

**The perceived position of moving objects:  
Visual prediction and its correction by transients**

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Thesis submitted to the University of Sussex  
for the degree of Doctor of Philosophy

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## Statement

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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.

Gerrit Maus

Brighton, April 28<sup>th</sup> 2008

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UNIVERSITY OF SUSSEX

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**The perceived position of moving objects:  
Visual prediction and its correction by transients****Summary**

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Despite processing delays in the neural pathways, moving objects are not seen as trailing their physical positions. Instead, they are perceived as shifted forward in the direction of motion. This shift becomes apparent in visual illusions such as the flash-lag effect. If, however, a moving object suddenly disappears from view or changes direction, there is usually no perceived overshoot of the object beyond extreme points of its trajectory. This thesis proposes a model based on two underlying mechanisms to explain these findings. The human visual system comprises a prediction mechanism that constantly shifts the perceived position of coherently moving objects forward in the direction of motion to compensate for processing delays. If an object suddenly disappears from view, these predictions become invalid and have to be corrected for. Transient signals resulting from the sudden disappearance are able to override ongoing prediction and facilitate accurate perception of the final position.

In a series of four articles this thesis presents empirical evidence for the proposed model. If a moving object disappears from view gradually, and therefore does not elicit a strong retinal transient, it is perceived to continue moving beyond the point where it is detectable on the retina. A functional imaging experiment showed that motion-sensitive area V3A in visual cortex represents moving objects in predicted positions. If a moving object disappears from view in the blind spot, it is seen in positions well inside the blind area. When two aligned objects move side by side and one of them disappears abruptly, the offset is perceived to lag behind. Intermediate situations, where moving objects elicit transients, but keep moving nonetheless, exhibit a competition between two positions based on prediction and transients. The implications of these findings for other theories of the flash-lag effect and localisation of moving objects are discussed.

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*“It is very difficult to make an accurate prediction, especially about the future.”*

Niels Bohr (1885 – 1962)

## A Introduction and Overview

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### A.1 Motivation and Outline of Thesis

Movement in the environment is one of the behaviourally most relevant stimuli for an organism. Movement in the peripheral space of sensory organs, for example on the skin of remote body parts or in the periphery of the retina, attracts attention and organisms direct their high-resolution sensory surfaces (e.g. finger tips or the fovea) to the locations of movement (James, 1890/1952). Movement is likely to stem from another organism, which could either be a conspecific, a potential mate or competitor, or another species, be it potential prey or predator. Even inanimate moving objects are likely to be of importance, as they could present an obstacle while the animal itself is in motion, or a possible threat. In all cases, having information about the exact position of anything that moves is a prerequisite for successful interaction with the moving object, be it avoidance or interception.

There are several problems the nervous system has to solve to determine the position of a moving object in the environment. One general principle in biological neural systems is that processing takes time. Processes such as phototransduction in receptor cells, signal conductance along nerve fibres and synaptic transmission between neurons all rely on electrochemical mechanisms that work in the order of several milliseconds and can add up to time spans of behavioural significance. During these time spans, the environment continues to change dynamically; other organisms and objects move and change position. In principle it is impossible for an organism to have absolute knowledge about the positions of all relevant objects. This is true even without

taking into account quantumphysical phenomena of uncertainty (Heisenberg, 1927).

However, to be able to interact with moving objects in a dynamic environment, organisms have developed sophisticated mechanisms to overcome these processing delays.

Without any kind of compensation for delays in neural processing it would be impossible for an organism to successfully interact with moving objects, as the position represented at any stage in the central nervous system would always lag behind the physical position of the object in the environment. Hence action directed at this lagging position would miss the object in question. Wild cats would jump short of fast moving prey animals; forest-dwelling animals would run into trees. Modern high-speed ball games provide nice examples to evaluate the potential error of localisations without compensation. If we assume neural delays from the retina to some cortical processing stage of about 100 ms, a tennis ball flying at a speed of 100 km per hour ( $27.8 \text{ ms}^{-1}$ ) would be misrepresented by 2.78 m. Obviously, in many cases predators are able to catch fast moving prey and tennis players are able to hit tennis balls. Compensation of delays at some stage of the neural processing is therefore a must.

Because of the sluggishness of muscle responses and inertia in the actual movement of limbs, compensation for delays in the motor system seems to be well established in neuroscience (Ghez & Krakauer, 2000). It is commonly assumed that delays in other parts of the nervous system are also compensated for at the motor stage of neural processing (Jordan, 1995). However, there is no a priori reason why all compensation should take place at one stage, as processing delays are prevalent in all parts of the nervous system. Observations of some visual illusions involving moving

objects have led to the proposal that sensory systems equally comprise prediction mechanisms to compensate for delays in efferent pathways and facilitate the accurate perception of positions (Nijhawan, 1994). One prominent illusion in this context is the flash-lag effect: When a brief flash is presented in alignment with a moving object, a gap is perceived between the flash and the moving object. The flash appears to lag behind the moving object. The argument goes as follows: Because the moving object moves on a consistent trajectory, the visual system is able to predict its position and compensate for processing delays. The moving object is therefore not seen in a position lagging behind the physical position, but close to its real position at any point along its trajectory. Because the flash is a sudden unpredictable event, delays cannot be compensated for in the same way and will only be perceived after a certain delay. The moving object will have moved on in this time, therefore a spatial gap between the flash and the moving object is perceived (Nijhawan, 1994).

This proposal has led to a considerable debate. Several alternative theories explaining the flash-lag effect have been brought forward (reviewed in section A.2.1). One finding in particular has been used to argue against the original prediction hypothesis: When the moving object abruptly disappears at the same time as the flash, no spatial gap between the two is perceived. All prediction is prone to errors in the case of abrupt events that lead to sudden changes in the state of the predicted system. If the perceived location of a moving object relies on a predictive mechanism, a perceptual overshoot of a moving object beyond its final presentation position would be expected, which is in stark contrast to most of the experimental findings. However, this finding does not rule out visual prediction in perception, if we assume that an additional mechanism exists that can correct for prediction errors (Nijhawan, 2002). Sudden

changes in the environment, like the abrupt disappearance of an object from view, are often associated with transient signals in neural pathways. In another perceptual phenomenon, namely backward masking, such transients are known to retroactively change the content of visual awareness. Perceptual localisation of moving objects might be based on a two-stage mechanism: A visual prediction mechanism localises consistently moving objects, and a correction mechanism based on transient signals corrects for prediction errors in the case of sudden unpredictable events. This thesis presents evidence for this proposal.

