject and confederate were then brought into the same room and seated a constant distance from one another. Those subjects who had viewed the 'threatening' video rated the confederate as being more threatening, and importantly, closer to them than those who had seen either the 'disgusting' or 'neutral' videos. As before, the disgust condition did not differ from the neutral condition. It is worth noting that a comparable experiment by Harber, Yeung, and Iacovelli (2011), found that depleting one's sense of self-worth made people more likely to underestimate the number of inches to a threatening object (a live tarantula). In numerous studies mentioned thus far, memory has been cited as a possible candidate for the observed paternalistic-like effects. This criticism is however less easily applied to any of these experiments, since position estimates are taken while the stimulus is still in full view of the subject. The problem here, it is suggested, is with the measure of proximity, which is potentially more cognitive than perceptual. Consider the size of the true distances to

the objects, which were held constant within each of the Cole et al. (2013) studies (156” from the tarantula in Experiment 1; 132” from the confederate in Experiment 2), and were jittered between several locations in the Harber et al. (2011) experiment (6”-56”). In the Harber et al. (2011) study subjects simply had to give a verbal estimate of the number of inches between them and the object, while in both Cole et al. (2013) experiments they were shown a one-inch sample line and asked to judge how many inches were between them and the stimulus. In all experiments, then, subjects had to formulate a number to ascribe to the distance between them and the stimulus. Shown a distance of, say, four inches, one may reasonably apply a perceptual judgment in reporting that either one’s internalised notion of an inch (in the case of Harber et al., 2011), or a sample inch (in the case of Cole et al., 2013), appears that it should fit approximately four times within the gap. However, since the true number of inches is considerably larger in the Cole et al., (2013) studies, and in most trials of the Harber et al. (2011) experiment, it is unlikely that this measure reflects in any meaningful way the contents of visuospatial perception. In this way the method is not unlike judging how many jellybeans fit in a jar. The point of the popular fairground game is that the number of jellybeans is not directly perceivable, and instead one has to make an informed guess, perhaps by drawing upon prior knowledge. It is argued therefore that reduced distance estimates for threatening stimuli using this method are less likely to reflect the effects of threat upon vision than they are the effects of threat upon cognitive mechanisms of generating numbers. Though perhaps challenging to implement, a psychophysical measure of perceptual comparison would have provided a more objective and direct assessment of perceived proximity.

It has been additionally claimed that size estimations are modulated by threat. For instance, after viewing a live tarantula the subjects in an experiment by Vasey et al. (2012) estimated the spider’s leg span by drawing a single straight line on a piece of card. It was demonstrated that spider-phobics judged the tarantula to be larger the higher their current levels of state anxiety. As articulated earlier, the method of removing the stimulus from view prior to making a spatial judgment permits only the remembered size of the stimulus to factor into people’s estimates, which may be more readily biased by threat. This is something that the authors themselves concede, though they still claim to have found evidence of a perceptual distortion. However, another paper suggesting an impact of affective content on size perception did not suffer from

potential confounding effects of memory (van Ulzen et al., 2008). Here it was shown that circles containing negative affective stimuli (e.g., spider or skulls) appeared larger than circles containing neutral (e.g., mug or mushroom) or positive (e.g., kittens or flower) affective stimuli. Size estimations were made by adjusting a concurrently visible comparison circle to match the size of a target circle containing the affective stimulus. Memory, then, is unlikely to be at the heart of the effect. It should be noted that the authors were careful not to claim that the perceived size of the affective stimulus itself is influenced, since the subjects only judged the size of the circle surrounding it. This study suggests therefore that emotional content can in certain circumstances impact upon visuospatial perception (perhaps mediated by attention, as van Ulzen et al., 2008 suggest), though perhaps not upon the perception of the threatening stimulus itself. The focus of this paper was also not specifically on threat, but on positive versus negative affective valence. The experiments used stimuli that were predefined as positive, neutral or negative in affective content, and no measures of threat or fear were taken. It remains to be seen therefore, whether threat itself can bias visuospatial perception.

Taken together, the aforementioned literature variously claims that threatening stimuli appear to move faster, to be closer to us, and to be larger in size, than non-threatening stimuli. In essence, it is said that fear-inducing objects are perceived in ways that makes them appear even scarier. The direction of all of these reported biases is therefore consistent with the literature used to support the paternalistic vision hypothesis, which proposes that vision provides us with percepts tailored to our behavioural requirements. Do we, then, literally see threatening objects as bigger, closer, and faster because this promotes their more prompt avoidance? The arguments of others (e.g., Durgin et al., 2009; Firestone, 2013a) have been cited and added to, claiming that much of the literature used to prop up paternalistic vision is flawed in that it allows for cognitive factors to impact judgments that are taken to reflect perception. It is additionally proposed that the largely separate literature on the effects of threat upon visuospatial perception is problematic in the same manner. Are any of the claims that threat value warps our spatial perception valid? The sheer number of robust, consistent effects reported across these two fields implies that paternalistic-like biases are not mere artefacts, but they may reflect, for example, task demands and memory more than they do vision.

In the present experiments we draw upon the flash-lag effect, a visual-perceptual illusion in which the position of a moving object appears forwardly displaced beyond that of a collocated flash (MacKay, 1958; Nijhawan, 1994). This is a very robust, and enormously replicated phenomenon (for an extensive review of empirical findings, see Hubbard, 2014), that scales up with the velocity of the moving object (Krekelberg & Lappe, 1999; Lee et al., 2008; Nijhawan, 1994; Wojtach et al., 2008). While a heated debate persists regarding the cause of the illusion, it is uncontroversial to assert that it is perceptual in nature, rather than being the result of, for instance, response bias, task demands, or memory (for reviews, see Krekelberg & Lappe, 2001; Nijhawan, 2002; Schlag & Schlag-Rey, 2002; Whitney, 2002). Judgments are made over multiple trials regarding the instantaneous relative positions of two concurrently visible stimuli, and evidence has indicated that the measure is robust against response bias (Kanai et al., 2004). Though most commonly investigated with moving visual stimuli that either rotate (e.g., Nijhawan, 1994) or linearly translate (e.g., Kanai, Sheth, & Shimojo, 2004) in the frontoparallel plane, flash-lag also occurs with stimuli that appear to change in depth (Harris, Duke, & Kopinska, 2006; Ishii, Seekkumarachchi, Tamura, & Tang, 2004; Lee et al., 2008), colour (Sheth et al., 2000), sound (Alais & Burr, 2003), and motor/kinaesthetic space (Nijhawan & Kirschfeld, 2003). The illusion is also not cognitively impenetrable, since higher-level stimulus attributes are able to affect it (for a review, see Hubbard, 2014). For example, when the moving and flashed stimuli together make up the components of a Japanese Kanji character, the flash-lag effect is reduced for Japanese speakers, but not for English speakers with no linguistic experience of the symbol (Noguchi & Kakigi, 2008). Similarly, it has been reported that when the bottom half of a frontal face image is in motion, and the top half is flashed, the flash-lag effect is reduced when both halves are from the same, rather than different faces (Khurana et al., 2006). Also demonstrating a role for prior knowledge, Nagai et al. (2010) showed that when the moving image was of a car, the flash-lag was greater during backwards rather than forwards motion, suggesting that knowledge of an object's typical motion characteristics is integrated into the percept. Given that these 'higher' cognitive factors are able to modulate the flash-lag effect, one might suppose that, if threat is able to impact visuospatial perception, it should also affect the size of the forward displacement in the flash-lag effect. The following experiments therefore do not necessarily bear on explanations for the flash-lag phenomenon, but instead use it to probe the question of whether threat influences visuospatial perception. If the flash-lag

effect is modulated by the fear content of the stimuli it would strengthen the overall footing of the paternalistic vision stance by suggesting that visual space can indeed be manipulated by threat, without concurrent effects from memory, for instance. More specifically, if the ‘known-quantity’ of flash-lag is enhanced or reduced depending on whether motion is towards or away from the subject, this would bear upon the paternalistic claims that threatening stimuli are perceived as closer, larger, and faster.

3.3 Experiment 1: Looming and receding motion

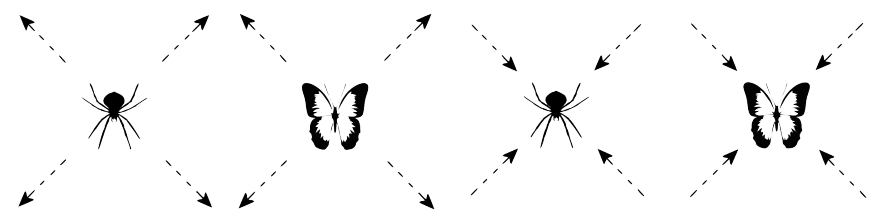
Outlined earlier were claims that people perceive threatening stimuli to be (1) closer, (2) larger, and (3) moving faster towards them than non-threatening stimuli. These will henceforth be referred to simply as claims (1), (2), and (3). This experiment explicitly addresses claims (1) and (2) in conjunction, and to a lesser extent, claim (3). The size of the flash-lag effect was investigated in subjects with a range of spider-phobia levels for a spider image and a butterfly image that either loomed or receded, while a flashed version of the same image was presented nearby for size comparison. Looming or receding motion could be seen as either motion in depth, or a change of size in the distal object. If the former is the case (as is the intention), claim (1) predicts an enhanced flash-lag (above equivalent motion for the butterfly image) in high-phobia subjects, since the effect should make the threatening stimulus appear closer. Claim (1) simultaneously predicts a reduced flash-lag for the receding spider image compared to the butterfly image in high-phobia subjects. Claim (2), on the other hand, suggests that threatening objects are seen as larger than non-threatening objects. Note that since the current stimuli do not clearly distinguish between motion in depth and size-change, the predictions of claim (2) are actually the same as claim (1).

Since flash-lag scales up with velocity (e.g., Nijhawan, 1994), the prediction that the motion of threatening objects towards the subject produces greater velocity estimates should also result in a magnified effect. Put simply, if something is perceived to move faster, it should produce a larger flash-lag. According to claims (1) and (2), motion of the spider away from high-phobia subjects should produce a relatively small flash-lag, because the effect of threat should make the spider seem less distant or less small.

However, the literature on the perceptual effects of threat has so far yielded no explicit claim about how the velocity of threatening objects moving *away* from the observer should be perceived. A null-result in this condition will therefore not be considered at odds with claim (3). The only prediction derived from claim (3), then, is that looming motion (to the extent that is perceived as approaching motion in depth) should produce a larger effect with spiders than with butterflies in high-phobia subjects. See Table 3.1 for a summary of the various predictions derived from paternalistic vision.

Table 3.1.

Experiment 1: Predicted differences in flash-lag magnitude for high compared to low phobia subjects derived from Claims 1, 2, and 3 of paternalistic vision. Key predictions are displayed in bold.

	Looming motion		Receding motion	
	Spider	Butterfly	Spider	Butterfly
				
Claim 1: Threatening objects appear closer	Larger FLE	Same/ similar FLE	Smaller FLE	Same/ similar FLE
Claim 2: Threatening objects appear larger	Larger FLE	Same/ similar FLE	Smaller FLE	Same/ similar FLE
Claim 3: Threatening objects appear to move faster towards you	Larger FLE	Same/ similar FLE	Same/ similar FLE	Same/ similar FLE

3.3.1 Methods

3.3.1.1 Subjects

Thirty-two naïve subjects (25 female) with normal or corrected-to-normal vision participated in exchange for payment or course credits.

3.3.1.2 Apparatus

Subjects sat at a desk with their head immobilised by a chin support while viewing a 21" Sony Trinitron Multiscan E500 CRT monitor (85Hz refresh rate, 1400 x 1050 resolution) from a distance of approximately 40cm. Responses were given with subjects' preferred hands by pressing the left and right keys on an Apple USB keyboard. Stimuli were presented using custom Matlab scripts, running with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

3.3.1.3 Stimuli and Procedure

Flash-lag task. On each trial a square clip art image of either a black spider or a black butterfly (see Figures 3.1 and 3.2) either loomed (expanded) out from or receded (contracted) towards a point 11.3° to the left or right of a central fixation cross. Only the black portions of the images were displayed, and the white regions shown in Figure 3.1 were shown in the neutral grey of the display background. After 2200ms the animal image disappeared. Measured between their most distant horizontal and vertical points the animal images were $1.5^\circ \times 1.5^\circ$ at their smallest, and $18^\circ \times 18^\circ$ at their largest. Rather than using an abstract shape as the control stimulus a butterfly was chosen because it has similar overall image complexity and, like spiders, butterflies are small, animate creatures.

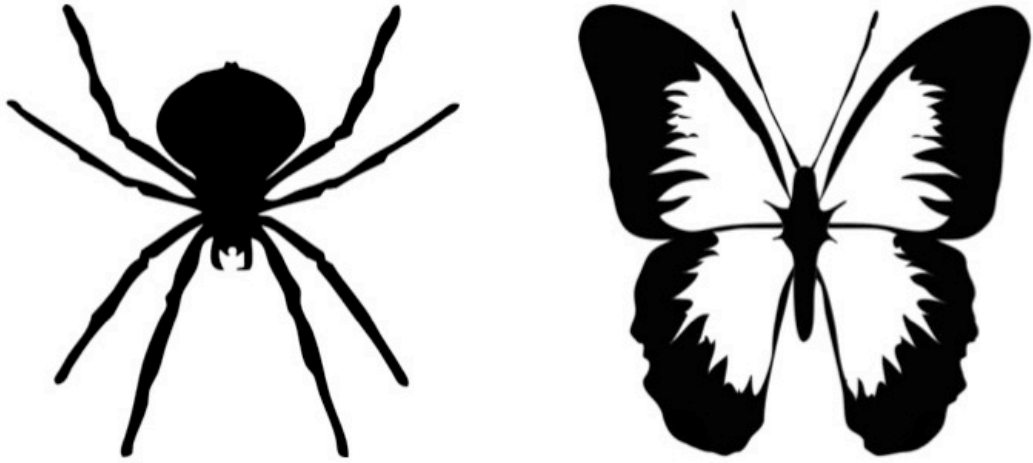


Figure 3.1. Spider and butterfly images used in Experiment 1.

While both axes of the image had the same amount added to or subtracted from them in each video frame, this quantity was varied over the course of the animation. If the image were to expand or contract by the same angular subtense in each frame it would produce the percept of an object either slowing down as it approached (during expansion) or speeding up as it receded (during contraction). The method of Regan and colleagues (e.g., Regan & Hamstra, 1993; Regan & Vincent, 1995) was used in order to produce a two-dimensional expansion or contraction animation consistent with motion in depth at a constant velocity. The variation in the angular subtense of the expanding image was thus described by the equation

$$\tan\theta_t = \frac{\tan\theta_0}{1 - t/T_0}$$

where the image's angular subtense at time t was $2\theta_t$ and $2\theta_0$ at $t = 0$, and the time-to-collision at $t = 0$ was given by T_0 . The resulting animation appeared consistent with an object moving towards the observer at a constant velocity. To produce the receding animation the looming animation was simply reversed. It has been shown that when faced with dynamic two-dimensional stimuli, perception prefers to interpret the simplest three-dimensional motion path that maintains an object's shape and identity (e.g.,

Attneave & Block, 1973; Bundesen, Larsen, & Farrell, 1983; Corbin, 1942; Shepard & Judd, 1976; Shepard & Zare, 1983). It is thus expected that subjects will perceive the stimuli as moving in depth, rather than as simply changing in size.

Halfway through the animation, a flashed version of the same image was presented for a single video frame (12ms) centred 11.3° to the opposite side of fixation. The size of the flash was equivalent to one of eight possible former or future sizes of the animated image, evenly distributed between 423ms in the past and 1056ms in the future (-423ms, -211ms, 0ms, 211ms, 423ms, 634ms, 845ms, and 1056ms). After the animation had finished, subjects pressed one of two keys depending on whether they perceived the left or the right image as larger at the time of the flash (binary choice). Since the stimuli were not stereoscopic, a judgment of relative size was considered to be more straightforward for subjects than a judgment of relative position in depth.

The side of the display on which the animated image was presented was alternated between trials to avoid a build up of motion aftereffects in one hemifield. After 16 practice trials, a total of 640 experimental trials were presented in random order ($2 \text{ animals} \times 2 \text{ motion directions} \times 8 \text{ flash sizes} \times 20 \text{ flash size repetitions}$), with a short break at the halfway point.

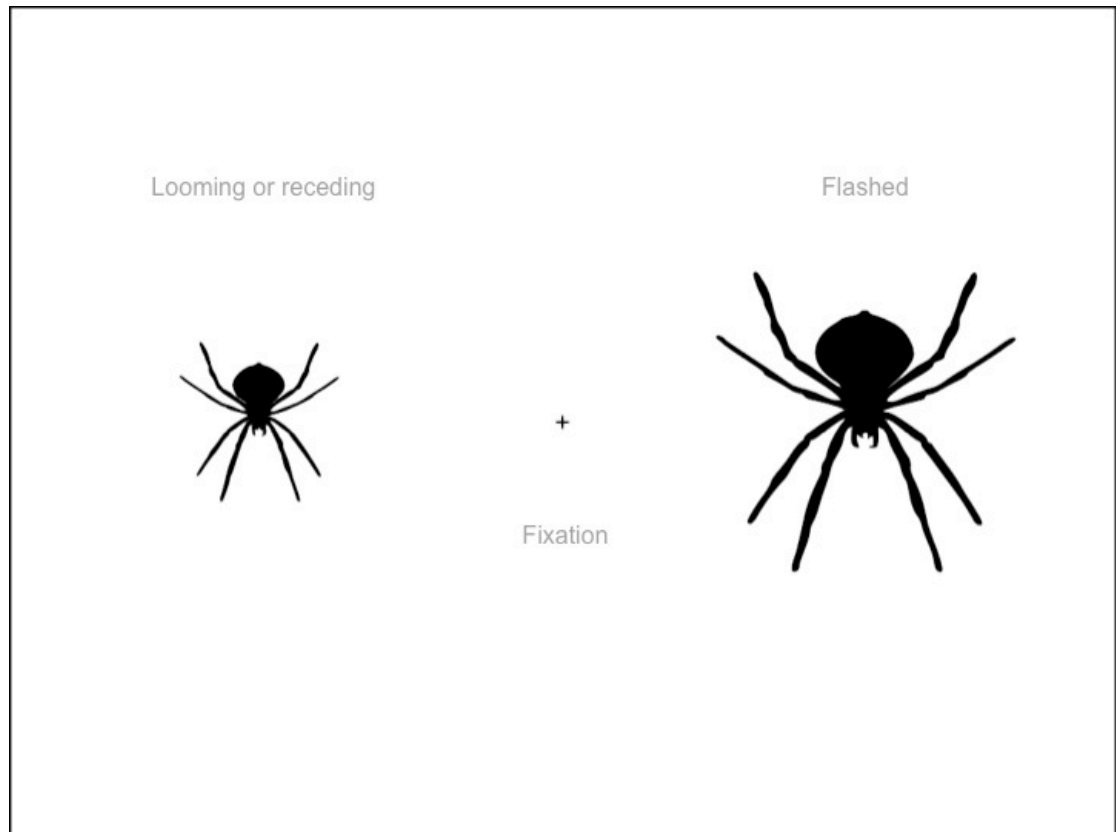


Figure 3.2. Experiment 1: Example of stimuli used in a spider trial. Only objects in black were shown.

Phobia level assessment. After completing the flash-lag task, subjects' phobia levels were assessed for both spiders and butterflies using the 18 standard items of the Fear of Spiders Questionnaire (Szymanski & O'Donohue, 1995) for spiders, and modified versions of the same 18 items for butterflies. Following Vagnoni et al. (2012), the butterfly items were identical to the spider items, except that the word "spider" was replaced by the word "butterfly." Some example items were therefore: "If I came across a spider now, I would get help from someone else to remove it," and "I would feel very nervous if I saw a butterfly now." Using a custom Matlab script, the 36 spider and butterfly items were shuffled together and presented on screen one at a time in random order above a 7-point Likert scale, ranging from "strongly agree" to "strongly disagree." Strong agreement with an item gave a score of +3 (indicating high-phobia), while strong disagreement gave a score of -3 (indicating low-phobia). After completing both sets of items the mean phobia score for each animal was calculated.

A paired samples t-test reveals that, across all subjects, spiders ($M = -1.09$, $SD = 1.72$) were considered to be more threatening than butterflies ($M = -2.31$, $SD = 0.87$), $t(31) = 4.49$, $p < .001$, $d = 0.9$. A significant paired samples correlation ($r = .46$, $p = .008$) also revealed that those who gave a high spider-phobia score, also tended to give a relatively high butterfly-phobia score. This suggests that the spider and butterfly phobia scores were not entirely independent – perhaps due to each subject being more or less likely than others to show agreement with statements given in questionnaires. The difference between the phobia scores for spiders and butterflies (i.e., spider score - butterfly score) was therefore taken to be the best measure of true spider-phobia level. Positive difference scores thus meant that spiders were considered more threatening than butterflies.

For some of the analysis to come subjects were separated into high- and low-phobia groups depending on whether their phobia difference score was above or below the median value, respectively. The high-phobia group had a significantly greater phobia difference score ($M = 2.41$, $SD = 1.33$) than the low-phobia group ($M = 0.03$, $SD = 0.29$), $t(16.4) = 6.98$, $p < .001$, $d = 2.93$. To ensure that the difference between spider and butterfly phobia scores was greater in the high-phobia group a 2×2 mixed-measures analysis of variance (ANOVA) was performed, with animal phobia score (spiders or butterflies) as a within-subjects factor, and phobia level (high or low) as a between-subjects factor. There were significant main effects of animal phobia score, $F(1, 30) = 51.25$, $p < .001$, $\eta_p^2 = .631$, and phobia level, $F(1, 30) = 12.3$, $p = .001$, $\eta_p^2 = .291$, and a significant interaction between them, $F(1, 30) = 48.65$, $p < .001$, $\eta_p^2 = .619$. An examination of the mean phobia scores for each animal from each group allows an interpretation of the interaction. While the low-phobia group produced very similar spider ($M = -2.28$, $SD = 0.91$) and butterfly ($M = -2.31$, $SD = 0.94$) scores, and the high-phobia group produced similarly low scores for butterflies ($M = -2.3$, $SD = 0.82$), the latter gave much higher scores for spiders ($M = 0.1$, $SD = 1.51$). This suggests that the aforementioned finding that spiders were considered more threatening than butterflies overall is almost entirely due to the difference in phobia scores from group labelled as ‘high-phobia’.

Data analysis. Responses regarding which image appeared larger were converted so that they equated to either ‘flash-ahead’ or ‘flash-behind’. So, for example, if a subject

reported that either a looming stimulus looked smaller than the flash, or that a receding stimulus appeared larger than the flash, it would be coded as a ‘flash-ahead’ response.

Psychometric curves were fit to the data from each condition (looming spider, receding spider, looming butterfly, receding butterfly) for each subject with a cumulative normal function (using the Palamedes toolbox for Matlab; Prins & Kingdom, 2009). Points of subjective equality (PSEs) and confidence intervals were estimated using a bootstrap procedure with 2000 iterations. PSEs corresponded to the size of the flash (in milliseconds of animation progress) that would receive 50% ahead and 50% behind responses. A PSE of 100ms therefore indicates that the two stimuli were perceived as equal when the flashed image was equal in size to that which the animated image would be expected to reach 100ms in the future.

For each subject PSE difference scores were calculated. These included the motion direction anisotropies associated with the spider image (looming spider PSE - receding spider PSE) and the butterfly image (looming butterfly PSE - receding butterfly PSE), and the difference between these anisotropies (spider anisotropy - butterfly anisotropy). A positive anisotropy difference therefore indicates that the spider produced a larger anisotropy than the butterfly. Also derived were the differences between the PSEs for the looming spider and looming butterfly (looming spider PSE - looming butterfly PSE), and the receding spider and receding butterfly (receding spider PSE - receding butterfly PSE). Positive values in both of these measures mean that the spider produced a larger flash-lag than the butterfly. Figure 3.3 shows psychometric curves from a representative subject.

3.3.2 Results

Correlations across all subjects. Phobia difference score did not correlate with anisotropy difference, $r = -.047$, $p = .799$, therefore implying no relationship between phobia level and the difference between one’s flash-lag anisotropies for the spider and butterfly images.

There was also no correlation between either the difference between one's looming spider and looming butterfly flash-lags, $r = .123, p = .502$. Additionally, there was no correlation between the difference between one's receding spider and receding butterfly flash-lags, $r = .141, p = .44$. Taken together, these two null results suggest that phobia level was not related to the difference between one's spider and butterfly flash-lags, in either direction of motion.

ANOVA with high- and low-phobia groups. A $2 \times 2 \times 2$ mixed design ANOVA was performed, with motion direction (looming or receding) and animal (spider or butterfly) as within-subjects factors, and phobia level (high or low) as a between-subjects factor.

There was a main effect of motion direction, $F(1, 30) = 6.58, p = .016, \eta_p^2 = .18$, a main effect of animal, $F(1, 30) = 19.17, p < .001, \eta_p^2 = .39$, and a significant 2-way interaction between them, $F(1, 30) = 16.55, p < .001, \eta_p^2 = .356$. An examination of Figure 3.4 indicates that the spider and the butterfly produced similar flash-lags for looming motion, and that while receding motion led to smaller effects with both images, it was more pronounced for the spider than the butterfly. There was no main effect of phobia level, $F(1, 30) = .26, p = .616, \eta_p^2 = .008$, nor did it interact with motion direction, $F(1, 30) = .35, p = .559, \eta_p^2 = .012$, or animal, $F(1, 30) = 2.28, p = .142, \eta_p^2 = .071$. There was furthermore no three-way interaction between motion direction, animal, and phobia level, $F(1, 30) = .01, p = .755, \eta_p^2 = .003$. In combination, these null results show that phobia level had no impact on flash-lag magnitude.

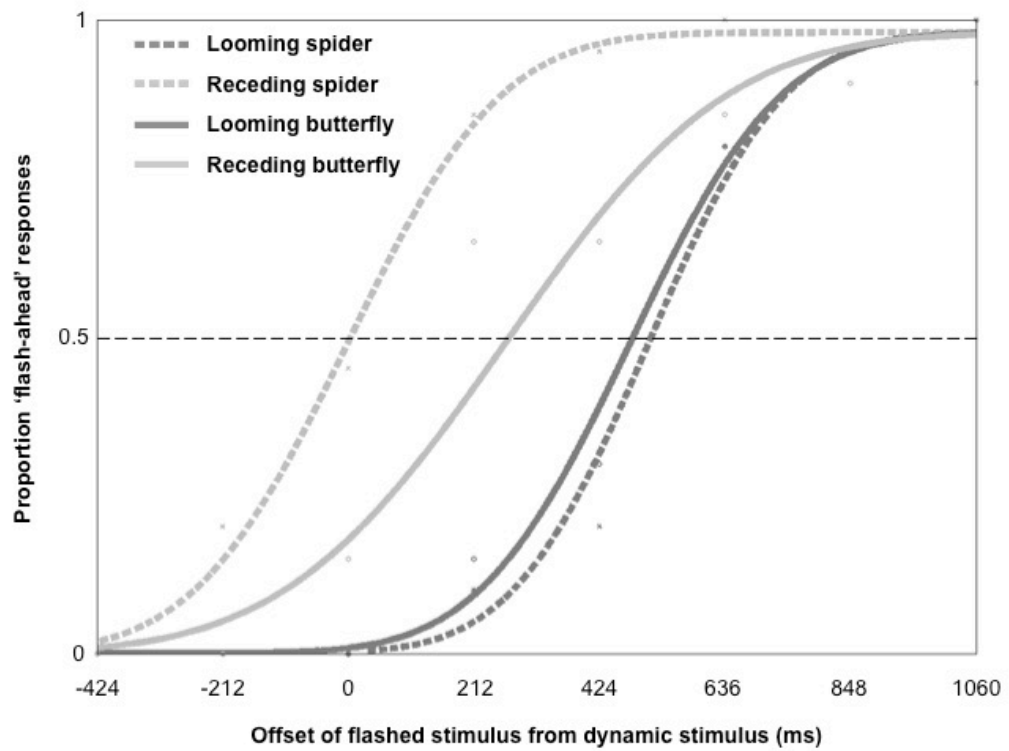


Figure 3.3. Experiment 1: Psychometric curves from a representative subject. Negative offsets represent flashes that lag behind the instantaneous size of the dynamic stimulus.

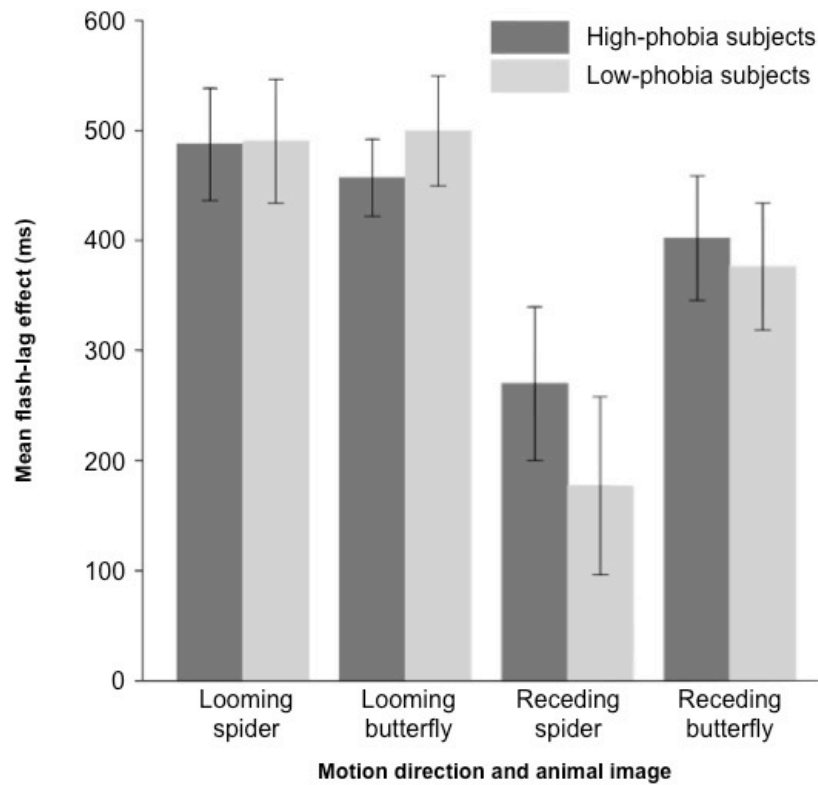


Figure 3.4. Experiment 1: Mean flash-lag effects for looming and receding spider and butterfly images for high- and low-phobia subjects. Error bars indicate ± 1 standard error.

3.3.3 Discussion

These findings are inconsistent with the paternalistic vision hypothesis, in that they imply that visual perception is not affected by threat. An unequivocally perceptual measure was used to probe instantaneously perceived spatiotemporal position and no effect of manipulating threat was found. Furthermore, contrary to the aforementioned studies, no evidence was found that threatening objects are perceived as closer, larger, or faster, than non-threatening objects. Phobia difference score did not correlate with the flash-lag anisotropy difference between the spider and the butterfly (as would be predicted by claims (1) and (2)), nor did it correlate with either the difference between the looming spider and the looming butterfly flash-lags (as would be predicted by claim

(3)), or the difference between the receding spider and the receding butterfly flash-lags. When subjects were split into high- and low-phobia groups, an ANOVA showed no effect of this between-groups manipulation, and no interaction between it and the other variables.

To the extent that the moving stimuli were perceived as moving in depth (as should be expected given the size-change profiles of the looming and receding animations) the current results bear most strikingly upon claim (1), that threatening stimuli are perceived to be closer to us than non-threatening stimuli. Our results suggest that this is not the case, i.e., that people do not underestimate the distance to threatening objects due to a perceptual bias. If, however, the looming and receding stimuli were actually perceived as changing in size rather than in depth, the present results would be evidence against claim (2), that threatening objects appear larger. Since this experiment does not distinguish motion in depth and size-change, the findings could potentially be taken as evidence against either claim (1) or (2), or both of them together. It is however more likely that the animations were perceived as motion towards or away from the observer, because the size-change profile was consistent with the simple, linear motion of an object moving in depth at a constant velocity.

The present results can also be taken as evidence against claim (3) – that incoming threatening stimuli appear to be moving faster – since high-phobia subjects should have seen looming spider stimuli as moving more quickly than low-phobia subjects, and thus displayed relatively augmented flash-lag effects. This is however a less direct implication of the present data since it has only been inferred that something perceived to move faster should produce a greater flash-lag effect. In defence of claim (3), Anstis (2010) has shown that when physical and perceptual motion directions are dissociated, flash-lag depends on the former, so it may similarly be that only physical velocity, and not perceptual velocity, is able to modulate the effect.

Despite our results being (on face value) contradictory to the paternalistic vision hypothesis, one may still argue that the interaction between motion direction and animal type could be explained from a paternalistic standpoint. Across all subjects, looming stimuli produced similarly large flash-lags that were greater than those for receding stimuli. However, the interaction shows that, across all subjects, the receding spider

gave a smaller flash-lag than the receding butterfly. It could be, then, that the spider was more threatening than the butterfly to everyone, regardless of their apparent phobia level, and that this made the spider appear less far along its trajectory and/or less small. If this was the case though, why was a difference between high- and low-phobia subjects not evident? As we saw earlier, the low-phobia group produced very similar phobia scores for both spiders and butterflies, while the high-phobia group gave considerably higher scores for spiders, but similarly low scores for butterflies. So, to the extent that the questionnaire was a valid measure of threat, the low-phobia group was equally intimidated by spiders and butterflies, while the high-phobia group was much more afraid of spiders. To maintain the paternalistic stance one could argue that the phobia measurements used herein did not reflect threat as it operated in the flash-lag task. The Fear of Spiders Questionnaire is, however, based on solid empirical footing (Szymanski & O'Donohue, 1995), and a similarly modified version was used by Vagnoni et al. (2012) to demonstrate the “affective modulation of the perception of looming stimuli” (p. R826). Given our almost identical use of the questionnaire to Vagnoni et al. (2012), one would have expected a comparably observable modulation of spatiotemporal judgments, though this was not the case. It may be retorted, however, that their measure of time-to-collision and our measure of flash-lag are simply not the same, and thus cannot be compared. Consider, though, that this would be inconsistent with the conspicuous analogies between our perceptual measures. Recall that in their experiment subjects viewed a stimulus looming for 1s before disappearing, then pressed a button to indicate when they thought it would have collided with them if it had continued to loom. The time between the stimulus offset and the button press was the time-to-collision measure. It should be highlighted that their measure of time-to-collision and the present measure of flash-lag are both judgments regarding the instantaneous spatiotemporal positions of two-dimensional objects appearing to move in depth at close proximity. It is posited therefore, that the starkest contrast between these two measures is that theirs involves a component of memory and mental imagery, while ours is a perceptual comparison. The present null-result, therefore, is most likely to reflect that spatiotemporal visual perception itself is not affected by threat. A plausible explanation for the interaction between motion direction and animal type might be that the low-level characteristics of the spider's shape (e.g., its outward-pointing legs) made it appear relatively larger during receding motion.

If one continues to entertain the possibility that spiders were scarier than butterflies for everyone, and that this explains the interaction effect outlined above, it may also be conjectured that a flash-lag difference between looming spiders and looming butterflies was not evident due to a ceiling effect. That is, perhaps an upper flash-lag limit for looming stimuli was hit. Consistent with this possibility, the present effects are considerably greater (up to ~800ms in some cases) than the sub-100ms effects commonly observed with either rotating or linear translating stimuli (e.g., Nijhawan, 1994). Larger-than-typical flash-lags have been observed previously in stimuli moving in depth (Harris et al., 2006). Encountering a flash-lag ceiling could have equalised the looming spider and looming butterfly effects, when the former would otherwise have had an advantage. The possibility of a ceiling effect cannot be discounted without further experiments.

An additional limit to this experiment becomes apparent when we consider the lesson of the El Greco fallacy outlined earlier (Firestone & Scholl, 2014; Firestone, 2013b). If the target and matching stimulus in a psychophysical task are analogous, then any perceptual effect should cancel out when the comparison is made. In the current experiment animated spiders were compared with flashed spiders, and animated butterflies were compared with flashed butterflies. The reasoning behind this decision was that for a valid size comparison to be made, the moving and flashed stimuli had to be the same shape. There is the potential, though, for a perceptual bias to be applied equally to both stimuli, thereby nullifying its appearance in the data.

Sample size might also be cited as a limiting factor in the present experiment. Given that considerable individual differences are commonly observed in the magnitude of the flash-lag effect (e.g., Kreegipuu & Allik, 2004; Nijhawan, 2001), it could be that thirty-two subjects provided insufficient power to reveal an effect.

A final point worth noting is that all subjects saw both the spider and the butterfly, and trials with each image were presented in random order. The spider or the butterfly could therefore appear on any given trial. It may be that at the beginning of each trial subjects were initially uncertain about whether they were seeing the spider or butterfly image in motion, since it was presented in the periphery. If confusion about the nature of the

image being shown persisted to the moment of the flash, this could have had negated perceptual differences between the images.

3.4 Experiment 2: Linear translation

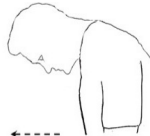
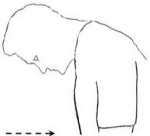






In the foregoing discussion it was argued that the spatiotemporal perception of threatening stimuli appears to be no different from that of non-threatening stimuli. However, the specific findings and the stimuli used also presented further issues that kept alive a potential role for paternalistic biases in visuospatial perception. Several possibilities were identified: everyone considered the spider more scary than the butterfly; ceiling effects equalised the looming flash-lags; the resemblance of the moving and flashed stimuli cancelled out perceptual biases; the sample was too small to reveal an effect; and seeing both threatening and non-threatening stimuli reduced effects. The current experiment attempts to circumvent these issues by presenting spider images that linearly translate up or down across displays that are either horizontally (i.e., flat) or vertically (i.e., standard) oriented. Flash-lag effects tend to be smaller when motion is in the frontoparallel plane (e.g., Nijhawan, 1994; Whitney & Murakami, 1998) than when motion is in depth (e.g., Harris et al., 2006), so by using the former it is hoped that ceiling effects will be avoided. For each subject the flash-lag effect is measured by briefly presenting two horizontal lines, one above and one below the translating spider image, and having the subject select which line had been closer to the spider at the time that they flashed. By having abstract (i.e., non-spider) shapes as the flashed stimuli, we avoid the potentially nullifying effect of identically shaped moving and flashed objects. Importantly, position in depth is also disentangled from instantaneous size. With the horizontal display, downwards motion is towards the subject, and upwards motion is away from the subject. Neither direction of motion is either towards or away from the subject's body when the display is vertically oriented. This experiment is therefore focused on testing claim (1), and not claim (2). Instead of having a within-subjects manipulation of threat as before (i.e., spider versus butterfly), a further between-group manipulation is added, so that some subjects view a less scary spider image, while others view a more scary spider image. The intention here is that there will be no moment of ambiguity about what image subjects are seeing in motion

since each individual always sees the same image. Finally, a larger sample is used to increase statistical power.

The specific predictions from the paternalistic vision stance are similar to those outlined for the previous experiment, except that the focus is now on testing claims (1) and (3), and not on testing claim (2). According to claim (1), high-phobia subjects should produce larger effects than low-phobia subjects for motion towards them (i.e., horizontal display, downwards motion), and smaller effects than low-phobia subjects for motion away from them (i.e., horizontal display, upwards motion). This anisotropy difference between phobia groups should therefore also be greater for subjects seeing the more scary spider than those seeing the less scary spider. This would suggest that, regardless of motion direction relative to their body, more threatening objects are perceived closer to high- than low-phobia subjects. The difference between downwards and upwards motion on the vertical display should differ less or not at all between subjects of different phobia levels and between subjects viewing the less and more scary spider images. Again, the specific prediction derived from claim (3) is that motion towards the subject should produce a larger flash-lag (because it should be perceived to move faster in that direction) to the extent that it is more threatening. See Table 3.2 for a summary of the various predictions derived from paternalistic vision.

Table 3.2.

Experiment 2: Predicted differences in flash-lag magnitude for high compared to low phobia subjects derived from Claims 1 and 3 of paternalistic vision. Key predictions are displayed in bold.