The thesis is structured as follows: Chapter A presents an overview of the work and provides a theoretical frame for the experimental studies. Section A.2 presents a detailed review of previous research in the field concentrating in particular on the debates circling around the flash-lag effect and related perceptual phenomena. Research on visual backward masking is also reviewed. Section A.3 presents the aims and general hypotheses of the thesis in detail and outlines the experimental work. Section A.4 summarises all findings and discusses their implications. The remaining chapters B to E present the experimental work in stand-alone research articles.

## A.2 Background

Visual motion can influence the perceived position of objects in the visual field in a variety of ways (see review by Whitney, 2002). Most important in the context of this thesis are the flash-lag effect (Nijhawan, 1994), in which a moving object is seen to be ahead of a flash that is presented in a physically aligned position, and representational momentum (Freyd & Finke, 1984), where the final position of a moving object is remembered to be further ahead than its actually presented final position. Research on

these two phenomena is reviewed in detail in sections A.2.1 and A.2.2. The following section A.2.3 mentions a few other phenomena where visual motion influences the perceived position of objects. Finally, section A.2.4 reviews research on visual backward masking, which is also important for the hypotheses of this thesis.

### **A.2.1 The Flash-Lag Debate**

#### *A.2.1.1 A historical perspective*

The last fourteen years have seen a considerable debate in the scientific literature on the underlying mechanism of the flash-lag effect. The recent arguments started with the publication of Nijhawan's (1994) motion extrapolation proposal. However, similar perceptual phenomena relating to the localisation of moving objects had been studied extensively much earlier (see next paragraph). Even the birth of experimental psychology itself might have depended on problems of perceptual localisation of moving objects. In astronomical measurements it was often necessary to record the accurate transit times of stars crossing the North-South meridian. To measure these time points astronomers had to record the time point when a star moved across a meridian wire in a telescopic view by estimating the perceived position of the star at certain clock beats (Mollon & Perkins, 1996). This method relied on the perception of the instantaneous visual position of a moving object at the incidence of an auditory time marker, and thus potentially gave rise to a cross-modal flash-lag effect (Alais & Burr, 2003). Observations of inter-subjective differences in this method triggered the first experimental investigations of reaction times and temporal order judgements and thus lay ground to the field of experimental psychology (Fröhlich, 1929; Mollon & Perkins, 1996).

*Measurement of the ‘sensation time’*

In the 1920ies and early 1930ies several researchers, mainly in Germany, set out to measure the time it takes from a physical event to the associated percept. This time was referred to as *Wahrnehmungszeit* ('perception time', Hazelhoff & Wiersma, 1924) or *Empfindungszeit* ('sensation time', Fröhlich, 1923); today it would most likely be called the *perceptual latency* of an event.

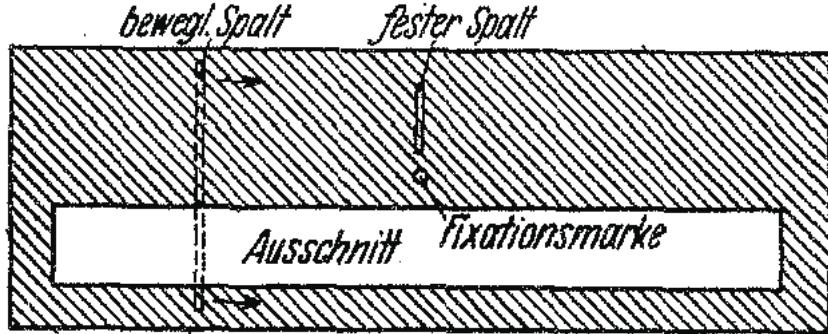
To determine the 'sensation time' Fröhlich used a simple visual stimulus of an illuminated bar moving from behind an occluder. The basic finding was that the bar did not seem to start moving right at the edge of the occluder, but at a position a short distance further ahead in the trajectory (Fröhlich, 1923). Many variants of this basic finding were reported in monograph length (Fröhlich, 1929). Fröhlich's assumption was that the time it takes the bar to move from the edge of the occluder to the first perceived position corresponds to the 'sensation time' of the bar. He argued that it takes time for the bar to be processed, and by the time the sensation is formed the bar has moved on and is therefore visible in the shifted position. This argument was criticised early on (Metzger, 1932; Rubin, 1929), as it is not entirely evident why after the 'sensation time' has passed the bar should be seen in a position shifted forward. However, what remains of Fröhlich's experiments in the context of this thesis is the prominent forward displacement of the first visible position of a moving object, today known as the 'Fröhlich effect'.

Hazelhoff and Wiersma (1924) used a different methodology to determine the time of perception. Their observers tracked a moving fixation mark with ocular movements. A briefly flashed target was presented at the position of the moving mark,

when it had traversed half of the visual display. The position of this flash was misperceived as shifted in the direction of the eye movement. Hazelhoff and Wiersma argued that in this case the position of the eye gaze moves before the flash is processed and perceived, and the flash is perceived at the position the eyes point to after this ‘perception time’ has passed.