		Horizontal display		Vertical display		
		Upwards motion	Downwards motion	Upwards motion	Downwards motion	
						
Claim 1: Threatening objects appear closer	More scary spider		Much smaller FLE	Much larger FLE	Same/ similar FLE	Same/ similar FLE
	Less scary spider		Smaller FLE	Larger FLE	Same/ similar FLE	Same/ similar FLE
Claim 3: Threatening objects appear to move faster towards you	More scary spider		Same/ similar FLE	Much larger FLE	Same/ similar FLE	Same/ similar FLE
	Less scary spider		Same/ similar FLE	Larger FLE	Same/ similar FLE	Same/ similar FLE

Note. Claim 2 was not tested in this experiment

3.4.1 Methods

3.4.1.1 Subjects

Eighty naïve subjects (56 female) with normal or corrected-to-normal vision participated in exchange for payment or course credits.

3.4.1.2 Apparatus

Two 21" Sony Trinitron Multiscan E500 CRT monitors with identical display settings (85Hz refresh rate, 1400 x 1050 resolution) were positioned side-by-side. One was arranged in a standard, vertical configuration, while the other was tilted forwards and viewed as a reflection in a half-silvered mirror, such that its image was projected in the horizontal plane of the desk (see Figure 3.5). For this latter display orientation, upwards motion was away from the subject's body, and downwards motion was towards the subject's body. For the vertical screen neither motion direction was explicitly towards or away from the subject. Stimuli presented on the horizontal display were inverted so that when reflected they projected the same retinal image as those on the vertical monitor. Subjects viewed the vertical display projected through a half-silvered mirror while their head was immobilised by a chin rest. When viewing the horizontal display, subjects sat at the same desk, also using a chinrest, but tilted their forehead forwards to rest on a support. They looked straight down towards the desk, where the screen was reflected. In both cases the subject's nasion was 35cm from the plane of the display. Responses were given with subjects' preferred hands by pressing the left and right keys on an Apple USB keyboard. Stimuli were presented using custom Matlab scripts, running with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

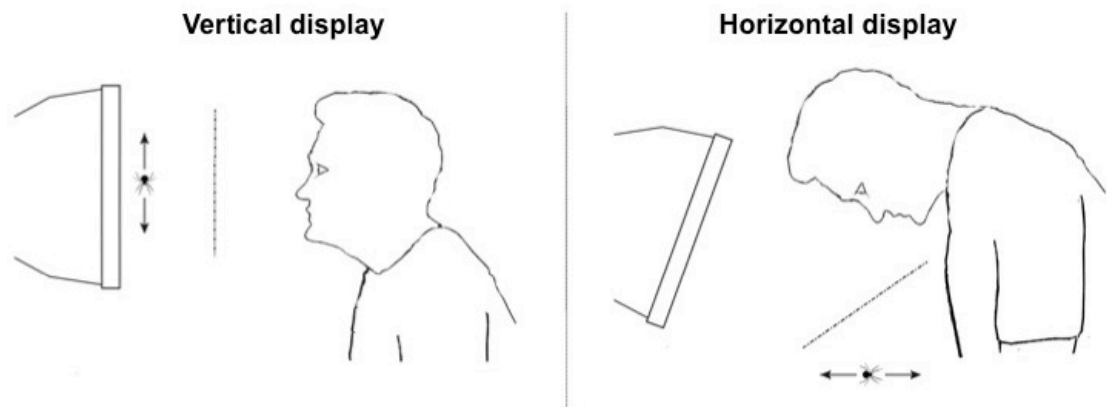


Figure 3.5. Experiment 2. Schematic diagram (not to scale) of display orientations used.

Dotted lines indicate positions of half-silvered mirrors. Arrows indicate visible trajectory of spider in each condition.

3.4.1.3 Stimuli and Procedure

Subjects saw one of two bird's-eye-view spider images (see Figure 3.6). One was the same clip art image used in the previous experiment (less scary), while the other was a photograph of a tarantula (more scary), modified slightly to appear more symmetrical about its vertical midline. Both spider images were square ($5.7^\circ \times 5.7^\circ$) and had transparent backgrounds, so that they appeared atop the neutral grey screen. Subjects began the session using one of the displays before switching to the other halfway through the main flash-lag task.

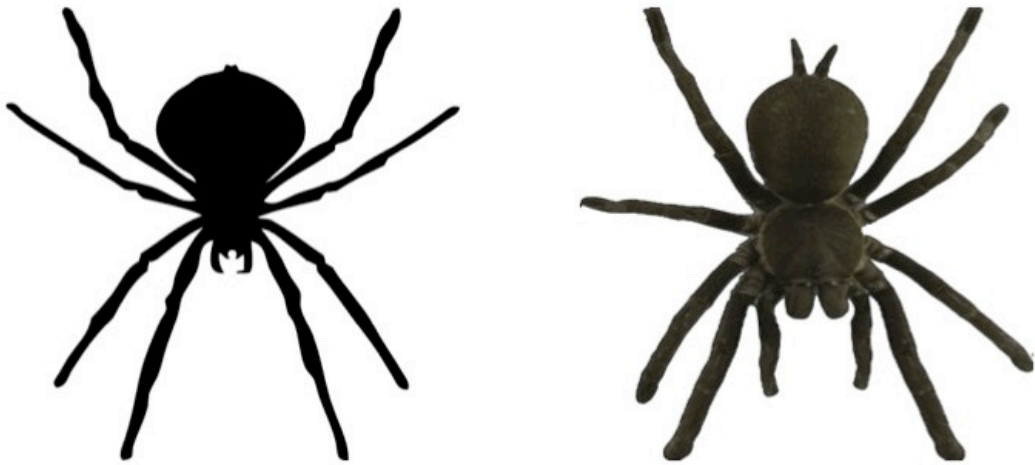


Figure 3.6. Experiment 2. Less scary (left) and more scary (right) spider images.

Alignment task. Using the first display orientation, subjects first performed a task in which they manually aligned the spider image they were to see in the flash-lag task between two horizontal lines. A fixation cross was presented with its centre 9.97° left of the display's vertical meridian, and vertically aligned with the display's horizontal meridian. Two lines ($5.7^\circ \times 0.5^\circ$) were aligned horizontally with the vertical meridian of the display, but separated vertically by 19.36° , and their overall vertical positioning was jittered so that the halfway point between them was somewhere between 2.24° below and 2.24° above the horizontal midline of the display. The two lines flashed for one frame (12ms) repeatedly, every 1 second. The spider image initially appeared with

its centre somewhere between 10.14° and 13.19° , either above or below physical alignment between the flashing lines. While fixating slightly to the left of the spider's vertical path, subjects took as much time as they needed to move the spider image so that it appeared equidistant between the two repeatedly flashing lines, using the keyboard's up and down keys. When subjective alignment was achieved subjects pressed the space key to complete the trial. Three upward-facing and 3 downward-facing trials were performed in alternation, with the first trial type (up or down) counterbalanced across subjects. The mean upwards-facing and mean downwards-facing value was calculated for each subject and these offsets from equidistance were used in the following flash-lag task in place of actual physical alignment. This task allowed subject-by-subject calibration of the stimulus positioning so that the flash-lag effect could be distinguished from subjective alignment without motion.

Flash-lag task. Flash-lag effects were measured using stimuli similar to those in the alignment task. At the beginning of each trial the same forwards-facing spider image moved onto the display from the edge and translated either upwards or downwards at $21.67^{\circ}/s$, for approximately 2000ms, before disappearing off the opposite edge of the display (see Figure 3.7). While the spider was moving, the same two lines used in the alignment task were flashed for one frame (12ms). The midpoint between the lines was jittered between three vertical positions, so that it could be either aligned with, or either 1.79° above or below the display's horizontal meridian. This was to make the position of the flashes unpredictable so that subjects could not simply judge the spider's location relative to fixation. The lines were presented when the spider reached one of 7 positions between them. The equidistance value was taken from the result of each subject's alignment task. In terms of milliseconds-from-equidistance, the offsets of the spider between the lines were -100ms, -50ms, 0ms, 50ms, 100ms, 150ms, and 200ms. Once the spider had disappeared off screen the subject was able to press the up or down key (binary choice) depending on whether they thought the line nearer to the top or bottom of the screen had been closer to the spider, respectively, at the time that they had flashed. After completing the first half of the flash-lag task on the first display orientation, subjects were moved to the second display for the rest of the session. Spider offset and motion direction were randomised across all trials performed on each display. Display orientation order (i.e., vertical then horizontal or horizontal then vertical) was counterbalanced across spider image and phobia level groups. Each subject performed a

total of 588 trials (2 display orientations \times 2 motion directions \times 7 spider offsets \times 3 jittered flash positions \times 7 repetitions of each spider offset at each flash position).

As in the previous experiment, cumulative normal functions were fit to the data from each condition for each subject using the Palamedes Toolbox for Matlab (Prins & Kingdom, 2009) and PSEs and confidence intervals were estimated using a bootstrap procedure with 2000 iterations. In this experiment, PSEs corresponded to the position of the spider image between the flashes that would receive 50% ‘ahead-of-equidistance’ and 50% ‘behind-equidistance’ responses. In this case, then, a PSE of 50ms would indicate that the spider image would have to be 50ms of animation progress behind the point of equidistance between the flashes in order to be perceived as equidistant. See Figure 3.8 for psychometric curves from a single representative subject.

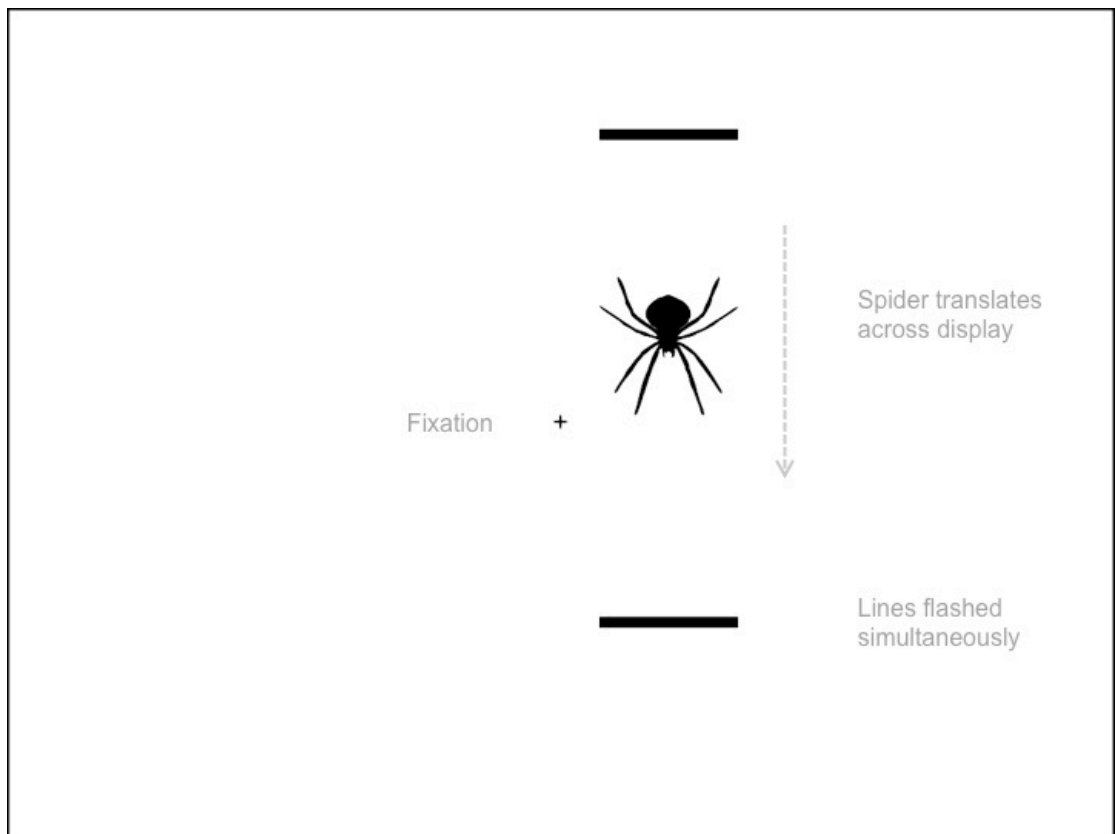


Figure 3.7. Experiment 2: Example of stimuli used. Only objects in black were shown. In this example the spider image is behind the point of equidistance between the flashes.

Fear of Spiders Questionnaire task. Continuing on the second display orientation, subjects performed the same Fear of Spiders Questionnaire (Szymanski & O'Donohue, 1995) task used in the previous experiment, but with only the 18 spider-related items. As before, subjects with a phobia score above the median were defined as “high-phobia”, and those with a score below the median were defined as “low-phobia”. An independent samples t-test confirmed that high-phobia subjects produced significantly higher spider-phobia scores ($M = 0.62$, $SD = 0.82$) than low-phobia subjects ($M = -2.1$, $SD = 0.58$), $t(78) = 17.23$, $p < .001$, $d = 3.91$.

Spider image relative scariness task. Subjects who performed the main experiment with the more scary spider were given a final additional task, in which they had to give a scariness rating for each of the spider images. The two $5.7^\circ \times 5.7^\circ$ spider images were presented side-by-side (less scary on the left, more scary on the right; 17.23° between their nearest edges) above a 7-point Likert scale, ranging from -3 (“Not scary at all”) to +3 (“Very scary”). A circle was initially presented surrounding the less scary spider on the left, with the question “How scary is this spider?” displayed above it. Once the subject had given a scariness rating for that spider, the more scary spider on the right was similarly highlighted, and a separate response was given. A 2×2 mixed-design ANOVA was performed on the scariness ratings for the two spider images, with phobia level (high or low) as a between-subjects factor, and spider image (more- or less scary) as a within-subjects factor. As expected, there was a main effect of phobia level, $F(1, 38) = 14.93$, $p < .001$, $\eta_p^2 = .282$, with high-phobia subjects finding both images scarier than low-phobia subjects. There was also a main effect of spider image, $F(1, 38) = 68.79$, $p < .001$, $\eta_p^2 = .644$, with the more scary spider appearing scarier to everyone. The two factors did not interact.

3.4.2 Results

Alignment task results. To investigate whether the display orientation or spider image used for the alignment task affected the alignments subjects made, a $2 \times 2 \times 2 \times 2$ mixed-design ANOVA was performed. Alignment task display orientation (horizontal or vertical), phobia level (high or low), and spider image (more or less scary) were

between-subjects factors, and alignment task direction (upwards or downwards) was a within-subjects factor. The means and standard deviations for each condition are shown in Table 4 below. This analysis revealed a significant main effect of alignment task display orientation, $F(1, 72) = 11.48, p = .001, \eta_p^2 = .138$, with subjects performing the horizontal alignment task producing estimates that were biased more towards the top of the display than those who performed the vertical alignment task. There was no effect of phobia level, spider image, or alignment task direction, and no interactions between any factors or combinations thereof. The main effect of alignment task display orientation implies that there was a general bias for subjects to perceive the spider closer to them by an average of 0.33° (2mm) when performing the horizontal rather than the vertical alignment task. Since these alignments were used to set the zero-offset position in the subsequent flash-lag task, this could have had a knock-on effect among subjects who performed the horizontal alignment task of enhancing flash-lag for upwards motion and reducing it for downwards motion. It should be noted, though, that this is a relatively small effect, translating to the distance travelled by the spider in approximately one 12ms frame in the flash-lag task. This finding will be readdressed in the flash-lag results section. Overall, excepting the main effect of alignment display orientation, this collection of results suggests that the subjective alignments made were not a function of either the direction the spider faced, or more notably, the subject's phobia level. This last point was corroborated by the lack of a correlation between spider-phobia score and the alignment made in either direction, either among all subjects, or when the data from those who performed each of the alignment tasks were analysed separately.

Table 3.3.

Experiment 2: Offset from alignment with horizontal meridian of display (mm) in each condition of the alignment task.

Alignment task display orientation	Phobia level	Spider image	Alignment task direction	Mean	SD
Horizontal	High	More scary	Upwards	4.9	11.95
			Downwards	9.1	14.3
		Less scary	Upwards	7.2	9.37
			Downwards	6.3	10.34
	Low	More scary	Upwards	6.7	11.85
			Downwards	9.8	14.62
		Less scary	Upwards	5.7	14.45
			Downwards	10.3	11.06
Vertical	High	More scary	Upwards	-3.1	8.7
			Downwards	1.9	12.27
		Less scary	Upwards	4.3	8.55
			Downwards	3.1	20.93
	Low	More scary	Upwards	-3.5	6.04
			Downwards	4.5	17.53
		Less scary	Upwards	-2.1	7.36
			Downwards	-3.5	13.53

Note. A positive offset from alignment represents a bias towards the top of the display

Flash-lag results: Correlations across all subjects. Phobia score did not correlate with the difference between the horizontal display flash-lag anisotropy and the vertical display flash-lag anisotropy, either overall, $r = .143$, $p = .206$, or when the data from the more scary, $r = .126$, $p = .438$, and less scary, $r = .161$, $p = .322$, spider images were examined separately. This is contrary to claim (1), which predicted a larger anisotropy on the horizontal display compared to the vertical display among subjects of higher phobia level.

Furthermore, there was no correlation between phobia score and the difference between downwards motion on the two displays, $r = .068$, $p = .546$, or upwards motion on the two displays, $r = -.151$, $p = .181$. These results were the same when the data from the more scary, (downwards difference, $r = .006$, $p = .972$; upwards difference, $r = -.168$, $p = .3$), and less scary (downwards difference, $r = .123$, $p = .448$; upwards difference, $r = -.146$, $p = .368$) spider images were analysed individually. According to claim (3), downwards motion should have produced a larger effect on the horizontal display than on the vertical display in subjects high in spider-phobia.

Flash-lag results: ANOVA with high- and low-phobia groups. A $2 \times 2 \times 2 \times 2$ mixed measures ANOVA was performed, with display orientation (horizontal or vertical) and retinal direction (up or down) as within-subjects factors, and phobia level (high or low) and spider image (more or less scary) as between-subjects factors. There was a main effect of retinal motion direction, $F(1, 76) = 13.6$, $p < .001$, $\eta_p^2 = .152$, with downwards motion producing larger flash-lag effects. This implies that the aforementioned bias in the alignment task among those who performed it on the horizontal display is unlikely to have had a major effect, since the highly significant difference in flash-lag effects is in the opposite direction to that expected. There was a significant main effect of spider image, $F(1, 76) = 5.61$, $p = .02$, $\eta_p^2 = .069$, with the more scary spider producing larger flash-lags than the less scary spider. There was also a significant interaction between phobia level and spider image, $F(1, 76) = 7.42$, $p = .008$, $\eta_p^2 = .089$, indicating that the main effect of spider image was entirely the result of differences exhibited by the high-phobia group. More specifically, the more scary spider image produced much larger flash-lags than the less scary spider, but only for the high-phobia group. To follow up this interaction the data were collapsed across display orientation and motion direction, so that there were four flash-lag observations from each subject. Separate independent samples t-tests were used to compare the complete sets of observations from the high- and low-phobia subjects for each spider image. These revealed that, compared to the low-phobia subjects, the high-phobia subjects produced significantly smaller flash-lags ($M_{\text{high-phobia}} = 17.55\text{ms}$, $SD = 57.78$; $M_{\text{low-phobia}} = 42.3\text{ms}$, $SD = 57.12$) with the less scary spider, $t(158) = 2.73$, $p = .007$, $d = 0.431$, and significantly larger flash-lags ($M_{\text{high-phobia}} = 66.16\text{ms}$, $SD = 48.02$; $M_{\text{low-phobia}} = 38.92\text{ms}$, $SD = 59.26$) with the more scary spider, $t(158) = 3.19$, $p = .002$, $d = 0.508$. Both findings remained significant with a Bonferroni-corrected α -level of 0.025.