Metzger (1932) explained the findings of Fröhlich and Hazelhoff as a special variant of the Hess phenomenon (1904). Stimuli of different contrasts have different ‘perception times’ and are therefore perceived to move at different speeds. He explained the basic findings of Fröhlich with the assumption that, initially, a newly appearing object has a longer ‘perception time’ than during later stages of its trajectory. In another experiment Metzger tested the prediction that a bar already in motion should perceptually lead a bar starting from behind an occluder. This prediction was experimentally confirmed. Following from this Metzger studied an additional stimulus, which seems to be the earliest example of a typical flash-lag display, as later used extensively in the flash-lag paradigm. A single vertical slit is moved behind a cardboard occluder with two cut-outs, one large horizontal cut-out, where the moving slit is seen as a moving bar, and a small one above the large cut-out, with the same width as the moving slit. Here the illuminated slit was seen as a flash (Figure A.1). Observers perceived the flash in the small cutout when the moving slit in the large cut-out was already in a position further along the trajectory of movement. Metzger argues that this phenomenon is in fact identical with Hazelhoff and Wiersma’s earlier findings. Although Metzger’s experiment did not involve any eye movements, the retinal stimulation was actually very similar to their earlier setup. In Hazelhoff and Wiersma’s experiment the moving object was stabilised on the retina by smooth pursuit eye

movements, the flash was briefly presented next to the fixation position, and the background was moving continuously on the retina due to the smooth pursuit eye movement.



**Figure A.1** To the best of my knowledge the first “flash-lag” stimulus display. A movable slit (*bewegl. Spalt*) is presented behind a cardboard occluder with two cut-outs: A large horizontal cut-out (*Ausschnitt*), where the slit is seen as a continuously moving object, and a small stationary slit (*fester Spalt*) above the fixation point (*Fixationsmarke*), where the moving slit appears as a brief flash. Metzger reported that observers saw the flash only when the continuously visible part of the slit was further ahead in the direction of motion. Source: Figure 3 from Metzger (1932).

Metzger concluded by pointing out that both Hazelhoff and Wiersma (1924) and Fröhlich (1929) had best measured the relative difference in the sensation time of a moving object and an abrupt onset. He deemed measurement of an absolute sensation time impossible. His explanation of the flash-lag phenomenon is therefore in principle identical with later proposals of differential latencies for moving objects and flashes (Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Murakami, 1998).

#### *Stroboscopically lit visual field*

Unrelated to the reports of the flash-lag phenomenon in the early literature on perceptual latencies, another similar finding was published in the late 1950ies. MacKay (1958) observed that when the eyes are moved involuntarily, e.g. by applying light

pressure with the finger to the side of the eyeball, continuously lit objects in the visual field are perceived to move, whereas a stroboscopically lit background (at 5-6 Hz) does not. Instead it seems to “move sluggishly to ‘catch up’ with the self-luminous objects” (MacKay, 1958, p. 507). These findings were interpreted as change and movement in the visual world having special significance and therefore being perceived saliently, whereas the comparative amount of information in the stroboscopically lit field is not actually changing as much from one flash to the next.

#### *Early eye movement research*

The early reports of the flash-lag phenomenon seemed to have gone unnoticed by much of the English language literature in the later twentieth century. However, citations for the findings on mislocalisations of flashes during smooth pursuit eye movements (Hazelhoff & Wiersma, 1924) can be found in some eye movement studies (e.g. Mitrani & Dimitrov, 1982). A later study by Mateeff and Hohnsbein (1988) also replicated Metzger’s first flash-lag finding and found differentially larger effects for motion towards the fovea compared to motion away from the fovea (see section A.2.1.3). The authors also interpreted these findings in terms of differential latencies.

#### *A.2.1.2 The rediscovery of the flash-lag effect*

In the early 1990ies Romi Nijhawan used a setup similar to MacKay’s use of continuously and stroboscopically lit visual scenes. A rotating rod in a dark room was illuminated continuously only in its central section, whereas the two ends could be illuminated by a brief stroboscopic flash. Observers reported to see the strobed parts of the rod to lag behind the continuously lit portion (Nijhawan, 1994). This paper was the first to use the term ‘flash-lag effect’, and also the first to propose a daring new explanation. Nijhawan proposed that the visual system comprises an extrapolation

mechanism for moving objects that is able to overcome transmission delays in the visual pathway from the photoreceptors in the eye to higher processing stages. The crucial difference for the perceived positions of the different parts of the rod in the experiment described lies in the predictability of the continuously visual part of the rod over the unpredictably occurring strobed parts. Whereas the visual system has formed a representation of the moving part that is extrapolated and corrected for processing delays, it cannot overcome the perceptual latency for the flashed parts of the rod. Therefore a spatial lag is perceived.

Motion extrapolation seems to be an early process, as it precedes influences of attention (Khurana & Nijhawan, 1995) and also colour integration. If a red flash is superimposed on a green bar, the flash is perceived as yellow, the sum of the two colours. If however the green bar is moving, and the flash, although superimposed on the bar, is perceived to lag the bar due to the flash-lag effect, the colours are decomposed to their constituent green and red components. A red flash is perceived lagging behind the green moving bar (Nijhawan, 1997).

At the time Nijhawan was unaware of the early findings from the 1930ies (personal communication), and apparently so were many others in the field who subsequently commented on Nijhawan's work. His paper was the starting point for an extended discussion in the scientific literature that continues to date.

#### *A.2.1.3 Stimulus dependencies and perceptual details*

This section will give a short overview of some of the findings concerning the perceptual details and stimulus dependencies of the flash-lag effect, before the different theories are discussed in the following sections.

*Speed dependence*

The magnitude of the spatial misalignment between the flash and the moving object scales with the speed of the motion (Krekelberg & Lappe, 1999; Nijhawan, 1994). This means the moving object is seen as shifted forward by a constant amount of time, rather than space. This time varies considerably between different stimulus configurations and also between observers. Typical values range between 40 and 80 ms.

*Eye movements*

The flash-lag effect seems to be dependent on retinal motion. When observers track the moving object in a typical flash-lag display with their eyes, no perceptual misalignment between the moving object and the flash is perceived (Nijhawan, 2001). However, as noted in early studies (Hazelhoff & Wiersma, 1924), in this case the perceived position of the flash can be mislocalised relative to the visual background, as the background is moving on the retina (see above).

*Circular and linear trajectories*

The flash-lag effect is a robust phenomenon and occurs for a large variety of motion trajectories. A lot of studies used rotational movement or objects on a circular trajectory, as this has the advantage of constant retinal eccentricity, when the centre of rotation is fixated. However, the flash-lag effect is also easily observed for objects translating on a linear trajectory (e.g. Watanabe, Nijhawan, Khurana, & Shimojo, 2001). There is an anisotropy in the size of the effect for motion towards versus motion away from the fovea, with larger effects measured for foveopetal than foveofugal motion (Brenner, van Beers, Rotman, & Smeets, 2006; Mateeff & Hohnsbein, 1988).

Another stimulus that has been used extensively is the so-called *ring-disc version* of the flash-lag effect: A black ring on a grey background moves on a circular trajectory, and at one instance a white disc is flashed very briefly filling the annulus of the ring. In this stimulus configuration observers see the black ring as not filled completely by the white disc. Instead they perceive the annulus as only partially filled, with the background colour in the leading portion of the annulus (Eagleman & Sejnowski, 2000). This is remarkable, as observers perceive an edge between the white disc and the ‘perceived void’ (Nijhawan, 2001) in the colour of the background. This edge is never projected on the retina.

### *The half cycle displays*

A lot of the discussion about different theories of the flash-lag effect focuses on the so-called *half cycle displays* (Khurana & Nijhawan, 1995; Nijhawan, 2002). The *flash-initiated cycle (FIC)* consists of a flash aligned with the first position of an object starting to move; the *flash-terminated cycle (FTC)* consists of a flash aligned with a moving object’s last position, i.e. the moving object disappears at the instance of the flash. Together these two half cycles form a *complete cycle (CC)* as used in Nijhawan’s (1994) original experiment.

In the FIC the effect is usually equivalent to the CC (Khurana & Nijhawan, 1995), although one study has reported larger displacements in the FIC (Ogmen, Patel, Bedell, & Camuz, 2004). In the FTC the flash-lag effect is usually abolished and the moving object is seen in a position aligned with the flash (Eagleman & Sejnowski, 2000; Nijhawan, 1992; Whitney, Murakami, & Cavanagh, 2000). However, these findings have caused considerable debate. In *representational momentum* the final position of a moving object is remembered to lie ahead of its last physical position (see section A.2.2

for a detailed discussion). Some studies also have found perceived overshoots (Fu, Shen, & Dan, 2001; Kanai, Sheth, & Shimojo, 2004) or undershoots (Baldo, Kihara, Namba, & Klein, 2002; Roulston, Self, & Zeki, 2006) for the last position of a moving object's trajectory. A large part of this thesis attempts a new interpretation for the findings of the flash-terminated flash-lag display.

*The flash-lag effect in other features and modalities*

The flash-lag effect occurs when observers compare the position of a continuously visible moving object with the position of a briefly flashed, static object. However, similar 'misalignments' occur for comparisons of other features in vision, and cross-modally.

Sheth, Nijhawan and Shimojo (2000) showed that other continuously changing features of an object are similarly 'extrapolated' as position in the standard motion flash-lag effect. When a visual stimulus patch continuously changes colour, luminance, spatial frequency or pattern entropy, and a second test patch with an identical feature value as in the changing patch is briefly flashed, observers perceive the continuously changing stimulus as further ahead in the dimension of change (Sheth et al., 2000). Although the amount of misalignment was highly variable depending on the feature in question, qualitatively all features tested showed the same effect.

Alais and Burr (2003) extended the flash-lag effect to the auditory domain. They found misalignments for both auditory frequency changes compared to a short burst of a single frequency, and auditory stereo position changes compared to a short tone from a static stereo position. Furthermore, when observers compared the position of an auditory stimulus moving in space to a visual flash, or a visual moving stimulus to an

auditory burst, the same typical flash-lag results were obtained, with the moving stimulus cross-modally leading the ‘flashed’ static stimulus (Alais & Burr, 2003). These cross-modal flash-lag effects were found to be bigger than uni-modal effects within vision or audition. In other stimulus configurations, however, an additional auditory tone at the time of the flash can decrease the flash-lag effect, which is thought to be a result of cross-modal temporal binding (Vroomen & de Gelder, 2004).

Other cross-modal flash-lag effects have been reported, when observers move their arm in the dark and compare the felt arm position to a visual flash ('motor flash-lag', Nijhawan & Kirschfeld, 2003), or when observers compare the position of a moving tactile object on their forearm to a visual flash (Rojas-Anaya, Thirkettle, & Nijhawan, 2005).

#### ***A.2.1.4 Attentional allocation***

Soon after the publication of Nijhawan's (1994) flash-lag paper, an alternative to motion extrapolation as the underlying mechanism was proposed by Baldo and Klein (1995). They showed that the illusory forward displacement of rotating moving dots relative to the perceived positions of flashed dots depends on the eccentricity of the flashes, with larger eccentricity leading to larger forward displacements. They argued that the time for the flashes to be perceived depends on their eccentricity, as it takes time to reallocate attentional resources to the more peripheral positions of the flashes. Due to this time cost in shifting attention from the moving object to the flash and back, the flash-lag effect is perceived.

In their reply Khurana and Nijhawan (1995) reported a similar stimulus, where flashing and moving objects were not presented in distinct spatial locations. In a

rotating line of dots, additional dots were flashed between the moving dots, and the flash-lag effect was still perceived. Furthermore, when the flashes were presented at the time the moving objects set into motion, termed a *flash-initiated* flash-lag display, an unabated flash-lag effect is perceived (Khurana & Nijhawan, 1995). In this case attention is oriented to neither of the two sets of objects (moving or stationary flashed), so there is no attentional disadvantage for one or the other. These findings argue against an explanation of the flash-lag effect solely in terms of the delays associated with attention shifts.

In these displays (Baldo & Klein, 1995; Khurana & Nijhawan, 1995) allocation of attention was manipulated rather implicitly. A later study manipulated attention in the flash-lag paradigm more explicitly by directing attention towards or away from the positions of flashes (Khurana, Watanabe, & Nijhawan, 2000). Although simple reaction times to flashes at cued locations were quicker than for un-cued locations, there were no differences in the measured size of the flash-lag effect depending on these manipulations. These findings argue against an explanation of the flash-lag effect solely in terms of delays in the redistribution of attentional resources from moving to flashed stimuli. In other studies it has been shown that the effect size can be modulated by voluntary attention (Baldo et al., 2002; Namba & Baldo, 2004). However, it is likely that attention here influenced perceptual latencies, and attention as such is not the underlying cause of the flash-lag effect, but has an additional influence on top (Namba & Baldo, 2004).