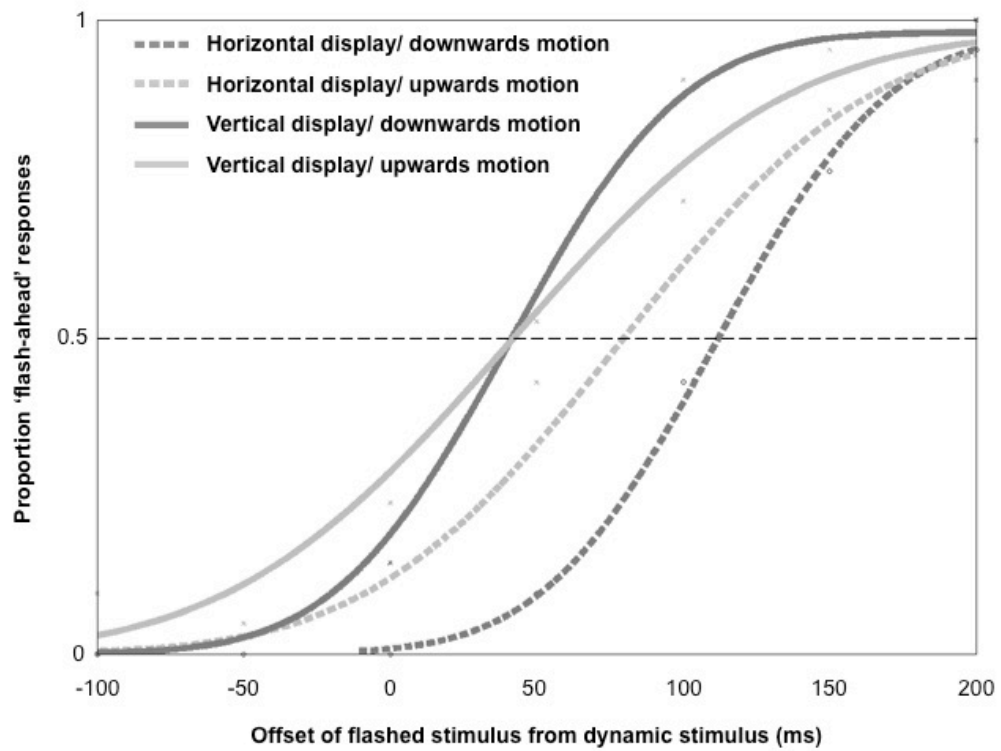


Figure 3.8. Experiment 2: Psychometric curves from a representative subject. Negative offsets represent flash positions in which the spider image was ahead of the point of equidistance.

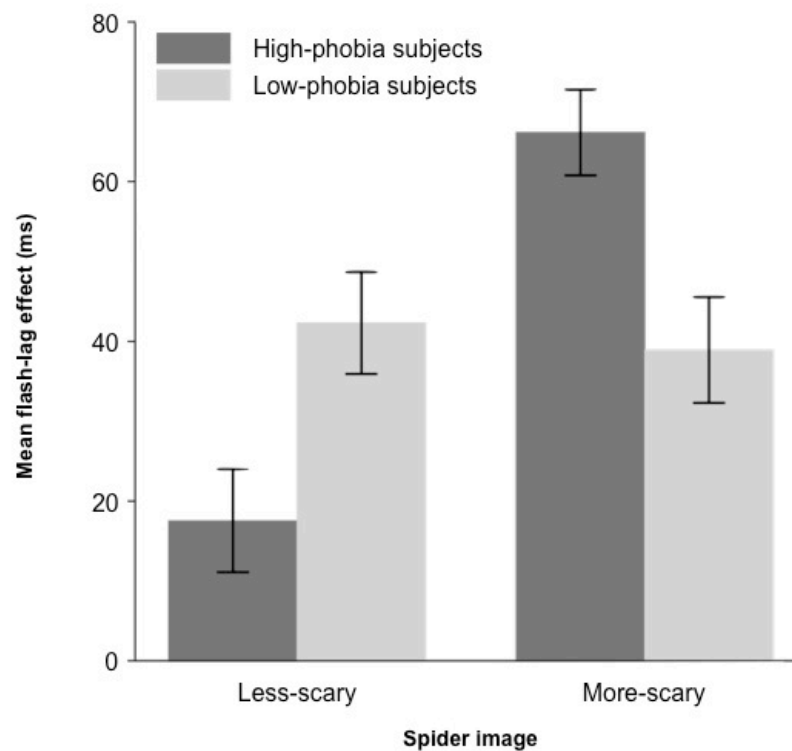


Figure 3.9. Experiment 2: Mean flash-lag effects from high- and low-phobia subjects for less- and more scary spider images, collapsed across display orientation and motion direction. Error bars indicate ± 1 standard error.

3.4.3 Discussion

The present results show that the flash-lag effect can be modulated by threat. Whether a moving spider image was more or less scary had little effect upon the flash-lags of low-phobia subjects, but among high-phobia subjects the scarier spider led to far greater flash-lags than the less scary spider (see Figure 3.9). These findings were only apparent in the ANOVA and not in the correlations because the latter looked at flash-lag differences between particular conditions, for example, whether horizontal downwards PSE - vertical downwards PSE correlated with phobia score. This method was intended to test the specific predictions from paternalistic vision that threatening objects are perceived be closer or to move faster towards oneself. However, the present ANOVA

results reveal a different picture; that flash-lag is simply enhanced as a function of threat, irrespective of motion direction relative to one's body.

Claim (1), that threatening objects are perceived closer to us, is not supported by these data. If this were the case, threatened subjects should have perceived the moving stimulus further down the horizontal display, closer to them, regardless of motion direction. This would have shown up in the horizontal display conditions of high-phobia subjects as a relatively augmented downwards motion flash-lag, and a relatively diminished upwards motion flash-lag, and especially so for the more scary spider image. Instead, it was found that downwards motion produced a larger flash-lag effect regardless of the display orientation, the subject's phobia level, or the scariness of the spider image. This effect is likely to be the result of retinal motion direction, something that has previously been shown to mediate flash-lag magnitude (e.g., Brenner, van Beers, Rotman, & Smeets, 2006; Kanai et al., 2004; Mateeff & Hohnsbein, 1988; Mateeff et al., 1991; Shi & Nijhawan, 2008). However, while previous studies have focused on how flash-lag is larger for motion towards, rather than away from fixation, the present findings additionally suggest that downwards retinal motion produces a larger effect than upwards retinal motion. The phenomenon of representational momentum, which exhibits numerous parallels with flash-lag (Hubbard, 2013; Munger & Owens, 2004), is also greater for downwards than upwards motion, and it has been suggested that this is because the visual system has an internalised model of the way that gravity acts upon real-world objects (De Sá Teixeira & Hecht, 2014; Hubbard & Bharucha, 1988; Hubbard, 1990, 2001). Under this interpretation then, it would be claimed that flash-lag is greater for downwards retinal motion because an object moving downwards on the retina is more likely to continue in that direction because downwards momentum works in conjunction with gravity, rather than against it.

There may still be scope however for the idea that we perceive threatening objects to be closer to us. Consider that the present findings support the basic premise that threat can influence low-level visual perception, and imply therefore that higher cognitive confounds may not explain all of the findings in the paternalistic vision literature. Given that this is the case, one may argue that the present results are not entirely contrary to claim (1), since static objects and objects in motion might be subject to different perceptual biases. For instance, when threatening objects are stationary there might be a

bias to perceive them closer to us, but when they are in motion another bias may dominate, so that threatening stimuli are seen further along their trajectory.

Claim (3), that we perceived threatening stimuli to move faster towards us, finds some support from these findings. It was reasoned that if claim (3) were true, threatening objects should produce a larger flash-lag under the appropriate motion conditions, since the flash-lag effect increases with the velocity of the moving target. Given that in this experiment threat augmented the flash-lag effect in general, it is possible that moving objects were perceived to move faster by those who felt threatened by them, regardless of direction. This is consistent with the conclusions of Witt and Sugovic (2013), though they only took velocity estimates for motion towards the subject, whereas our findings might imply that a threatening object moving away is also perceived to have a higher velocity.

Why then, did this experiment reveal an effect of threat, when the previous one did not? As highlighted earlier, there were several potential issues with the previous stimuli that were not present in the current investigation. Firstly, ceiling effects may have been avoided by using linear translation, thereby allowing higher-end differences to manifest. Also, the present experiment used flashed lines, rather than flashed versions of the moving stimuli, thereby removing the possibility that effects were cancelled out because both stimuli were perceived with the same bias. Presenting images of different threat levels as a between-subjects manipulation may also have meant that even when the moving stimulus was relatively peripheral, subjects could identify it.

An additional possibility is that the greater power provided by the larger sample size in Experiment 2 meant that it was able to reveal an effect that Experiment 1 was not. It should also be acknowledged, though, that the larger sample size may also have led to a Type 1 error; that is, the significant results might not reflect actual, real-world differences. This may be considered unlikely though, given the ample effect sizes (Cohen, 1988) accompanying the statistical significance.

It is not clear why the effects of phobia level differed between the two spider images. Why, for instance, did high-phobia subjects produce smaller flash-lags than low-phobia subjects with the less scary spider, but greater flash-lags than the low-phobia group with

the more scary spider? It could be that the high-phobia subjects realised that the less scary stimulus (a monotone clip art spider) was so evidently not real that they were able to overcompensate in their responding for what would otherwise be an enhanced flash-lag. The more realistic, more scary spider, on the other hand, may have been too threatening to permit such a compensation. This is of course entirely speculative, and post-hoc, and it is an open question why the flash-lags for the less scary spider should be smaller for the high- than the low-phobia group.

3.5 General Discussion

Two experiments have been reported. The first showed no evidence that threat modulated the flash-lag effect, while the second ironed out several issues present in the first, and revealed that threat augmented the flash-lag effect, irrespective of the direction of motion relative to the observer. This evidence suggests, therefore, that visuospatial perception can indeed be affected by threat – a core requirement of the paternalistic vision hypothesis. As mentioned in the introduction, several researchers have claimed that many apparently ‘perceptual’ findings used to support paternalistic vision could actually reflect the workings of cognitive factors. It was further argued that this criticism could be applied to much of the research used to claim that threatening stimuli are perceived as closer, larger, and faster. To the extent that the flash-lag effect reflects visual perception, then, these findings provide general support for the idea that visuospatial perception itself can be influenced by threat. This said, evidence that threatening objects are perceived as closer or larger was not found, though our data are consistent with the possibility that they appear to move faster.

3.5.1 Theories of the flash-lag effect

The flash-lag effect was not augmented or diminished depending on the direction of motion, but was modulated on the basis of how threatening the moving stimulus was to

the observer. While these results do not explicitly arbitrate between different explanations for the flash-lag effect, it will be useful now to consider some of those accounts in order to help elucidate the nature of the effect reported herein.

One theory for the occurrence of the flash-lag effect is that our visual systems compensate for neural transmission delays by extrapolating the positions of moving objects so that their perceived positions more closely approximate their real positions (Nijhawan, 1994, 2008). Without such a prediction, it is reasoned that the perceived positions of rapidly moving objects would trail behind their real positions to an extent that would render interaction with them problematic. According to this account, the prior trajectory of the moving object allows an extrapolation of its future position, which means that its retinotopic cortical representation does not lag behind its retinal location. We see a spatial separation, then, because the unpredictable flash reaches perception later, after a delay of approximately 100ms. While this explanation initially appealed to early visual mechanisms (e.g., Berry, Brivanlou, Jordan, & Meister, 1999), later reasoning has argued that compensation for the delays of moving objects may occur at multiple levels of the nervous system (Nijhawan et al., 2004; Nijhawan, 2008). Shi and Nijhawan (2008) furthermore argued that flash-lag motion direction anisotropies relative to the fovea are a sign of the visual system's sensitivity to the behavioural significance of stimuli. From this perspective, the mechanisms of visual prediction might further extrapolate the positions of threatening objects to err on the side of caution, because they are more behaviourally significant. It is perhaps safer to for the observer to perceive a scary-looking moving spider as having travelled slightly further than it actually has. If this occurred prior to the integration of body position signals, it would explain the lack of a difference between motion towards and away from the body. This interpretation would be consistent with the claims of the paternalistic vision literature pertaining to threat. These suggest that we perceive threatening or potentially dangerous things in ways that promote behavioural responses that safeguard us from harm (e.g., Cole et al., 2013; Teachman et al., 2008; Vagnoni et al., 2012; Witt & Sugovic, 2013).

Movement of attention has also been invoked to explain the flash-lag effect. Baldo and Klein (1995) firstly suggested that the flashed stimulus draws attention away from the moving stimulus, which moves some distance in the time it takes to shift attention and

make a perceptual comparison – thereby resulting in a misalignment. It was further highlighted that focusing attention on the moving object would reduce its perceptual latency, thus making it appear advanced beyond the relatively delayed flash. While later evidence has indicated that attentional processes do not cause the flash-lag effect (e.g., Khurana & Nijhawan, 1995; Khurana, Watanabe, & Nijhawan, 2000), it is still acknowledged as a modulatory factor (Baldo et al., 2002; Baldo & Klein, 2010; Namba & Baldo, 2004). In light of this position it is interesting to note that it takes longer to disengage attention from a threatening stimulus (Fox, Russo, Bowles, & Dutton, 2001; Fox, Russo, & Dutton, 2002; Georgiou et al., 2005). Given that the attentional shift account of flash-lag suggests that the effect is proportional to the time taken to shift attention from the moving to the flashed stimulus, a tendency for attention to linger on the threatening stimulus would increase the effect. Furthermore, it could be that a more acute focus of attention upon the threatening stimulus reduces its perceptual latency beyond that of the less threatening stimulus, allowing it to reach perception even earlier before the flash. This interpretation overlaps with that which follows from another explanation of the flash-lag effect: that of differential latencies for moving and flashed stimuli. The idea here is simply that moving stimuli are perceived with a lower latency than flashed stimuli, without invoking a role for attention (Purushothaman et al., 1998; Whitney, Murakami, et al., 2000; Whitney & Murakami, 1998). It could also be, then, that perceptual latencies for threatening stimuli are lower than those for non-threatening stimuli, without a mediating effect of attention.

Several other theories of flash-lag have at their heart the notion that the visual system must integrate position signals over time in order to generate a motion percept. While disagreeing on when the integration window begins and ends, these theories propose that flash-lag occurs because the average position of the moving object during this time period is beyond the position of the stationary flash (Eagleman & Sejnowski, 2000a, 2007; Krekelberg & Lappe, 1999, 2000a, 2000b; Lappe & Krekelberg, 1998). These theories would ascribe a larger flash-lag to a longer temporal integration window, such that the average position of the moving object was perceived even further beyond the flash. However, it is unclear why such a low-level attribute should be affected by threat in the way demonstrated in the current study.

3.5.2 Neuroanatomical pathways

A further consideration of interest in explaining how threat could enhance the flash-lag effect lies in the neuroanatomical pathways that could underpin such an interaction between emotion and vision. It has been shown, for instance, that projections from the amygdala to the visual cortex facilitate the recognition of emotional facial expressions (e.g., Morris et al., 1998; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). While these findings mostly demonstrate functional connections between the amygdala and the ventral visual stream, there is also anatomical evidence of projections from the amygdala to dorsal areas (Amaral, Behniea, & Kelly, 2003) responsible for processing information relevant to spatial relationships and action (Goodale & Milner, 1992). It is also worth noting that the flash-lag effect is modulated by activity in area V5/hMT+ (Maus, Ward, Nijhawan, & Whitney, 2013), which has separately been shown to interact with the amygdala in processing simultaneous motion and emotion (Hindi Attar, Müller, Andersen, Büchel, & Rose, 2010). An influence of amygdala activity upon the dorsal visual stream or V5/hMT+ could potentially underlie the threat-enhanced flash-lag effects observed herein.

3.5.3 Limitations and future directions

Attention was drawn earlier to some of the advantages of Experiment 2 over Experiment 1 in an effort to explain why it exhibited an effect of threat that was not initially apparent. Consideration will now be given to the limitations common to both experiments, and some directions for future research will be suggested in light of these.

Two of the main arguments put forward to explain where paternalistic visual effects might come from, if not perception, are that either task demands (e.g., Durgin et al., 2009; Firestone & Scholl, 2014) or memory (e.g., Cooper et al., 2012) are behind the biases. The flash-lag effect involves a relative position judgment of two stimuli presented simultaneously, so it is unlikely that memory, or associated mental imagery, are able to explain the current findings. What about task demands, though? Critics of the paternalistic vision literature contend, with experimental support, that subjects might

often guess the experimenters' hypotheses, and then produce responses in accordance with that expectation (Durgin et al., 2009; Firestone & Scholl, 2014; Firestone, 2013a; Russell & Durgin, 2008). It is possible that the experiments reported herein may too have suffered from this problem. Subjects in both experiments were recruited with the knowledge that the experimenter sought people with a range of levels of spider-phobia, which may, in conjunction with the methods, have indicated to them something about the purpose of the experiment. That said, judgments were not explicitly in reference to one's body, as was the case in previous experiments (e.g., Cole et al., 2013; Vagnoni et al., 2012). Had the subjects been required to judge, for example, the positions of spiders relative to themselves, it would have perhaps been more suggestive of the underlying hypotheses, e.g., that high-fear people underestimate the distance to scary objects. Future experiments may go some way to avoiding this possibility by not mentioning anything about, for example, spiders, prior to the experimental session.

As discussed, a possible issue with these experiments that keeps in play the potential for threatening objects to be perceived closer to us is that threatening objects in motion may be subject to different biases than static threatening objects. This could perhaps be investigated with a static version of the second experiment, in which the position of a stationary, continuously visible spider is judged relative to lines flashed above and below it on the display. If threatening stimuli are perceived closer to us, high-phobia subjects should estimate that the spider is closer to the lower line when the display is horizontal, compared to when it is vertical, and more so than low-phobia subjects.

To measure the flash-lag effect one must perform a number of trials with the same moving and flashed stimuli. It is possible that repeated exposure to the threatening stimulus might have meant that subjects became desensitised to the threat, or gained an implicit understanding that the stimulus was not to be feared. In fact, these very outcomes are some of the principal aims of exposure therapy for treating emotional and anxiety disorders (Richard & Lauterbach, 2007). Such an effect may have abolished the influence of threat on the flash-lag effect in the first experiment, and reduced it in the second. Such effects could perhaps be alleviated by using an adaptive measure of flash-lag (e.g., Nijhawan, 1994) to reduce the required number of trials. In addition, only subjects with either very high, or very low phobia levels could be tested in an effort to enhance between-group differences. The potential for over-exposure is however a

notable limit of the flash-lag method for investigating the effects of threat. Vagnoni et al. (2012), on the other hand, who measured time-to-collision, were able to present each of their threatening and non-threatening images only once, thus avoiding the potential for exposure effects to reduce the influence of threat.

Finally, and very briefly, it should be highlighted that while spiders are frequently a source of threat, evidence that other commonly feared objects (e.g., needles, or snakes) can have a similar effect on flash-lag magnitude would greatly strengthen the findings reported.

3.6 Conclusions

It was argued in the introduction that many experiments in the paternalistic vision literature likely suffer from possible confounding effects of cognition, such as task demands, memory, and mental imagery. The first experiment – with looming and receding spider and butterfly images – appeared supportive of this contention, since the flash-lag effect, an unequivocally perceptual illusion, was not modulated by threat. The second experiment used an alternative method, however, in which separate groups of high- and low-phobia subjects saw either a more or a less scary spider image that either moved up or down, or towards or away from them. This, it was argued, controlled for some of the potential issues with the first experiment. It was found that flash-lag effect was in general boosted when the moving stimulus was threatening to the observer. This strongly supports a basic premise of paternalistic vision – that visuospatial perception is sensitive to our behavioural needs. However, no evidence was found for the specific claims that threatening stimuli are perceived as closer, or larger, though the findings are consistent with the possibility that threatening objects are seen to move faster, regardless of the direction relative to the observer. These findings imply, therefore, that the paternalistic vision hypothesis need not be considered groundless, and that many of the findings that appear susceptible to cognitive influence, may not actually reflect it.

Paper III: Additive and subtractive effects of gamma movement on the forward displacement of size-changing stimuli

4.1 Abstract

Previous findings show that expanding or contracting stimuli that abruptly disappear are perceptually displaced in the direction of size-change, so that their final size appears larger or smaller, respectively. Experiments reported here make use of the flash-lag effect and related illusions to demonstrate that this forward displacement is greater for contracting stimuli than expanding stimuli, but only when the size-changing stimulus disappears at the moment of perceptual comparison. The aforementioned directional anisotropy is shown to be present when size-changing stimuli are compared to references that disappear at (Experiments 1 & 2) or continue after (Experiment 3) their offset. It is then shown that when the size-changing stimulus continues after the disappearance of the reference, the difference in effects between directions is abolished (Experiment 5). The findings are explained in terms of the apparent contraction (gamma movement) of abruptly disappearing stimuli. More specifically, it is suggested that at the moment of disappearance, the formerly expanding or contracting objects undergo a rapid perceptual contraction, which augments the forward displacement of contracting stimuli and diminishes it for expanding stimuli. Finally, a novel account of gamma motion is given that suggests we perceive abrupt disappearance as contraction because objects in the environment do not frequently instantaneously vanish. Rather, their retinal images tend to contract before going out of sight.

4.2 Introduction

A crucial task of the visual system is to accurately localise the positions of moving objects in space. Numerous illusions reveal that when something is in motion its percept is biased forwards along its trajectory, relative to its real position or to other stimuli (for reviews, see Nishida, 2011; Whitney, 2002). Of particular interest here is that the final size of an expanding or contracting object that suddenly disappears is misperceived in the direction of size change (Whitaker et al., 1999). It is shown further on in a series of experiments that this forward displacement is greater for contracting than for expanding stimuli when the dynamic stimulus disappears at the moment of perceptual comparison. However, before reporting the current findings in detail it will be helpful to briefly recap some of the prominent literature on forward displacements.

Ramachandran and Anstis (1990) showed subjects displays with square arrays of 4 square windows. Behind each window was a field of horizontally translating random dots. When the dots in the upper windows moved towards the middle of the display and the dots in the lower windows moved away from the middle of the display, the upper windows were perceived closer together than the lower windows. Similarly, De Valois and De Valois (1991) found that when gratings moved in opposite directions within two adjacent, aligned windows, the windows themselves were perceived as misaligned, each biased in the direction of the motion they contained. If a moving pattern is seen through a window, then, the shape of the window itself is perceived as shifted in the same direction. Explanations for this motion-induced position shift are debated, with accounts appealing to, for example, forward shifts of visual cortical receptive fields (Fu, Shen, Gao, & Dan, 2004), and contrast enhancement at the leading edges of moving stimuli (Arnold, Thompson, & Johnston, 2007).

Comparably, the final position of a sequence of progressively displaced shapes is biased in the direction of apparent motion (*representational momentum*; Freyd & Finke, 1984; Hubbard & Bharucha, 1988; Kelly & Freyd, 1987). In a particularly influential experiment, Freyd and Finke (1984) showed subjects a sequence of three snapshots of a progressively rotated rectangle separated by brief intervals. A fourth rectangle was then shown – its orientation consistent with either a continuation or a reversal of rotation.

Subjects were more likely to judge the fourth rectangle as being the same as the third when it was oriented further in the direction of implied rotation. This effect was also found to occur with smooth linear translation (rather than discrete rotations), and furthermore, that it was greater for downwards than for upwards motion (Hubbard & Bharucha, 1988). A wealth of findings has since led to the claim that high-level internalisations of simple physical properties, such as momentum and gravity, are responsible for the bias (for reviews, see Hubbard, 1995, 2005).

In addition to motion endpoints, it has been shown that smoothly moving stimuli are biased forwards in perception both at the start of motion (Fröhlich, 1923; Kirschfeld & Kammer, 1999), and relative to other stimuli presented during motion (Nijhawan, 1994). The latter example here has been termed the flash-lag effect, and is exemplified by the perceived spatial advance of a moving stimulus beyond a briefly aligned flash. While it was initially thought that flash-lag did not occur when the flash occurred in synchrony with the disappearance of the moving stimulus (*flash-terminated condition*, or *FTC*; Eagleman & Sejnowski, 2000; Whitney, Murakami, & Cavanagh, 2000), it has subsequently been shown that a flash-lag can be elicited in the FTC, for example, when the stimuli are at a considerable eccentricity (Kanai et al., 2004). Forward displacements of moving stimuli endpoints have also been observed without flashed comparisons when the moving stimuli are blurred (Fu, Shen & Dan, 2001), or when their offset is made less perceptually abrupt, for example, by fading out instead of instantaneously disappearing (Maus & Nijhawan, 2006; 2008; 2009; Shi & Nijhawan, 2012).

We shift focus now to an assortment of findings that show that expanding and contracting stimuli are misperceived as shifted in the direction of their size change. For instance, it was recently shown that the flash-lag effect occurs in expanding and contracting lines (Kafaligönül et al., 2010). Subjects fixated centrally while a vertical line (with one of its ends fixed at the horizontal meridian) expanded or contracted on one side of the screen. Another line on the opposing side flashed briefly during the first line's ongoing motion. When the lines were the same size at the time of the flash, the size of the flash was perceived to lag behind that of the dynamic line. This effect was larger for expanding than contracting objects, which the authors suggested was consistent with the finding that flash-lag is larger for approaching than receding stimuli (e.g., Harris, Duke, & Kopinska, 2006).

Kelly and Freyd (1987) also found evidence of representational momentum with expanding and contracting stimuli. Squares either grew or shrunk in size over the course of three sequential inducer presentations, before a fourth probe-square was presented. Subjects judged whether the size of the fourth square was the same as or different to that of the remembered third square. They found that subjects tended to overestimate the size of the third square in ‘grow’ trials and underestimate it (though not significantly) in ‘shrink’ trials. The larger forward displacement in expanding motion is consistent with the aforementioned finding in expanding and contracting flash-lag (Kafaligönül et al., 2010).

Whitaker et al. (1999) similarly demonstrated that smoothly expanding and contracting stimuli are biased in their direction of size change at the moment of their disappearance. This was the case when the whole stimulus expanded or contracted, when it was just the internal texture (but not its window – akin to the motion-induced position shift), and when the movement was in the form of a motion aftereffect. However, of most interest here is their first experiment, in which subjects fixated between two radial Gabor patterns (6° centre-to-centre), one of which was static (reference) while the other was changing in size (dynamic). The reference stimulus was approximately 3.5° in diameter, while the dynamic stimulus either expanded from $0.5\times$, or contracted from $2\times$ its size. At some point, both stimuli disappeared and subjects had to decide whether the dynamic stimulus had been larger or smaller than the reference stimulus at the moment of their mutual disappearance. It was found that the size of the expanding stimulus was overestimated by 7.2%, while the size of the contracting stimulus was underestimated by 9.7%. So, inasmuch as there is a forward displacement of the size of the dynamic stimulus, this result is in accordance with the aforementioned findings from Kafaligönül et al. (2010) and Kelly and Freyd (1987). However, whereas the tendency in those studies was for a greater expanding than contracting effect, the bias here, to anticipate the present findings (see further on) appears to be in the opposite direction. It should be noted, though, that Whitaker et al. (1999) did not report a difference between the effect magnitudes in each direction.

Here experiments are reported showing that the forward displacement of contracting stimuli is greater than that of expanding stimuli, specifically when the size-changing stimulus disappears at the instant the observer has to make a perceptual judgment

(hereafter termed the *moment of comparison*). To begin, informal observations suggest that a flash-lag effect occurs for both expanding and contracting stimuli in the FTC, and that it is larger in the latter than it is in the former. The initial experiment is intended to formally test this possibility, and represents the first formal investigation of flash-lag in the FTC with expanding and contracting stimuli.

4.3 General Methods

4.3.1 Subjects

Subjects with normal or corrected-to-normal vision participated in exchange for money or course credits. All were naïve to the purpose of the experiments. Different groups of subjects were used in each experiment.

4.3.2 Apparatus

In all experiments subjects rested their chin on a support while viewing a 21” Sony Trinitron Multiscan E500 CRT monitor (85Hz refresh rate, 1400 x 1050 resolution) from a distance of 350mm. Stimuli were presented using custom Matlab scripts, running with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Responses were made using the left and right keys on an Apple USB keyboard.

4.3.3 Stimuli and Procedure

Stimuli were black on a neutral grey background. On each trial a dynamic stimulus was presented at 8° eccentricity, either to the left or right of fixation. A reference stimulus appeared at the same eccentricity in the opposite hemifield. In a binary choice paradigm, subjects were required to judge whether the left or right stimulus was longer (Experiments 1, 2, 3, & 5), more distantly spaced (Experiment 4a), or closer to the edge

of the display (Experiment 4b) at a *moment of comparison*. This moment was specified differently between experiments. Subjects responded by using the left or right hand to press the left or right keyboard key, respectively.

Excepting Experiment 4b (see Section 4.8.1), immediately following the first appearance of the dynamic stimulus, each of its ends either moved vertically away from, or towards the horizontal meridian at a constant rate of $3.65^\circ/\text{s}$. This meant that the separation between the ends of the stimulus changed at $7.3^\circ/\text{s}$. The animation proceeded for one of 5 randomly jittered durations (1386ms, 1468ms, 1550ms, 1632ms, or 1714ms) before the moment of comparison was signalled (see individual methods sections). This meant that the midpoint of the dynamic stimulus was always on the horizontal meridian of the display.

The length of the reference stimulus at the moment of comparison was varied between trials so that it was equal to one of 7 size offsets (based on pilot observations) from the instantaneous length of the dynamic stimulus. Excepting Experiments 4a, 4b, and 5 (see Sections 4.7.1, 4.8.1, and 4.9.1, respectively), the reference could range from 1.3° shorter (longer) than, to 2.6° longer (shorter) than the dynamic stimulus in expanding (contracting) motion, in 7 equal steps. The 7 size offsets used in each condition were equivalent to time offsets of -188ms, -94ms, 0ms, 94ms, 188ms, 282ms, and 376ms. So for instance, an offset of 376ms would mean that the reference line would have to continue for another 376ms into the future to achieve the same length as the reference stimulus. In this example therefore, the reference would be 376ms ‘longer’ than the instantaneous size of the dynamic stimulus in the expanding condition, and 376ms ‘shorter’ than it in the contracting condition. As the time offsets used were the same in both directions of size change these (rather than size offsets) will be referred to henceforth.

On each trial the side on which the dynamic line was presented was alternated in order to prevent a build-up of motion aftereffects. After 12 training trials, subjects performed a total of 560 experimental trials (2 directions of size change \times 2 hemifields \times 7 reference stimulus offsets \times 4 repetitions at each offset \times 5 moments of comparison) with a short break at the halfway point.

4.3.4 Data analysis

Raw data based on whether the left or right stimulus appeared larger or more widely spaced were converted into responses consistent with the reference stimulus appearing either ahead of or behind the dynamic stimulus. If the reference stimulus appeared smaller than the dynamic stimulus in a contracting trial, for instance, this would be converted to a ‘reference-ahead’ response. Psychometric curves were fit to individuals’ data using a cumulative normal function implemented in the Palamedes set of Matlab routines (Prins & Kingdom, 2009). Points of subjective equality (PSEs) and confidence intervals were estimated using a bootstrap procedure with 2000 iterations. All PSEs are expressed in milliseconds (ms) of lag of the reference behind the dynamic stimulus. See Figures 4.2, 4.6, and 4.9 for examples of psychometric curves from representative subjects in Experiments 1, 4a, and 5, respectively.

4.4 Experiment 1: Flash-terminated condition

4.4.1 Methods

Nine subjects (2 female) participated. The dynamic stimulus was a vertical line of constant width (0.41°) that changed in length from either 0° (expansion) or 22.64° (contraction) to reach either 10.52° , 11.15° , 11.78° , 12.41° , or 13.03° (depending on the jittered time measure; see General Methods) before the moment of comparison was signalled by a flashed reference line (single frame flash duration = 12ms). See Figure 4.1 for a diagram of the stimuli. Immediately following the flash, both stimuli disappeared simultaneously. The length of the reference line was randomly varied between 7 length offsets from the dynamic line at the moment of comparison (see Section 4.3.3). The subjects judged whether the line on the left or right of the screen was longer at the time of the flash.

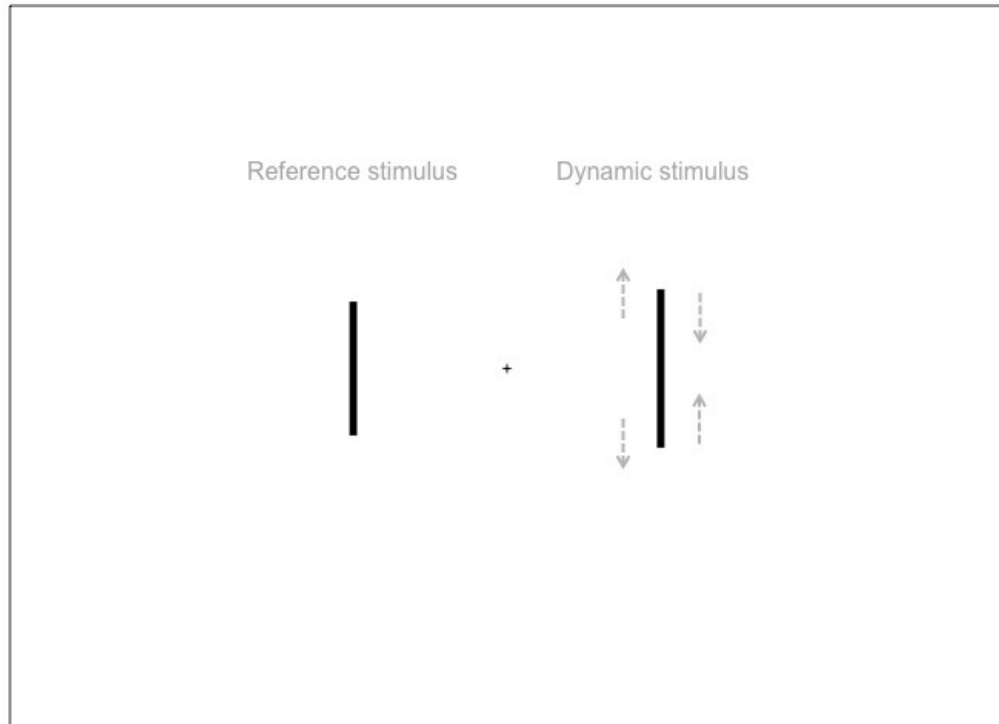


Figure 4.1. Example of line stimuli used in Experiments 1, 2, 3, and 5. Only objects displayed in black were visible during the experiments. Reference stimulus was either flashed or continuously visible (see individual methods sections).

4.4.2 Results

One-sample t-tests show that the mean PSEs for expanding [$M = 83.35\text{ms}$, $SD = 49.95$, $t(8) = 5.01$, $p = .001$, $d = 3.54$] and contracting [$M = 171.45\text{ms}$, $SD = 42.49$, $t(8) = 12.1$, $p < .001$, $d = 8.559$] motion were significantly different from zero, indicating a strong flash-lag effect in both directions. A paired samples t-test further reveals that the reference was perceived to lag behind the dynamic stimulus more so for contracting lines than it did for expanding lines, $t(8) = 3.87$, $p = .005$, $d = 1.293$. Figure 4.3 shows plots of the mean flash-lag effects in each direction.

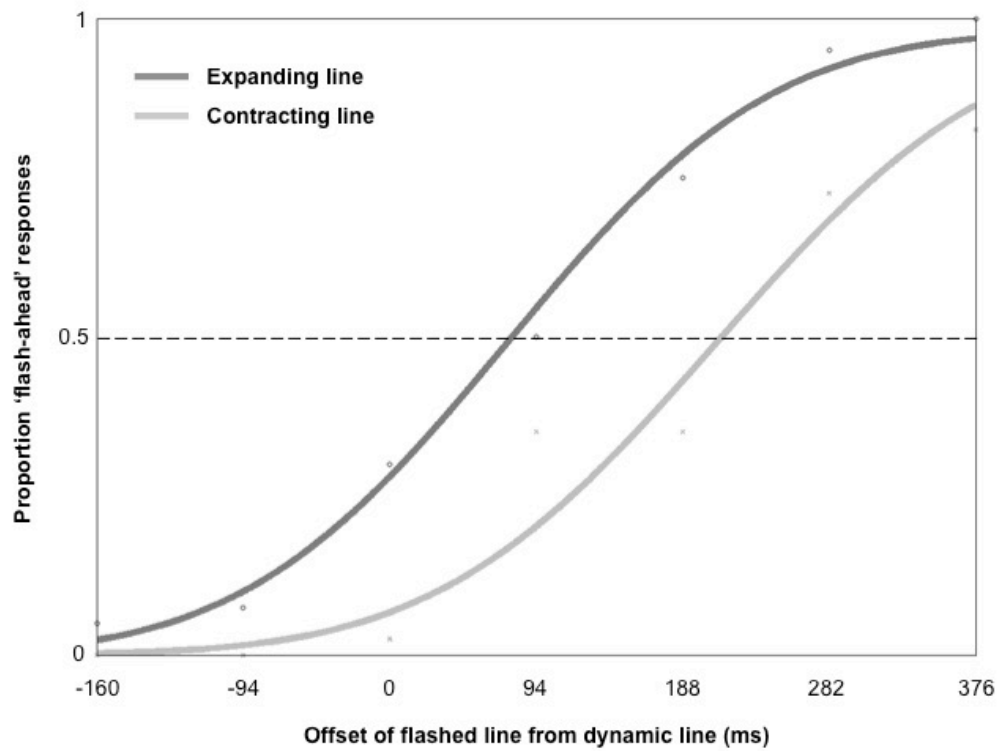


Figure 4.2. Experiment 1: Psychometric curves from a representative subject. Negative offsets represent flashed stimuli that physically lagged the instantaneous size of the dynamic stimuli.

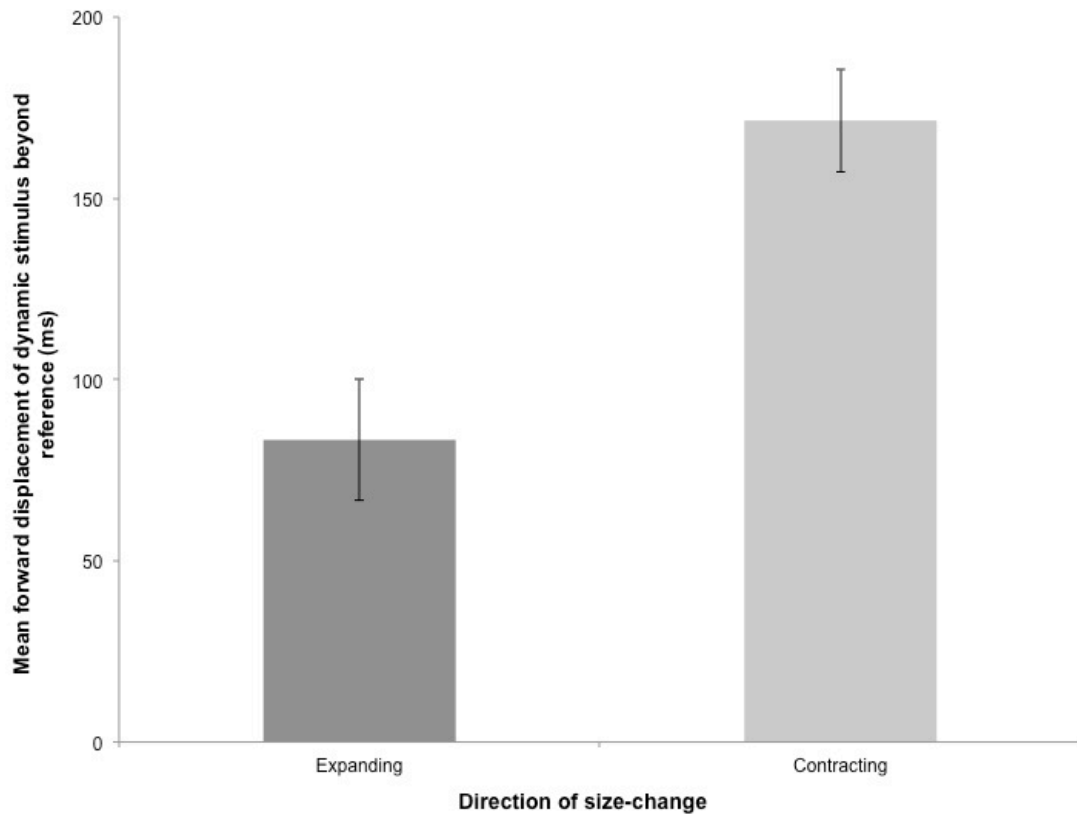


Figure 4.3. Experiment 1: Mean forward displacements observed in Experiment 1, in which the reference flashed synchronous with dynamic stimulus offset. Error bars indicate ± 1 standard error.