Voluntary attention, as discussed above, has to be distinguished from bottom-up or stimulus-based attention, which has been implicated as the mechanism behind the

line-motion illusion (Hikosaka, Miyauchi, & Shimojo, 1993). ‘Cue-induced visual focal attention’ has been suggested as a mechanism to accelerate perceptual processing of a moving object along its trajectory (Kirschfeld & Kammer, 1999). This proposal is discussed in more detail in the next section.

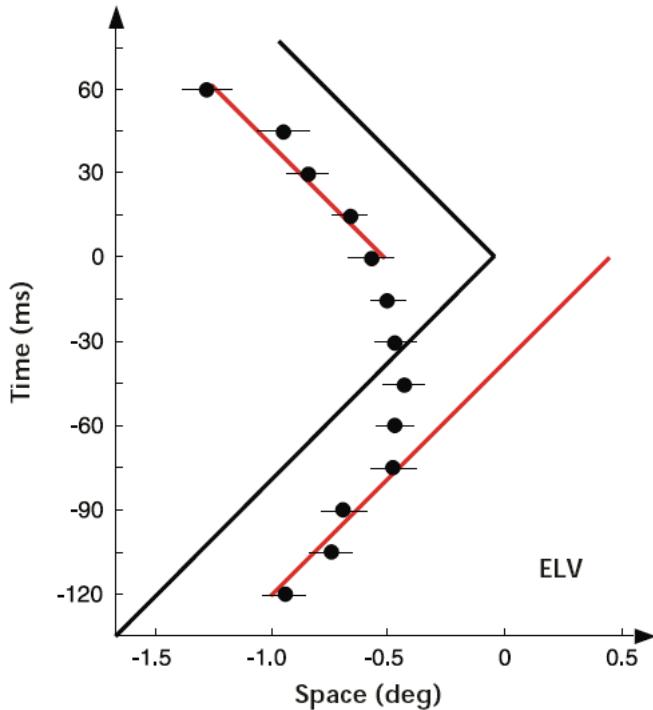
#### *A.2.1.5 Differential latencies*

Another alternative account of the flash-lag effect posits that moving objects are simply processed with shorter latencies than static flashes. This idea is identical to earlier theories about the phenomenon (Mateeff & Hohnsbein, 1988; Metzger, 1932), but has been independently re-stated in response to Nijhawan’s (1994) flash-lag paper (Purushothaman et al., 1998; Whitney & Murakami, 1998).

The motion extrapolation account of the flash-lag effect posits that a moving object is spatially shifted forward in the direction of motion based on information from the past trajectory. Therefore it predicts that a moving object that abruptly reverses the direction of movement should perceptually overshoot the point of reversal based on the past trajectory, and only later be perceived as shifted forward in the new direction. In a new variant of the flash-lag display, the moving object abruptly reversed the direction of motion, and flashes were presented at various timings before and after this reversal (Whitney & Murakami, 1998). In this experiment the positions of flashes were determined that caused the moving object to appear aligned with the flash at each of these timings. For the object in continuous motion flashes had to be presented about 45 ms ahead into the trajectory (the flash-lag effect). However, the flashes never had to be presented beyond the position of reversal to appear aligned, i.e., the moving object did not overshoot the reversal position (Whitney & Murakami, 1998). Instead, even before the object reversed its motion direction, the forward displacement effect diminished (see

Figure A.2). Similar findings were obtained for flash-lag displays, in which the moving object increased or decreased velocity at the time of the flash (Brenner & Smeets, 2000), or abruptly disappeared from view (Eagleman & Sejnowski, 2000; Whitney et al., 2000). Whitney and Murakami (1998) were the first to point out that these findings are incompatible with the motion extrapolation model and argued that differential latencies explain the data best. However the ‘rounding’ of the perceived positions near the point of reversal (Figure A.2) is not predicted by differential latencies either. In a later study the same researchers argued for an additional involvement of a temporal integration mechanism (Whitney et al., 2000, see next section).

Purushothaman and colleagues used different stimuli to come to the same conclusion, that the flash-lag effect is caused by differential latencies for moving and flashed objects (Purushothaman et al., 1998). Starting from the well-known fact that the perceptual latency of visual stimuli depends on their luminance (e.g. Hess, 1904), they hypothesised that increasing the luminance of the moving object, but not of the flash, should shorten its perceptual latency and therefore result in a larger flash-lag effect. Equivalently, increasing the luminance of the flash, but not of the moving object, should decrease the flash-lag effect. This hypothesis was confirmed in experiments (Purushothaman et al., 1998). The authors argued that a motion extrapolation mechanism that compensates for perceptual latency would need to have access to information about the change in latencies due to the change in luminance. This is physiologically implausible, and the fact that a change in latencies brings about a change in the size of the flash-lag effect, leads them to conclude that differential latencies themselves are the cause behind the flash-lag phenomenon.



**Figure A.2** The typical result of flash-lag experiments involving an abrupt reversal of the direction of movement (taken from Whitney & Murakami, 1998). The solid black line depicts the trajectory of a moving object, reversing motion direction at time 0 in position 0. The red lines depict the perceived positions as predicted by motion extrapolation, spatially shifted forward in the direction of motion to compensate for neural delays. The black dots (with errorbars) are the perceived positions of the moving object as measured by the positions of flashes that appear aligned with the moving object at time points around the point of reversal (Whitney & Murakami, 1998).

A possible mechanism that achieves shorter latencies for moving objects has been described by Kirschfeld and Kammer (1999). Re-investigating the Fröhlich effect they claimed that an interplay of cue-induced focal visual attention and metacontrast causes the forward displacement of the first perceived position of a motion trajectory (Fröhlich, 1923). The moving object itself acts as a cue to the subsequent presentation of the same object in a neighbouring position. This cuing facilitates and accelerates the perception of the moving object. Furthermore, the moving object acts as a metacontrast mask for

previous presentations of the same object in earlier positions of the trajectory, and thus reduces visual persistence at earlier positions and contributes to the deblurring of motion (Burr, 1980). The same mechanism would also explain the forward displacement of the moving object in the flash-lag effect (Kirschfeld, 2006; Kirschfeld & Kammer, 1999). Subsequently other groups made similar suggestions (Kanai et al., 2004; Sheth et al., 2000).