4.4.3 Discussion

These results, like Kanai et al. (2004), demonstrate that there can be a flash-lag effect in the FTC. The size of the flashed reference line was perceived to lag behind the instantaneous size of both expanding and contracting lines, even though the moving and flashed stimuli disappeared simultaneously. The effects reported previously (25ms; Kanai et al., 2004) were considerably smaller than those observed here (grand mean = 127.4ms, $SD = 63.87$) – requiring some explanation. Importantly, it has been shown that the flash-lag effect increases with the separation between the moving and flashed stimuli (Baldo et al., 2002; Baldo & Klein, 1995; Kanai et al., 2004) and that both a large stimulus separation and eccentricity contribute to eliciting a flash-lag effect in the FTC (Kanai et al., 2004). In the current experiment both the eccentricity of each

stimulus (8°), and the interstimulus separation (16°) were even greater than those used in Kanai et al. (2004), so it is likely that these factors amplified the flash-lag in comparison to their findings. It may still be that expanding and contracting stimuli, *per se*, produce flash-terminated flash-lag effects even when the stimuli are close together in central vision, but the current experiment has not tested this possibility. It is an open question for future research.

Of greater interest, however, is that the forward displacement for contracting motion was more than double that observed during expanding motion. This is inconsistent with the findings of Kafaligönül et al. (2010), who used similar stimuli but found the opposite results. However, two conspicuous distinctions between this experiment and theirs should be noted. Firstly, they used a full-cycle flash-lag display, in which the moving stimulus continued for some time and distance after the flash occurred, while here the flash and dynamic stimulus disappeared simultaneously. Secondly, although the authors used vertical lines that grew longer or shorter, only one end of the line moved (the other was fixed). In this experiment, on the other hand, the centre of the line was fixed at the meridian, while both ends moved simultaneously towards or away from it. Either of these discrepancies may have been sufficient to produce the conflicting results. It is argued later (see Section 4.9.3), however, that the first of these points is more likely to be at the root of the difference.

It has been shown that the flash-lag effect is larger for foveopetal than foveofugal linear translation in both full-cycle (Mateeff & Hohnsbein, 1988; Shi & Nijhawan, 2008) and flash-terminated conditions (Kanai et al., 2004). In the present experiment the only motion present in any given trial was of the ends of the dynamic line, either moving towards (contracting) or away from (expanding) each other. When one also considers that the ends of the lines simultaneously moved either towards or away from the display's horizontal meridian, the possibility emerges that the present anisotropy was a manifestation of the previously reported capacity for foveopetal motion to produce a larger effect than foveofugal. That is, it could be that motion-towards-the-meridian is a close enough approximation of foveopetal motion that it leads to an enhanced flash-lag effect. This would, though, be in conflict with the results of Kafaligönül et al. (2010), mentioned above. In their experiment, contracting motion still involved the motion of one end of a line towards the meridian and yet expanding motion produced the larger

effect. The size-changing stimulus was also at a considerably smaller eccentricity than that used here, and so the motion of the end of the line was even more directly foveopetal or foveofugal. The possibility that the motion of the ends of the line relative to fixation is responsible for the anisotropic flash-lag found here is further discounted in a series of control experiments reported later on (Experiments 4a and 5).

So, if not motion direction relative to fixation, then what causes the difference between expanding and contracting stimuli? It has been demonstrated that objects approaching a visual landmark undergo greater representational momentum than objects receding from a landmark (Hubbard & Ruppel, 1999). Similarly, and as mentioned previously, the flash-lag effect is relatively enhanced in motion towards, rather than away from, the fixation (Kanai et al., 2004; Mateeff & Hohnsbein, 1988; Shi & Nijhawan, 2008). Comparable to motion-towards-a-landmark, and motion-towards-fixation, contracting motion has a point of reference – an implied endpoint. That is, if an object continues to contract, it will eventually reach a vanishing point. While it is rejected further on (Experiments 4a and 5) that motion-towards-an-endpoint, in general, is responsible for the anisotropy, a slightly different notion remains tenable. Retinal images undergoing contraction are implicitly approaching a moment of disappearance. Indeed, it is likely that contraction even predicts disappearance. In support of the compatibility between disappearance and contraction, it has been claimed for a long time that abruptly disappearing stimuli are actually perceived to rapidly contract – a phenomenon referred to as *gamma movement* (Baldwin & Tinsley, 1965; Bartley & Wilkinson, 1953; Bartley, 1936, 1941; Hartmann, 1938; Kanizsa, 1979; Kenkel, 1913; Lindemann, 1938; Winters, Jr. & Gerjuoy, 1965; Winters, Jr., 1964). The implication here is that the visual system assigns a contraction percept to something that instantaneously, uniformly disappears. So, in the present experiment, if the dynamic stimuli were subject to gamma contraction at the moment of comparison, it would make them appear to quickly (but not instantly) contract to down to ‘zero’ size. In the contracting condition, this was the implied endpoint of the dynamic stimulus anyway, but the endpoint of the expanding stimulus was less clear, and would, if anything, have been in the opposite direction. Gamma contraction upon offset would therefore have facilitated the transit of the contracting stimulus to its implied endpoint, but inhibited that of the expanding stimulus. Such an interaction between forward displacements and gamma motion could explain why the present effect was larger for contracting than expanding stimuli.

Here, though, it should be noted that in Experiment 1, flashed references were used for perceptual comparison with dynamic stimuli, while the experiments of Whitaker et al. (1999) made use of continuously visible reference stimuli. Since no statistically-significant difference in the forward displacements of expanding and contracting motion was reported by Whitaker et al. (1999), it follows that the anisotropy found presently may be a result of using flashed reference stimuli. Experiment 2 tests this with a method analogous to Whitaker et al. (1999), in which subjects compare a dynamic stimulus to a continuously visible reference that disappears in conjunction with it.

4.5 Experiment 2: Continuous reference/synchronous offset

4.5.1 Methods

Nineteen subjects (12 female) participated. This experiment was identical to Experiment 1, except that instead of flashing the reference line, it was visible throughout each trial, from the onset to the offset of the dynamic stimulus. The moment of comparison was the time at which both stimuli disappeared simultaneously.

4.5.2 Results

The results of Experiment 2 are plotted in Figure 4.4, further on. As before, one-sample t-tests reveal that the size of the reference stimulus was perceived to lag behind that of the dynamic stimulus for both expanding [$M = 136.61\text{ms}$, $SD = 89.68$, $t(18) = 6.64$, $p < .001$, $d = 3.13$] and contracting [$M = 209.49\text{ms}$, $SD = 86.18$, $t(18) = 10.6$, $p < .001$, $d = 5$] motion. A paired-samples t-test shows that the forward displacement was larger for contracting than expanding motion, $t(18) = 2.37$, $p = .029$, $d = 0.544$. For the purpose of comparison with the data of Whitaker et al. (1999), the mean percentage of

misjudgment of the size of the dynamic stimulus was calculated for expanding and contracting motion. This calculation made use of the mean dynamic line length at the moment of comparison (11.78°) and the constant rate of size-change ($7.3^\circ/\text{s}$). The size of the contracting stimulus was underestimated by approximately 12.98%, while the size of the expanding stimulus was overestimated by around 8.47%. In Whitaker et al. (1999) these misjudgments were 9.7% and 7.2%, respectively.

4.5.3 Discussion

This experiment resulted in the same pattern of findings as Experiment 1, suggesting that they were not a product of using flashed reference stimuli. Replicating Whitaker et al. (1999), stimuli in both conditions were forwardly displaced in their direction of size-change. However, extending those findings, it was additionally found that the forward displacement during contracting motion was larger than it was during expanding motion, echoing the data from the Experiment 1.

As before, these findings are in line with the suggestion that the consistent direction of contracting motion and gamma contraction (upon physical disappearance) leads to a larger forward displacement than expanding motion prior to sudden offset. However, if gamma movement is indeed occurring in the dynamic stimulus, it should also be affecting the size percept of the reference stimulus. Take Experiment 2, for example, in which both stimuli were visible for the same amount of time, and abruptly disappeared in synchrony. If both dynamic and reference stimuli were subject to gamma contraction at their offset, their percepts would have raced each other to ‘zero’ size; that is, they would have looked more similar to each other than they might have done otherwise. This would serve to relatively diminish the apparent forward displacement for contracting motion, while augmenting it for expanding motion, thereby resulting in a smaller anisotropy. In the next experiment the dynamic stimulus expands or contracts as before, and must be compared to the reference at the moment it disappears, but the reference is visible continuously, throughout, and for some time after the offset of the dynamic line. The prediction is that, if gamma movement is no longer also applied to the reference stimulus at the moment of comparison, an even larger forward

displacement should be observed for contracting motion, and an even smaller one should be seen for expanding motion.

4.6 Experiment 3: Continuous reference/ no offset

4.6.1 Methods

Fourteen subjects (11 female) participated. This experiment was identical to Experiment 2 except that the reference line persisted on screen for some time after the disappearance of the dynamic line, which was itself jittered randomly between 5 durations as before. In each trial the reference line was visible for 3100ms, instead of up to the moment of comparison, which here was the time at which the dynamic stimulus disappeared from screen. Subjects had to wait until both stimuli had disappeared before making their response.

4.6.2 Results

One-sample t-tests show that the length of both expanding [$M = 92.92\text{ms}$, $SD = 80.65$, $t(13) = 4.31$, $p = .001$, $d = 2.39$] and contracting [$M = 273\text{ms}$, $SD = 111.58$, $t(13) = 9.16$, $p < .001$, $d = 5.08$] lines was perceived advanced beyond that of a static reference that endured on screen after the moment of comparison. A paired-samples t-test again showed that this forward shift was greater for contracting than it was for expanding motion, $t(13) = 4.66$, $p < .001$, $d = 1.259$.

To compare the results from Experiment 2 with those from Experiment 3 the data were submitted to a 2×2 mixed-measures analysis of variance (ANOVA), with direction of size-change (expanding or contracting) as a within-subjects factor, and experiment (2 or

3) as a between-subjects factor (see Figure 4.4). As expected, there was a significant main effect of the direction of size change, $F(1, 31) = 26.9, p < .001, \eta_p^2 = .465$, with contracting motion leading to larger forward displacements than expanding motion, but no main effect of experiment, $F(1, 31) = .22, p = .645, \eta_p^2 = .007$. More importantly, however, there was a significant interaction between the direction of size change and the experiment, $F(1, 31) = 4.83, p = .036, \eta_p^2 = .135$, showing that the difference between the expanding and contracting forward displacements was larger in Experiment 3 than it had been in Experiment 2. While follow-up t-tests however revealed that the differences between the expanding effects from each experiment, $t(31) = 1.44, p = .159, d = 0.512$, and the contracting effects from each experiment, $t(31) = 1.85, p = .074, d = 0.637$, were not significant, the effects were nevertheless medium in size (Cohen, 1988).

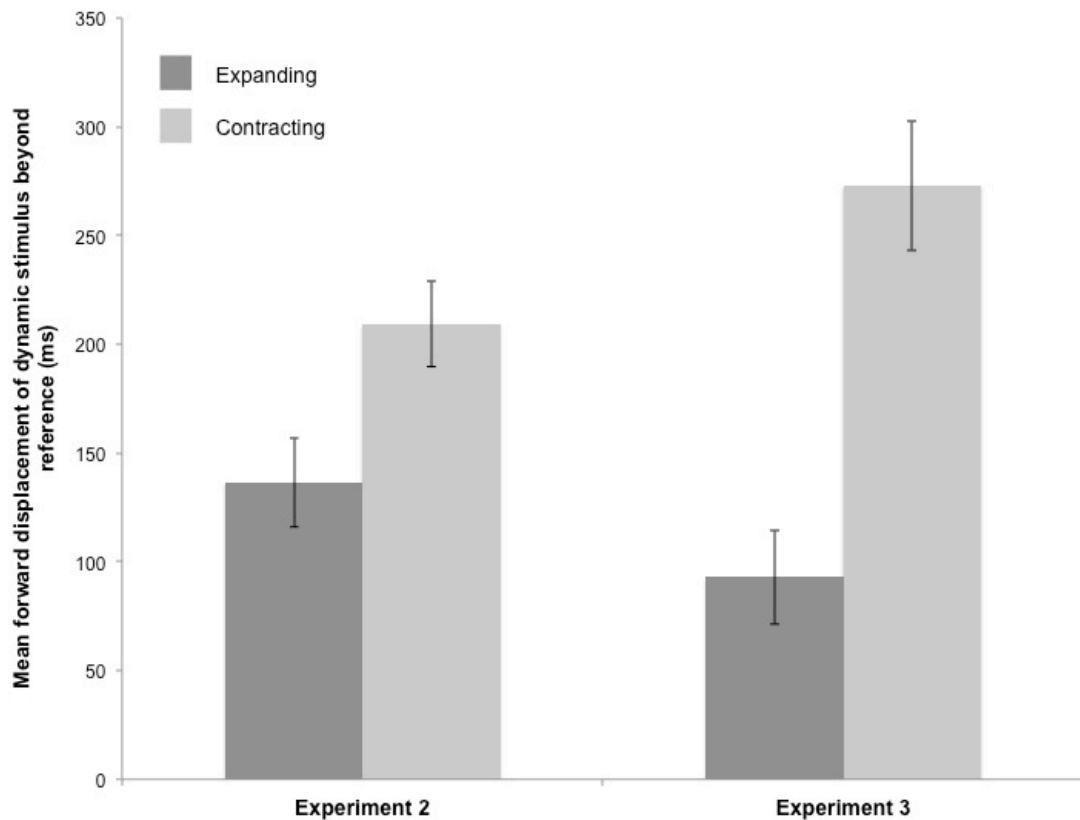


Figure 4.4. Mean forward displacements observed in Experiments 2 and 3, in which a continuous reference disappeared in synchrony with, or some time after dynamic stimulus offset, respectively. Error bars indicate ± 1 standard error.

4.6.3 Discussion

It is of particular interest that the anisotropy was larger in Experiment 3, in which the reference line persisted on screen after the moment of comparison, than it was in Experiment 2, in which the reference line disappeared in conjunction with the dynamic line. It is argued here that this is because the reference line was not subject to gamma motion at the moment of comparison, on account of it persisting after the dynamic line disappeared. Since the reference line appeared longer at the moment of comparison, the forward displacement of expanding and contracting lines were relatively diminished and enhanced, respectively, leading to a larger anisotropy. This therefore supports the claim that gamma contraction is responsible for the forward displacement advantage of contracting objects over expanding ones observed consistently in Experiments 1, 2, and 3.

Earlier it was highlighted that the stimuli in the current experiments involve simultaneous motion of the ends of the dynamic lines either towards or away from the horizontal meridian of the display. Even though the ends of the lines did not move *directly* towards or away from fixation, the possibility was raised that the greater forward shifts seen in contracting stimuli may be due to the ends of the lines moving obliquely, ‘more’ towards the fovea than they do in expanding stimuli. This would be contrary to the explanation given herein, that contracting objects are biased more forwards than expanding objects because gamma contraction upon their disappearance works in combination with a more basic forward displacement. Implicit in this interpretation is that perceptual systems assume the distal stimulus is a coherent object. From this assertion it follows, then, that the anisotropy observed thus far should be reduced or eliminated if the dynamic stimulus is not perceived as a single object with an expanding or contracting retinal image. The next experiment tests this prediction by using the same stimuli as Experiment 1, but presenting only the top and bottom portions of each line. Instead of dynamic stimuli being coherent objects that expand or contract, they are simply pairs of small squares that translate away from, or towards each other, respectively. Gamma motion is the distinct contraction of individual objects, and so should not bias such stimuli towards each other upon offset. On the other hand, an explanation of the anisotropy invoking an advantage for foveopetal movement would

predict that the anisotropy should remain, because retinal motion direction is the same relative to fixation.

4.7 Experiment 4a: Two translating squares/ FTC

4.7.1 Methods

Nine subjects (6 female) participated. This experiment was identical to Experiment 1, except that rather than showing the full line stimuli as before, only the uppermost and lowermost square sections of the dynamic and reference lines were displayed (see Figure 4.5). These squares therefore subtended $0.41^\circ \times 0.41^\circ$ of visual angle, and moved vertically in opposite directions - away from each other in the expanding condition and towards each other in the contracting condition. As before, the moment of comparison was when the dynamic stimuli disappeared in synchrony with the flashed reference stimuli. In this case, however, subjects judged whether the left or right pair of dots looked more distantly spaced.

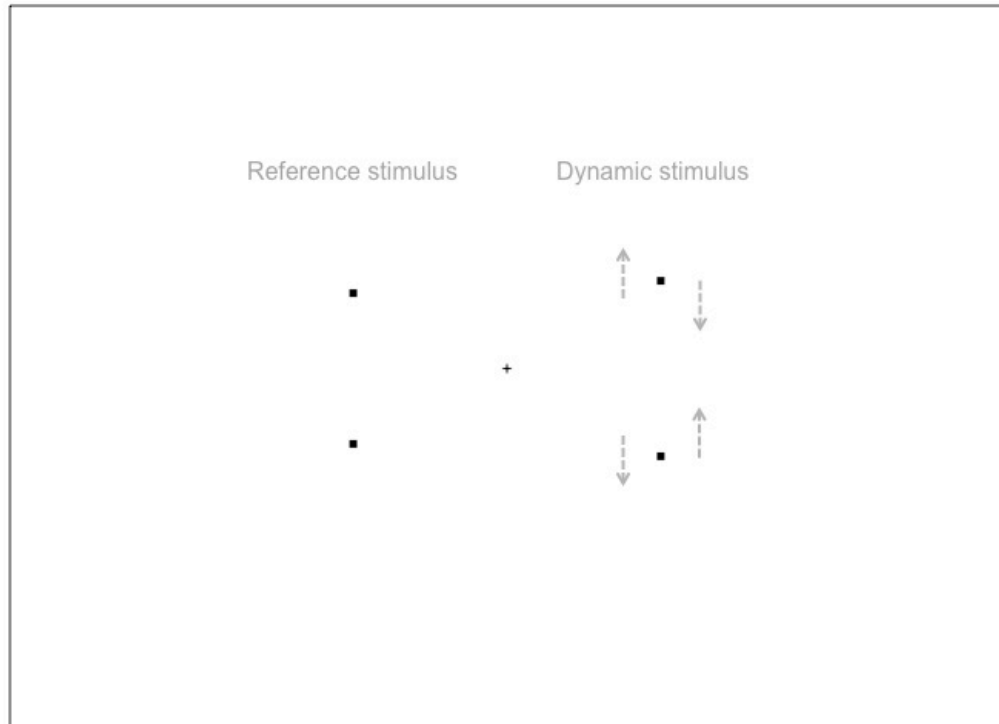


Figure 4.5. Experiment 4a: Example of square stimuli used. Only objects displayed in black were visible during the experiment. Reference stimulus was flashed in synchrony with dynamic stimulus offset.

4.7.2 Results

The overall results of Experiment 4a are displayed in Figure 4.8, further on.

Psychometric curves from a representative subject are shown below in Figure 4.6.

Consistent with previous experiments, one-sample t-tests show that the vertical separation of squares moving both away from [$M = 80.93\text{ms}$, $SD = 79.41$, $t(8) = 3.06$, $p = .016$, $d = 2.162$] and towards [$M = 109.66\text{ms}$, $SD = 83.37$, $t(8) = 3.95$, $p = .004$, $d = 2.79$] each other was forwardly displaced in the direction of change. However, a paired-samples t-test shows that the difference in forward displacement between squares moving towards and away from each other (equivalent to previous experiments' expanding and contracting conditions, respectively) was not significant, $t(8) = .67$, $p = .52$, $d = 0.224$.

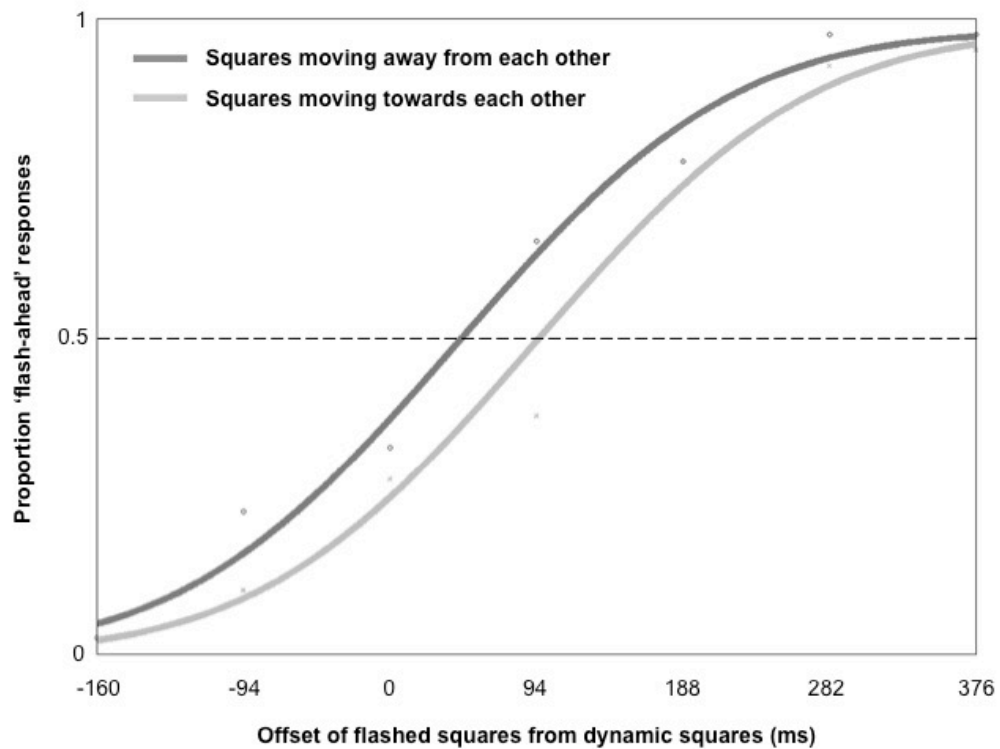


Figure 4.6. Experiment 4a: Psychometric curves from a representative subject. Negative offsets represent flashed stimuli that physically lagged the separation of the dynamic stimuli.

4.7.3 Discussion

As before, Experiment 4a demonstrates a forward displacement for both directions of motion, but unlike in previous experiments, no difference in the magnitude of the effects was observed. This implies that when the motion is limited to the end portions of the lines, the anisotropy between contracting and expanding (in this case, towards and away from each other) disappears. While the motion relative to fixation was the same as in Experiment 1, presenting the stimuli as squares translating towards or away from each other, rather than as coherent lines, meant that the anisotropy was abolished. This is in support of the claim presented earlier that gamma movement is ultimately responsible for the greater forward displacement of contracting than expanding stimuli.

One should additionally note that the flash-lag effects found here are comparable in size to those in Experiment 1. This suggests that expanding or contracting motion was not the critical factor in eliciting a flash-lag effect in the FTC in the first experiment. As argued earlier, it is more likely to be the result of – simultaneously – a large eccentricity and a large separation between moving and flashed stimuli (see Kanai et al., 2004).

Another inference that can be taken from this result is that motion-towards-an-endpoint is not sufficient to explain the greater forward displacement in contracting than expanding conditions observed in the preceding experiments. Here, when two squares moved towards each other such that they appeared as if they would imminently collide, no greater flash-lag effect was evident, even though their collision was an implied, shared endpoint of their linear motion trajectories.

This experiment has suggested that the larger forward displacement in contracting stimuli cannot be explained by way of it being partially confounded with foveopetal motion, though another experiment will be useful to further examine this issue. The next experiment presents only one of the two squares in motion towards or away from the horizontal meridian. The prediction is that, if previously reported forward displacement differences between foveopetal and foveofugal motion play no part in the current experiments, a single square translating towards the meridian (i.e., ‘more’ towards fixation) should not produce a larger flash-lag than a square moving away.

4.8 Experiment 4b: Single translating square/ FTC

4.8.1 Methods

Ten subjects (8 female) participated. This experiment was identical to Experiment 4a, except that only one of the two square end portions of the dynamic line from the preceding experiments was presented in any given trial (see Figure 4.7). A single square

($0.41^\circ \times 0.41^\circ$) could thus translate either towards or away from the horizontal meridian, in either the upper or lower hemifield (counterbalanced), before a square on the opposite side of the screen flashed at its time of offset. Subjects had to report whether the left or right square appeared closer to the top (if stimuli were in the upper hemifield) or the bottom (if stimuli were in the lower hemifield) of the display.

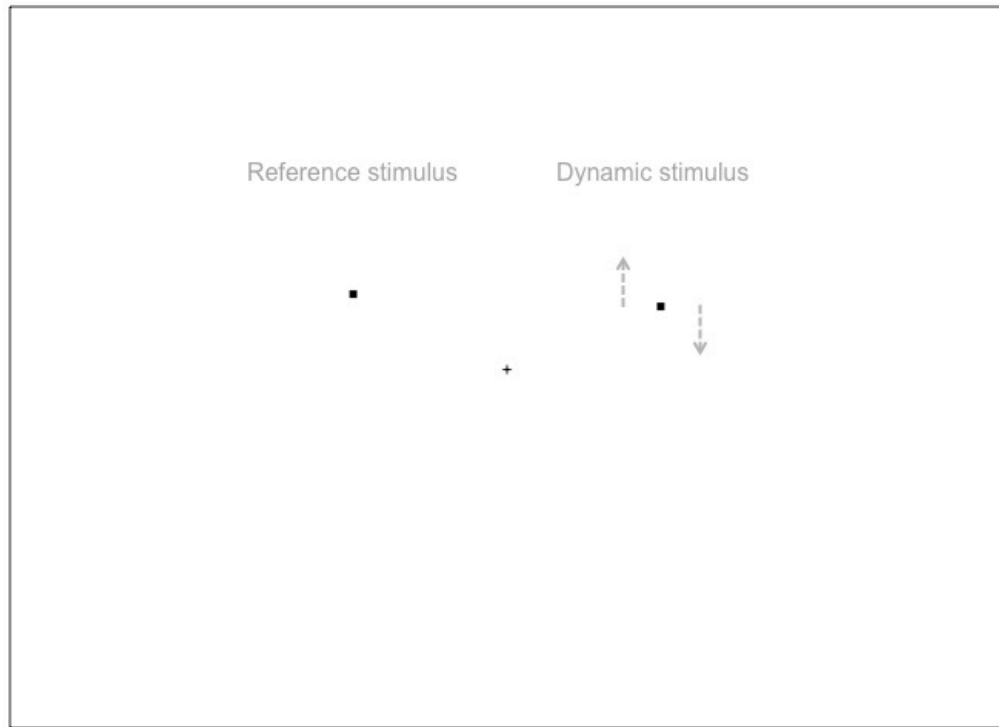


Figure 4.7. Experiment 4b: Example of square stimuli used. Only objects displayed in black were visible during the experiment. Reference stimulus was flashed in synchrony with dynamic stimulus offset.

4.8.2 Results

One sample t-tests reveal that squares moving towards the horizontal meridian produced a significant flash-lag effect [$M = 185.12\text{ms}$, $SD = 142.63$, $t(9) = 4.1$, $p = .003$, $d = 2.736$], but that squares moving away did not [$M = 37.22\text{ms}$, $SD = 75.26$, $t(9) = 1.56$, $p = .152$, $d = 1.043$]. A paired-samples t-test furthermore shows that the difference

between these displacements was significant, $t(9) = 3.21, p = .011, d = 1.09$. The results of Experiment 4b are plotted in Figure 4.8.

In order to compare the results of Experiment 4a with Experiment 4b, a 2×2 mixed measures ANOVA was performed, with direction of motion (away from or towards the meridian) as a within-subjects factor and experiment (4a or 4b) as a between-subjects factor. There was a main effect of direction of motion, $F(1, 17), p = .012, \eta_p^2 = .315$, with motion towards the horizontal meridian producing a larger effect than motion away. There was no main effect of experiment, $F(1, 17) = 7.81, p = .64, \eta_p^2 = .013$, and no interaction between direction of motion and experiment $F(1, 17) = 3.56, p = .077, \eta_p^2 = .173$. Independent samples t-tests show that neither the expanding effects from each experiment, $t(17) = 1.23, p = .235, d = 0.565$, nor the contracting effects from each experiment, $t(17) = 1.39, p = .184, d = 0.646$, differed significantly from one another.

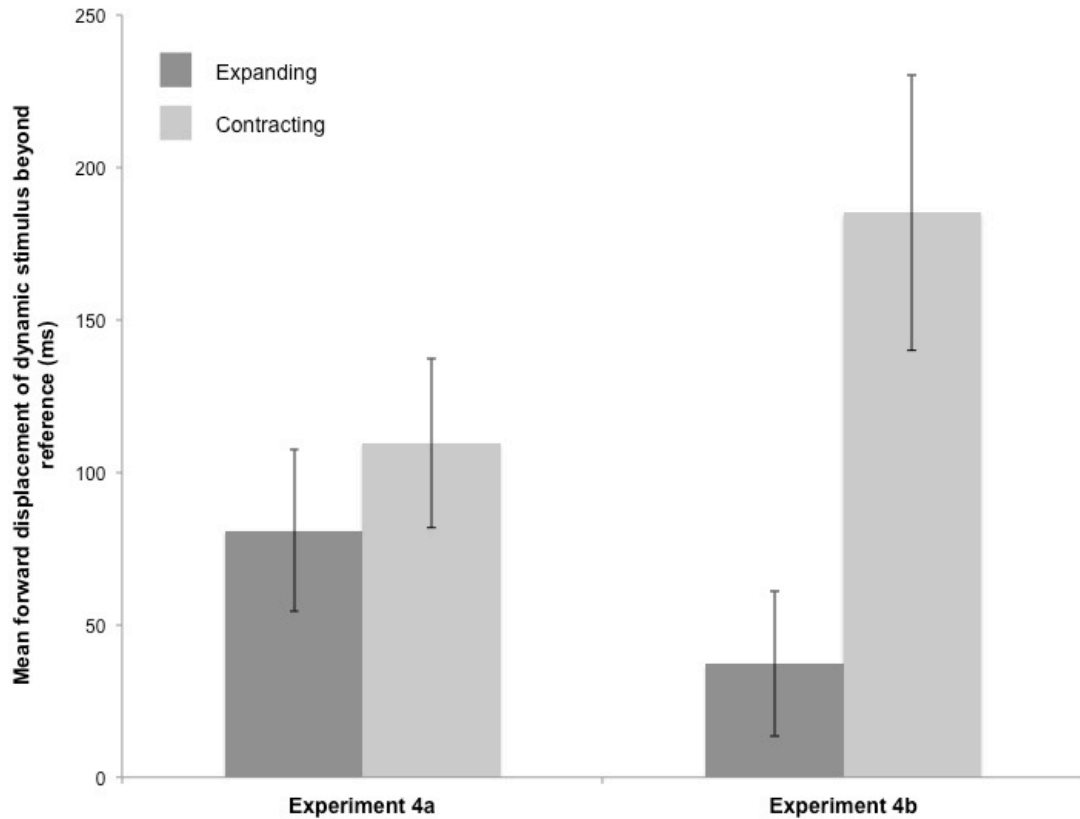


Figure 4.8. Mean forward displacements observed in Experiments 4a (two translating squares) and 4b (single translating square) when the reference flashed in synchrony with dynamic stimulus offset. Error bars indicate ± 1 standard error.

4.8.3 Discussion

These results do not fit with the predictions outlined above. While Experiment 4a showed that two squares translating vertically towards or away from each other do not produce the same flash-lag anisotropy observed with a single line, Experiment 4b has shown that when just one of these squares is visible, the anisotropy appears to return. The most parsimonious explanation, and that submitted to here, appeals to the perceptual similarity of motion towards and away from the meridian with foveopetal and foveofugal motion, respectively. That is, to the extent that motion towards the meridian is ‘more’ foveopetal than motion away, it should produce a larger flash-lag effect. This experiment therefore replicates previous findings in the FTC (Kanai et al., 2004). The possibility is therefore left open that in Experiments 1-3, motion direction of

the ends of the lines relative to the fovea contributed to the magnitude of the observed effects.

Why, though, do we see 1), a greater forward displacement in contracting than expanding lines (Experiments 1-3); 2), no such anisotropy when only the ends of the lines are visible (Experiment 4a); and 3), the reemergence of the anisotropy when only one of the ends is presented (Experiment 4b)? It is proposed here that the anisotropy evident in Experiments 1-3 is of a different nature to that seen in Experiment 4b. An explanation for the former anisotropy was outlined earlier (i.e., gamma motion interacting with forward displacements), and a different, simple explanation for the anisotropy in Experiment 4b presents itself in the form of direction relative to fixation. However, there is reason to believe that these effects are caused by different mechanisms, since Experiment 4a does not show a corresponding anisotropy, even though it emulates both the line stimuli from Experiments 1-3, and the individual square stimuli from Experiment 4b. Prior to Experiment 4a, it was predicted that motion of two squares towards each other should not produce a larger forward shift at offset than two squares moving away, because the moving stimuli were not a single coherent object. This argument stands, though an explanation is required for why the findings should be incongruent with those in Experiment 4b. Consider that in Experiment 4b, two dynamic stimuli were seen on each trial, each moving in opposite directions. It has been shown that motion in one part of the visual field can influence the perception of motion (Murakami & Shimojo, 1993; Ramachandran & Cavanagh, 1987; Whitney & Cavanagh, 2002) and position (Durant & Johnston, 2004; Whitney & Cavanagh, 2000a; Whitney, 2002) in other regions. It has further been demonstrated that the magnitude of the flash-lag effect depends on motion in distant parts of the visual field (Maiche, Budelli, & Gómez-Sena, 2007; Shioiri et al., 2010). It is not implausible, therefore, that motion in one region can also affect the forward shift magnitude of a stimulus in another part. In Experiment 4a, in particular, the upwards motion of one square may have interfered with the forward displacement of the other, downwards moving square, and vice versa. If this interference effect was greater when the squares moved towards each other than when they moved away it would explain why the flash-lag effects did not differ, but were of comparable size overall to those in Experiment 1 (i.e., the full line equivalent of Experiment 4a). So, it is argued that a foveopetal advantage may not have manifested in Experiment 4a as it did in Experiment 4b because of the presence of

two stimuli translating in opposite directions. However, making this case precludes the earlier suggestion that the null result in Experiment 4a disproves that a bias relative to fixation is at the heart of the anisotropies seen in Experiments 1-3. Further research on this would therefore be required.

As mentioned earlier, it has been reported that foveopetal motion results in a larger flash-lag effect than foveofugal movement, both when the moving stimulus disappears with the flash (FTC; Kanai et al., 2004), and when it carries on after the flash (full-cycle; Mateeff & Hohnsbein, 1988; Shi & Nijhawan, 2008). In light of the latter of these two findings, if the direction of motion relative to the fovea is responsible for a larger forward displacement in contracting than expanding lines, this should be the case in both the FTC, and full-cycle flash-lag displays. Conversely, it has been suggested here that the forward displacement of contracting (expanding) objects is augmented (reduced) when they suddenly disappear due to gamma contraction. If this is the case, size-changing stimuli that do not disappear at the moment of comparison should not display the same anisotropy as those that do. The next experiment therefore uses a full-cycle flash-lag display, in which the expanding or contracting line continues after the moment of comparison (i.e., a flashed line). This experiment is comparable to that of Kafaligönül et al. (2010), who found a greater effect for expanding than contracting lines, which they attributed to its perceptual similarity to looming motion, which leads to a greater flash-lag than receding motion (Harris et al., 2006). It may be expected, then, that this experiment will also produce a greater forward displacement for expanding than contracting stimuli, which would oppose the suggestion that the findings of Experiments 1-3 are the result of motion direction relative to fixation. At the same time, such a finding would conflict with the possibility mentioned earlier that motion-towards-an-endpoint, per se, results in larger forward displacements. Since a contracting line still has an implied point of disappearance regardless of whether it abruptly disappears before reaching it, this perspective would predict that it should yield a greater flash-lag.

4.9 Experiment 5: Full-cycle flash-lag

4.9.1 Methods

Ten subjects (6 female) participated. This experiment was very similar to Experiment 1, in that a line expanded or contracted on one side of the screen before another line flashed on the other side. Here, however, the dynamic line continued in its direction of size-change after the flash, so that it was on screen for a full 3100ms. As in previous experiments, the timing of the flash was jittered randomly between 5 times to prevent it becoming predictable. Pilot observations suggested that, on the whole, this experiment would produce larger forward displacements than the previous experiments.

Accordingly, the spread of offsets of the reference from the dynamic stimulus was increased to better measure the flash-lag effect. The length of the flashed line could therefore differ from the dynamic stimulus by -258ms, -129ms, 0ms, +129ms, +258ms, +388ms, or +517ms of size-change. The moment of comparison was the time of the flash, and subjects gave their responses after both stimuli had disappeared from screen.

4.9.2 Results

One-sample t-tests show that both expanding [$M = 346.52\text{ms}$, $SD = 125.72$, $t(9) = 8.72$, $p < .001$, $d = 5.811$] and contracting [$M = 279.05\text{ms}$, $SD = 110.54$, $t(9) = 7.98$, $p < .001$, $d = 5.322$] lines produced significant flash-lag effects. Although there was a tendency, a paired-samples t-test shows that the difference between the flash-lag effects in the two directions was not significant, $t(9) = 1.03$, $p = .331$, $d = 0.325$. Psychometric curves from a representative subject are plotted in Figure 4.9, and the mean flash-lag effects across all subjects are plotted in Figure 4.10.

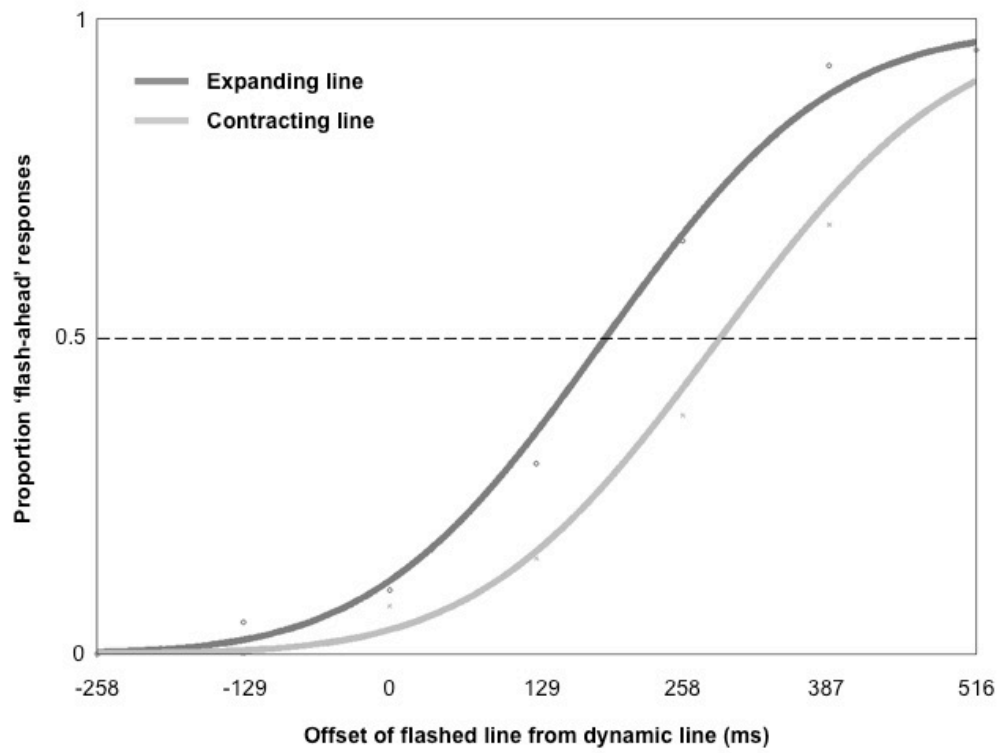


Figure 4.9. Experiment 5. Psychometric curves from a representative subject. Negative offsets represent flashed stimuli that physically lagged the size of the dynamic stimuli.