#### *Evidence against differential latencies*

Despite its simplicity and intuitive appeal, the differential latency account of the flash-lag effect faces several problems. For example, Eagleman & Sejnowski (2000) presented a flash followed by the onset of a moving object in the same position after varying delays. Giving the flash a ‘headstart’ in this way should annihilate the flash-lag effect, if it relied on differential latencies, but the size of the flash-lag effect remained unchanged by this manipulation (Eagleman & Sejnowski, 2000). In a similar flash-initiated display there was no measurable difference in reaction times to either the motion onset or the flash, and temporal order judgements revealed a slight processing advantage for the flash (Nijhawan, Watanabe, Khurana, & Shimojo, 2004). Note that early on Rubin (1929) reported that in a similar display he could bias either stimulus to be perceived first, and concluded that there are no systematic differences in the time to perception for static vs. moving objects.

#### *Physiological measurements of response latencies*

Physiological evidence for faster processing of moving objects is sparse. Several studies reported spike latencies for single neurons in primate visual cortex in response to visual stimulation (Maunsell & Gibson, 1992; Raiguel, Lagae, Gulyas, & Orban, 1989; Raiguel, Xiao, Marcar, & Orban, 1999; Schmolesky et al., 1998). In comparison,

responses to moving stimuli seem to be slower than responses to transient stimuli, but comparisons between studies are difficult. The only study to compare latencies for flashed and moving stimuli directly, found slightly longer ( $\sim 5$  ms) response latencies for moving stimuli in neurons of area MT (Raiguel et al., 1999). This advantage for flashed stimuli is the opposite of what is needed for a differential latency account of the flash-lag effect.

In single cell recordings of isolated rabbit and salamander retinae it has been shown that the peak spiking rates of retinal ganglion cells in response to a moving stimulus are achieved, when the leading edge of the moving stimulus enters the receptive field, or even slightly before (Berry, Brivanlou, Jordan, & Meister, 1999). The authors interpreted this as neural anticipation of a moving stimulus in the retina. Similarly, in cat primary visual cortex the responses of populations of neurons to moving squares are faster than for flashed squares (Jancke, Erlhagen, Schoner, & Dinse, 2004b). Whereas here the authors argue for shorter latencies for moving stimuli, their design does not allow distinguishing between their explanation and the alternative of a spatial extrapolation causing the shortened delays.

Indeed, the accounts using differential latencies and motion extrapolation as explanations for the flash-lag phenomenon are not always easily distinguishable and might not be mutually exclusive (Nijhawan, 2002; Nijhawan et al., 2004). If a moving object is extrapolated, this will result in measurements of shorter latencies, and vice versa, if moving objects had shorter latencies, this could be interpreted as a spatial forward shift in comparison to an object with ‘standard latency’.

#### A.2.1.6 Temporal integration

One further influential theory of the flash-lag effect, and of visual localisation of moving objects in general, is *temporal integration*. Several researchers have formulated different versions of this theory, but common to all is that the perceived position of a moving object is the outcome of an averaging process that samples positions over an extended period of time.

A set of studies published between 1998 and 2000 argued heavily against the motion extrapolation explanation of the flash-lag effect. Their arguments relied on the results of experiments introducing abrupt changes in the trajectory of the moving object at the time of the flash. The flash-lag effect scales linearly with speed (Nijhawan, 1994). If the speed is abruptly changed at the time of the flash, the speed after the flash determines the size of the illusion (Brenner & Smeets, 2000). When the motion reverses direction, the moving object is never perceived to overshoot the point of reversal, as motion extrapolation would predict (Whitney & Murakami, 1998; Whitney et al., 2000). Similarly, when the moving object disappears abruptly at the time of the flash, the so-called flash-terminated display, the object does not overshoot its final position and there is no apparent lag between the moving object and the flash (Eagleman & Sejnowski, 2000; Whitney et al., 2000). In general these experiments revealed that the perceived position of the moving object at the time of the flash is determined by the events happening after the flash.

In the direction reversal experiments (Whitney & Murakami, 1998; Whitney et al., 2000) the perceived position of the moving object near the point of reversal seems to be ‘rounded’ (see Figure A.2), i.e., even before the physical reversal the moving object is

perceived as shifted less, never reaches the true reversal point, and only after some considerable time is perceived in baseline flash-lag positions. Whitney and colleagues noted that this finding cannot entirely be explained by differential latencies, and proposed that additionally a spatiotemporal filtering mechanism must be involved to cause the ‘perceptual blunting’ (Whitney et al., 2000).

Lappe and Krekelberg (Krekelberg & Lappe, 1999, 1998) conducted experiments on the flash-lag effect, in which they used repeated flashes or stroboscopic motion at different frequencies. Analogously to earlier stimuli by Baldo and Klein (1995) they used a rotating line of dots and flashed additional dots further out from the central fixation point. Here the outer dots were ‘flashed’ repeatedly at frequencies from 1 to 16 Hz. In another condition the frequency was held constant at 1 Hz, but the duration for which the outer dots were visible was varied from 28 ms to over 600 ms. During this time, the outer dots were not stationary, but moved in the same way as the inner dots. Longer presentation or higher frequency of presentation of the outer dots led to a reduction of the flash-lag effect, with presentation durations of 500 ms and longer or presentation frequencies of 16 Hz and higher leading to no perceptual lag. It is the total duration of visibility of the outer dots that determines their lag. These results are not easily explained by either motion extrapolation or differential latencies, but the data can be fitted convincingly by a spatiotemporal filtering model (Krekelberg & Lappe, 1999; Lappe & Krekelberg, 1998). In a later paper this model was developed into a full computational model of relative position judgements based on a local energy detection model (Krekelberg & Lappe, 2000). However, some of the model’s specifications seem implausible. To fit the data it has to assume an unconvincingly long integration time of about 500 ms, and it has to assume that a position signal persists for extended periods at

the last visible position of a moving object after it has disappeared (Krekelberg, 2001; Krekelberg & Lappe, 2000). The flash lag-effect, in this view, occurs when the spatiotemporally filtered position of the moving object is compared to the persisting position of the flash, which is no longer visible.