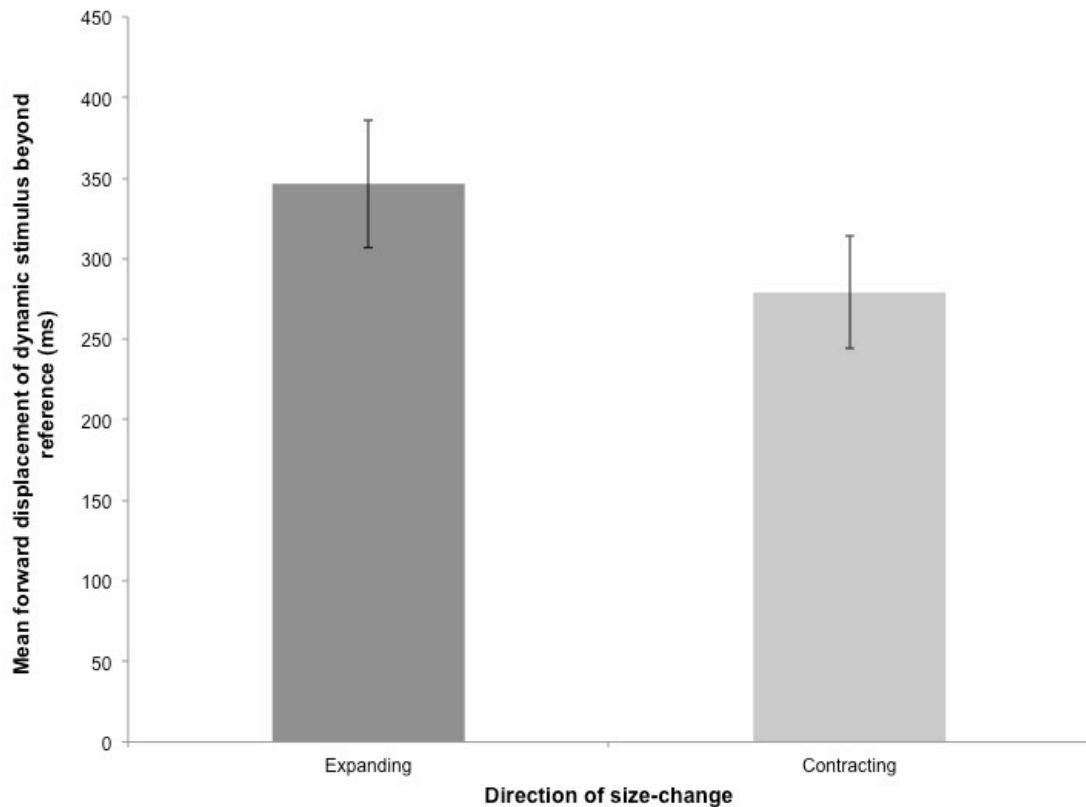


Figure 4.10. Mean forward displacements observed in Experiment 5, in which the reference flashed partway through the dynamic stimulus animation. Error bars indicate ± 1 standard error.

4.9.3 Discussion

That the flash-lag effects were considerably larger in this full-cycle experiment than they were in the FTC (Experiment 1) is consistent with the finding that, when a flash-lag effect is elicited in the FTC, it is smaller than it could have been if motion continued after the flash (Kanai et al., 2004).

More interestingly, these findings show unequivocally that, when a size-changing stimulus does not disappear at the moment of comparison, a contracting line produces no greater effect than an expanding line. In fact, in this full-cycle flash-lag experiment the effect was slightly in the opposite direction, though not significantly so. While the ends of the lines moved – as before – towards or away from the horizontal meridian,

there was no forward displacement advantage of one direction over the other. Since it has been shown that foveopetal motion leads to a greater flash-lag than foveofugal motion (Mateeff & Hohnsbein, 1988; Shi & Nijhawan, 2008), the implication is that this factor is not responsible for the greater forward displacement of contracting lines observed in Experiments 1-3. That is, in the present experiment, the ends of the dynamic line still moved towards or away from the meridian ('more' or 'less' towards fixation, respectively), but these two directions produced similarly sized effects. In discussing Experiment 4b, it was argued that Experiment 4a was, in hindsight, not a good control for the possibility that contraction and expansion had been confounded with foveopetal and foveofugal motion in Experiments 1-3. The findings of Experiment 5, however, suggest more strongly that this was not the case, and more broadly, that contraction and expansion produce a different class of motion percept to linear translation.

In accord with the null result of Experiment 4a, however, the current finding suggests that motion-towards-an-endpoint is not, in itself, what leads to a relatively enhanced forward shift in contracting lines in Experiments 1-3, since contracting motion in this experiment also had an implied endpoint.

How does continuation of the animations after the flash lead to similar contracting and expanding motion effect? As mentioned earlier, it has been demonstrated elsewhere that abruptly disappearing stimuli are perceived to quickly shrink in size (e.g., Kenkel, 1913). The sudden disappearance of the stimulus that was previously contracting enhances its forward displacement. When considered alongside the strong advantage for contracting motion seen in Experiment 1, the present null-result is in support of this position. Here, the moving stimulus did not disappear at the moment subjects had to make a perceptual comparison. This prevented the occurrence of high-speed gamma contraction that would have resulted in stimulus disappearance, and thus reduced the magnitude of the flash-lag effect. Additionally, that the flash-lag of the expanding line was considerably larger than it had been in any of the preceding experiments suggests that its forward displacement was not perceptually cut-short by gamma contraction at disappearance, as was the case previously.

The current finding is also consistent with that mentioned earlier, that full-cycle motion with expanding and contracting lines leads to a larger expanding than contracting flash-lag effect (Kafaligönül et al., 2010). While the difference between the directions did not reach significance here, the discrepancy between the present findings and those of Kafaligönül et al. (2010) is really one of degree, rather than kind, and could have been due to inconsistencies between the two sets of stimuli, such as the larger eccentricity used in the current studies.

4.10 General Discussion

The preceding experiments have shown that a contracting object that abruptly disappears at the moment of perceptual comparison is perceived further along its trajectory than a similar object that had previously been expanding. Conversely, when a size-changing stimulus continues after the moment of comparison, whether it had been contracting or expanding makes little difference. It is argued here that gamma movement (Kenkel, 1913), a form of apparent motion, adds to the underlying forward displacement of contracting stimuli upon disappearance, and subtracts from it in expanding stimuli. This explains the forward shift advantage for contracting stimuli when they disappear at the moment of comparison, and the lack of such when they do not. This account was outlined in part earlier on, though a more detailed overview will be given now of both gamma movement, and why it should differentially affect the forward displacements of formerly contracting and expanding images. Further discussion will then be given of the nature of gamma movement, and a novel interpretation will be proposed that aligns it with other apparent motion phenomena.

When something instantaneously vanishes, its percept undergoes a rapid contraction (Baldwin & Tinsley, 1965; Bartley & Wilkinson, 1953; Bartley, 1936, 1941; Hartmann, 1938; Kanizsa, 1979; Kenkel, 1913; Lindemann, 1938; Winters, Jr. & Gerjuoy, 1965; Winters, Jr., 1964). This phenomenon was first studied formally by Kenkel (1913), who gave it the term *gamma movement*, in light of its parallels with other forms of apparent motion, such as alpha and beta phenomena. Studies showed that when a stimulus was

illuminated for a brief period of time, its onset and offset were accompanied, respectively, by apparent expansion and contraction (e.g., Bartley, 1941; Hartmann, 1938; Lindemann, 1938). Though initial experiments used very subjective, introspective measures of perceived motion, such as asking subjects to report whether they were seeing the movement or not, later studies used more robust psychophysical methods. Winters, Jr. (1964), for instance, presented a circle, followed after 800ms by another circle. After a further 200ms, both circles disappeared simultaneously. Subjects tended to estimate that the later-appearing circle had been larger than the initial circle, even when it had actually been identical, or even slightly smaller. This was in spite of the subsequent finding that stimuli of longer duration tend to be perceived as larger (e.g., Thomas & Cantor, 1975). The conclusion was that since the later stimulus had more recently appeared, it was still in the process of gamma expansion at the time the two objects had to be compared, and was thus perceived as larger.

It follows from the reasoning of Winters, Jr. (1964), mentioned above, that if the final size of a recently disappeared object must be judged, the ongoing process of gamma contraction will make it appear smaller than its actual size at offset. Additionally, as has been shown previously (Whitaker et al., 1999), and replicated in the present experiments, the final sizes of expanding and contracting stimuli are biased in their direction of size-change. So, for example, contracting stimuli are perceived smaller at offset than they actually are. The argument to be made here to explain the current findings was also given, in part, in the discussion of Experiment 1 (Section 4.4.3). It was suggested there that the greater forward shift for contracting stimuli stems from the consistent direction of perceived size-change between ‘real’ contraction and ‘illusory’ gamma contraction (see Figure 4.11). That is, when something is contracting and suddenly disappears, it is seen to continue contracting (through gamma motion), if at a higher rate. The specific explanation given here, then, is that when something is contracting towards a vanishing point, and gamma motion expedites its transit to that destination, a larger forward displacement is seen. When something expands before disappearing, however, its direction of perceived size-change reverses at the time of offset. So, while there is still a forward displacement in the direction of pre-offset motion, it is comparatively reduced because it is cut-short by gamma contraction working in opposition. In such a case the forward displacement is diminished because gamma contraction subtracts from its magnitude. It is claimed, then, that motion-

towards-an-endpoint alone is not sufficient to explain the current set of results, but that motion-towards-an-endpoint working in conjunction with a percept that helps it reach that endpoint more quickly (gamma motion) provides a robust account.

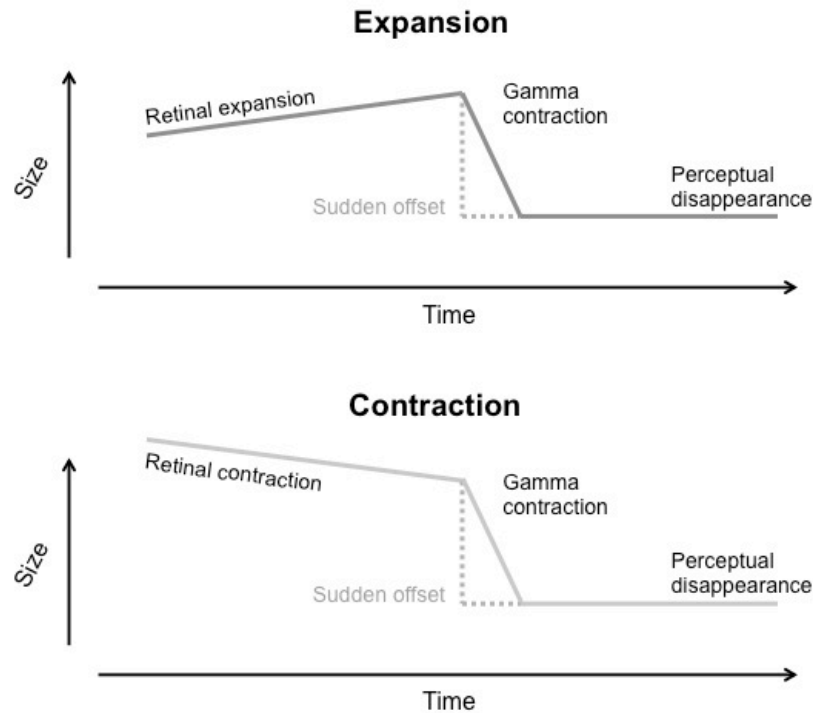


Figure 4.11. Schematic diagram of the proposed relationship between perceived size of the dynamic stimulus and time in Experiments 1-3. Note that in the lower pane the direction of perceived size change is consistent before and after the sudden offset.

A further possibility that does not rely on the occurrence of full gamma motion (i.e., contraction down to 'zero' size), is that local motion signals arise at the locations of the edges of a recently disappeared stimulus and are interpreted as contraction. Indeed, Grossberg and Rudd (1992) have put forward a similar account to explain gamma motion in general. Whether a recently disappeared stimulus is perceived to contract partially (due to real motion signals) or fully (due to apparent motion) is a question for future research.

4.10.1 The nature of gamma movement

There has been little recent attention given to the processes underlying gamma movement. Originally, the Gestaltists explained it as a central psychological phenomenon that occurs whenever a figure emerges on, or disappears from, a background (e.g., Harrower, 1929; Hartmann, 1938; Kenkel, 1913; Koffka, 1935; Lindemann, 1938). This was later challenged by accounts owing the percept to more peripheral aspects of the visual system (e.g., Baldwin & Tinsley, 1965; Bartley & Wilkinson, 1953; Bartley, 1936, 1941). Since these interpretations were put forward, however, the nature of gamma movement has received little attention. Here a novel explanation is given that is consistent with a wide range of well-established phenomena in the apparent motion literature.

Let us first consider a type of phenomenon closely related to gamma movement, which has been variously termed *polarised gamma motion* (Kanizsa, 1979), *line motion* (Hikosaka, Miyauchi, & Shimojo, 1993), *motion induction* (Faubert & von Grünau, 1995; von Grünau & Faubert, 1994), and more generally, either *transformational apparent motion* (Tse, Cavanagh, & Nakayama, 1998; Tse & Logothetis, 2002; Tse, 2006) or *morphing* (Baloch & Grossberg, 1997; Holcombe, 2003). Hikosaka and colleagues provided a good example when they showed that if a square is flashed, promptly followed by the uniform instantaneous appearance of a line, with one end abutting the square's location, the line is seen to expand into existence from the end nearest the square (Hikosaka et al., 1993). So, as with gamma motion, an abruptly appearing stimulus is seen to expand in a continuous motion. Several authors have claimed that this illusion is best described as a manifestation of processes attempting to determine the most likely external cause of perceptual events (e.g. Downing & Treisman, 1997; Holcombe, 2003; Tse et al., 1998; Tse & Logothetis, 2002; Tse, 2006). Consistently, Tse and Logothetis (2002) provided evidence that this type of motion can be perceived to extend out of the picture plane, in depth, implying that a full three-dimensional object representation is involved. More recently this has been supported by functional neuroimaging data that suggest an interaction between high-level form (posterior fusiform gyrus) and motion (V5/hMT+) processing cortical areas during the perception of transformational apparent motion (Tse, 2006).

Expanding on this position, it is proposed here that gamma movement stems from the visual system's attempt to disambiguate the state of objects in the environment. As an interpretation of apparent motion in general, this is backed by a substantial literature. For example, if the displacement between two alternating stimuli is great, the rate of alternation that produces optimal apparent motion must be proportionately low (Korte, 1915) – as would be expected if a single physical object moved across the same distance in space. Other findings have accumulated to suggest that the objects and paths of apparent motion are governed by the principles that underpin the motion of real-world objects (Attneave & Block, 1973; Bundesen et al., 1983; Farrell & Shepard, 1981; Foster, 1975; Shepard & Cooper, 1982; Shepard & Judd, 1976; Shepard & Zare, 1983; Shepard, 1981).

It has been argued that since we have evolved in an environment populated by persistent, rigid, three-dimensional objects, we are also inclined to interpret discrete, successive views of things in these terms (Shepard, 1981). On this account, apparent motion occurs because the brain easily accepts the disappearance and appearance of stimuli as representing the start and end positions of continuously moving objects. Shepard (1984) took a Helmholtzian likelihood approach to explain this, suggesting that the visual system internalises statistical regularities inherent in the environment in order to disambiguate the external state of things. The idea is that if something is unclear, the perceptual system will seek an interpretation by referring back to prior experience. How, though, does this apply to an interpretation of gamma motion? Consider first that our visual systems have not developed in an environment in which stimuli instantaneously vanish. When the images disappear from the retina, it tends to be at the end of a continuous process of contraction. Additionally, distal objects themselves do not tend to pop out of existence instantaneously; they will usually become *less* visible before becoming *invisible*, as when moving behind an occluder. Contraction of a retinal image is therefore predictive of that image's imminent disappearance, and more generally, of the disappearance from view of the distal object it represents. If a stimulus is presented electronically, however, it can be made to instantly vanish without any gradual retinal diminishment, even though this is something that does not occur naturally. It is suggested therefore that, in the absence of a more likely interpretation, an object that suddenly appears or disappears is perceived to expand or contract because the visual system associates these respective phenomena. Thinking about this in terms

of the states of distal objects, the most likely perceptual solution to something that has abruptly appeared or disappeared is that it has rapidly approached or receded away from the observer. This final point is consistent with the observation that gamma movement is easily perceived as motion in depth (e.g., Allen & Kolers, 1981; Bartley, 1941; Kanizsa, 1979).

It is worth briefly noting that the present results represent only the second instance (as far as is known) of an ‘objective’ measure of gamma motion. As mentioned earlier, previous investigations (e.g., Bartley, 1941) made use of subjective, introspective methods to probe the effect, which are vulnerable to considerable bias. Like Winters, Jr. (1964), the current experiments employed a binary choice method of constant stimuli, though improving on that earlier study, psychometric functions were also fit to the data and used to estimate PSEs. It is suggested that the current method of examining differences in the forward displacements of size-changing, disappearing stimuli may rekindle interest in the study of gamma motion, which has received little attention for many years.

In summary then, this study provides three key contributions. First, it is shown that the little-studied phenomenon of gamma motion interacts with forward displacement effects, which have been of considerable interest to vision scientists in recent times. More specifically, gamma motion is found to enhance a forward shift when the two percepts work in a consistent direction. Secondly, it is argued that gamma contraction occurs in general because the visual system is naïve to instantaneous disappearance, and so infers that the recently vanished object actually rapidly receded. Finally, the methodology used herein provides an objective measure of gamma motion, which may be adopted in further study of its effects elsewhere.

4.10.2 Future directions

A number of avenues of research pertaining to the current finding and claims could be pursued. For example, one could look in more detail at the possibility that the motion direction of the ends of the stimuli impact the magnitude of the anisotropy. Similar

experiments in which size-change occurs in two dimensions could help with this. Such a method would mean that opposing edges of the dynamic stimulus move simultaneously in foveopetal and foveofugal directions, and would thereby control for motion direction relative to fixation. This may not be a full solution though, because evidence suggests that forward displacements are greater in the periphery than in central vision (e.g., Kanai et al., 2004). Thus it might be expected that the forward shift of the more peripheral edge of the stimulus would be greater than that of the more central edge moving in the opposite direction. Another approach would be to use stimuli similar to those used here but to shift them up or down on the screen, so that both ends of the stimuli are not moving simultaneously foveopetally or foveofugally.

To investigate further where gamma contraction is at the heart of the forward displacement anisotropy observed in Experiments 1-3, further experiments could look at whether the anisotropy is present when neither stimulus disappears at the moment of comparison. This could be done with similar expanding and contracting stimuli, and a continuous, static reference stimulus off to one side visible for the same epoch as the dynamic stimulus. Instead of signalling the moment of comparison by having one of the stimuli flash or disappear, it could be signified by, for instance, a change of colour of the background, or the flashing of a third stimulus. Here there would be no gamma contraction in the stimuli to be compared, and so it would be predicted that there should be no difference in forward displacement between expanding and contracting motion.

4.11 Conclusions

A series of experiments has been reported that show expanding lines produce a smaller forward displacement in their direction of size change at offset than do contracting lines. This was not the case when only the end portions of the lines were visible, or when the dynamic lines did not disappear at the moment of comparison. It was argued that the latter of these findings, in particular, suggests that the larger forward displacement in contracting lines in the preceding experiments was not due to the direction of motion of the ends of the lines towards fixation. Instead, it was suggested

that the rapid apparent contraction (gamma motion) of abruptly disappearing stimuli adds to the forward displacement of contracting lines and subtracts from the forward displacement of expanding lines. Put differently, while contracting lines have an implied endpoint, which is reached all the more quickly via gamma motion at sudden offset, expanding lines have no clear endpoint, and gamma motion at offset works in opposition to their forward displacement. A novel interpretation of gamma motion was also offered on the basis of a wealth of literature that suggests objects and paths of apparent motion are disambiguated on the basis of the ways that objects in the world tend to endure and move. In terms of gamma motion, it was thus argued that the visual system's unfamiliarity with sudden disappearance leads to an interpretation on the basis of statistical regularities in the ways that distal objects tend to project upon the retina as they move in 3-D space. Finally, the methodology introduced here can be easily adopted for the 'objective' study of a long known effect (gamma motion) that has not just received scant attention in recent times, but also most of the studies on it have used a subjective method of introspection.

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