Based on findings that the amount of forward mislocalisation in the flash-lag effect is based on the speed of motion after the flash, Brenner and Smeets (2000) also criticised the motion extrapolation and differential latencies models. While it might be readily assumed that the visual system uses a ‘snapshot’ of the scene to judge the apparent alignment of the moving object and the flash, Brenner and colleagues hypothesised that such a snapshot is not easily available, but has to be computed ad hoc, when a judgement about the position is needed (Brenner & Smeets, 2000; Brenner et al., 2006). This computation is triggered by the flash and supposedly relies on a sampling of positions from the trajectory. As the sampling is triggered by the flash, only positions from after the flash can contribute to the sample and hence the flash-lag effect is perceived. A similar argument has been made by Eagleman and Sejnowski (2000, see next section). However, it does not entirely stand that only events from after the flash contribute to the flash-lag effect. When in a flash-initiated display the moving object is presented statically in its first position before starting to move, this reduces the flash-lag effect (Chappell & Hine, 2004; Whitney & Cavanagh, 2000b). Also, under certain stimulus configurations a flash-lag effect can be observed in the flash-terminated condition, when there is no motion after the flash (Kanai et al., 2004; Munger & Owens, 2004).

Another variant of temporal integration has been advanced by Roulston, Self and Zeki (2006), who proposed that temporal averaging is weighted towards the most recently sampled positions. This explains, as they argue, a small undershoot of the final perceived position of a moving object (Baldo et al., 2002; Roulston et al., 2006), as well as the Fröhlich and standard flash-lag effects. In this variant of temporal integration it also needs to be assumed, that the integration interval extends to times after the flash.

#### **A.2.1.7 Postdiction**

As mentioned above, the movement of the object after the flash seems to determine the size of the flash-lag effect (Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000). Paradoxically this means, that the perceived position of the moving object is based on the future, i.e., on events that have not yet taken place at the time of the flash. This is of course metaphysically impossible. Brenner et al. (2000) therefore argue that the perceptual determination of an instantaneous position is only started once a temporal marker (e.g. a flash) has been perceived.

Similarly, in their influential paper Eagleman and Sejnowski (2000) claim that a flash interrupts the visual system's continuous motion integration of the moving object. After the flash the integration starts anew, and the new sampling outcome is ‘postdicted’, or reassigned, to the time, when the flash was perceived. *Postdiction* here is to be understood as the conceptual opposite of prediction: Rather than anticipating an event that is about to take place in the future, postdiction means that an event is registered after it has taken place with the knowledge that its time of occurrence was earlier. There are a number of postdictive phenomena in perception, in which the conscious percept is only determined in retrospect. For example in backward masking the subsequent presentation of a mask can render a previously presented target invisible,

although this target would clearly be perceived without the mask (Alpern, 1953; Breitmeyer, 1984). In the colour phi phenomenon a dot subsequently presented in two distinct positions and different colours is seen to change colour on its apparent motion path half way between the two presentation positions (Kolers & von Grünau, 1976). In the cutaneous rabbit illusion a tactile stimulus is perceived to move continuously along the forearm, although stimulation occurs only at two discrete positions (Geldard & Sherrick, 1972). The controversial Libet experiments about the origin of free will (Libet, 1981) and several other phenomena (reviewed in Dennett & Kinsbourne, 1995) can similarly be explained by a retrospective determination of the content of conscious perception, or postdiction.

Eagleman and Sejnowski (2000) concluded that all conscious perception is postdictive and lags the physical events of the world by about 80 ms. This fact alone, however, would not explain the flash-lag effect, if the perception of both the flash and the moving object was delayed by the same amount. So additionally it has to be assumed that the flash interferes with ongoing motion processing and causes the sampling of positions to be restarted when the flash is perceived.

The postdiction account has been formalised computationally. Applying computational principles from the engineering literature, Rao, Eagleman and Sejnowski (2001) simulated the direction reversal experiments by Whitney and Murakami (1998) with an optimal smoothing model. Their model combines a Kalman filter to calculate a prediction for the position of a moving object from the past trajectory (Kalman, 1960) with a smoothing model that uses future data for a more accurate estimation of position. The output of such a model with access to about 80 ms of future input data accurately

simulates the experimental data from direction reversal stimuli (Whitney & Murakami, 1998). This in turn requires the conscious percept to be delayed by at least the amount of time from the future that is used in the smoothing model. Rao et al. (2001) speculated, that a fixed lag of about 80 ms represents an optimal trade-off between spatial and temporal accuracy in biological perception. However, as Grush (2005) pointed out, a fixed lag does not necessarily have to be assumed in such a model, as it would easily allow for multiple estimates of the events at one physical time to be computed at several time points, as more and more sensory data becomes available. This idea is compatible with Dennett's multiple drafts model for consciousness (Dennett, 1991; Dennett & Kinsbourne, 1995).

More recently Eagleman and Sejnowski published a slightly different account of the flash-lag effect (Eagleman & Sejnowski, 2007). Here they claimed that motion signals from after the flash bias the localisation of the moving object forward in the direction of motion. This account arises out of a comparison of the flash-lag effect with other mislocalisation phenomena involving visual motion, in which static flashes or objects can be 'dragged' along with the motion of a stimulus (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990; Whitney, 2002). This proposal is essentially a *spatial* account of the flash-lag phenomenon, whereas the earlier postdiction model relied on *temporal* integration to cause the misalignment between the flash and the moving object. A similar conclusion was reached in another study re-examining the dependence of the flash-lag effect on the distance between flashed and moving object (Linares, Lopez-Moliner, & Johnston, 2007).

#### *A.2.1.8 Computational models of the flash-lag effect*

Many of the theories of the flash-lag effect remain on a rather descriptive level. Only a few studies in the literature actually attempted to formalise a theory into a computational framework that could be tested against experimental data. This section describes some of these studies in more detail.

##### *Temporal Integration*

As described in section A.2.1.6 Krekelberg and Lappe (2000) developed a computational model for the perceived relative position between two objects. They combined temporal and spatial filters that mimic receptive field properties of visual neurons with a local energy model for edge detection (Morrone & Burr, 1988) to determine the position of objects in the visual field. In the final stage of their model the difference in the position of two objects is averaged over a long integration time window of approximately half a second. This model accurately simulates the behavioural data of experiments, in which the position of a continuously moving object is compared to an intermittently presented moving object or a repeatedly flashed object (Krekelberg & Lappe, 1999). Additionally, however, it has to be assumed that an amodal position signal persists in the last presentation position of an object that abruptly disappears from view (Krekelberg, 2001).

##### *Models for retinal ganglion cell responses*

Some efforts have been undertaken to model the neural responses of retinal ganglion cells in response to moving stimuli. In single cell recordings from ganglion cells of isolated salamander and rabbit retinae, Berry, Brivanlou, Jordan and Meister (1999) found the peak firing rate response to occur before the moving stimulus actually reached the neuron's receptive field centre. Berry et al. (1999) modelled this response

by assuming a spatio-temporal filter, plus a non-linear contrast gain control mechanism that modulates the increase in firing rate in response to extended stimulation by inhibitory feedback. Their model accurately captures the physiological data, and the authors conclude that such a mechanism is underlying the physiological extrapolation of moving objects in the retina.

In a behavioural study, Fu, Shen and Dan (2001) showed that the last position of a stopping object is perceived as shifted forward, when its edges are blurred, rather than sharp-edged as usually in studies on the flash-terminated flash-lag display (Eagleman & Sejnowski, 2000; Whitney et al., 2000). Fu et al. (2001) used a similar model to Berry et al. (1999) incorporating a spatio-temporal filter with a biphasic temporal impulse response function. This filter consists of an early excitatory phase and a delayed inhibitory component. Their model accurately fits the behavioural data for sharp-edged and blurred visual targets. The delayed inhibitory component of the temporal impulse response obliterates the need for non-linear feedback like the contrast gain control mechanism used in Berry et al.'s (1999) model. In further experiments Fu et al. (2001) found that the final position of blurred *second order* motion targets was also perceptually shifted forward from the stopping position. Second order motion is not defined by moving luminance contrast and thus can only be detected at cortical sites. So although biphasic impulse response functions can be physiologically measured in retinal ganglion cells, Fu et al. (2001) argued for the involvement of cortical mechanisms in motion extrapolation. It has to be noted, however, that their model does not predict the linear speed dependency of the forward displacement as found in the flash-lag effect (Nijhawan, 1994). To account for more behavioural data on the dependency of the flash-lag effect on spatial frequency and different velocity ranges, Cantor and Schor

(2007) proposed to combine biphasic temporal impulse response function filters with a position averaging model (Krekelberg & Lappe, 2000).

#### *Motion extrapolation in Wilson-Cowan type networks*

Wolfram Erlhagen (2003) proposed that the perceived forward shift in the flash-lag effect could be explained by an internal model that predicts the motion of the moving object, equivalently to forward models predicting the movements of limbs in the control of action (e.g. Wolpert, Ghahramani, & Jordan, 1995). He used a two-layer neural field model with one excitatory and one inhibitory layer based on the Wilson-Cowan network architecture (Wilson & Cowan, 1973) that has been designed to implement some basic features of cortical processing. Similar network architectures have also been used to model such diverse visual phenomena as orientation selectivity or backward masking (Ernst & Eurich, 2002; Herzog, Ernst, Etzold, & Eurich, 2003). Each neuron of the excitatory layer integrates inputs from its neighbours and projects to the inhibitory neuron in the same cortical column (or retinotopic position). Inhibitory neurons additionally integrate inputs from adjacent excitatory neurons, but project back to the excitatory layer only locally. Interactions within the excitatory layer are gated by a *shunting threshold* that effectively prohibits excessive lateral spread of activity (Erlhagen, 2003). In response to a moving stimulus this network exhibits a travelling wave of activity, representing the movement of the stimulus. Due to the lateral spread of excitatory activity in the network, there is a subthreshold ‘preativation’ leading the peak of the travelling wave that shortens the latency to peak for a moving stimulus compared to a static flashed stimulus presented in isolation. This feature of the network is akin to cue-induced visual focal attention (Kirschfeld & Kammer, 1999). Additionally, there is a shortening of the response duration for a moving stimulus due to the later onset of inhibition from the second layer in the network that leads to a

deblurring of the moving stimulus (Burr, 1980). In these respects the model achieves equivalent behaviour to the models mentioned above (Berry et al., 1999; Fu et al., 2001).

For different parameter values, especially for lower shunting thresholds, self-stabilised waves of activity can continue to move in the network even in the absence of continued bottom-up stimulation. Erlhagen (2003) speculates that such an internal model of a moving stimulus can be used in cognitive tasks such as predicting the positions of a moving object passing behind an occluder. Furthermore, Erlhagen proposes a multi-layered architecture, in which self-sustained waves of activity in higher layers feed back to a *position field* that also receives bottom up input from the retina. If the internal model in a higher layer predicts moving stimulus positions, the architecture can achieve a complete compensation for processing delays in the activity of the position field (Erlhagen, 2003).

#### *Feed-forward neural network*

A much simpler feed-forward neural network model can also exhibit some of the perceptual features of the flash-lag and Fröhlich effects. Baldo and Caticha (2005) implemented a three-layer feed-forward network of leaky integrate-and-fire neurons. Neurons in each layer receive strong excitatory connections from the neuron of the preceding layer in the same ‘retinotopic’ position, and weaker excitatory connections from laterally adjacent neurons of the preceding layer. To implement antagonistic center-surround receptive fields there are additional inhibitory connections from laterally more distant neurons of the preceding layer. Despite the remarkable simplicity of the network the activity of neurons in the output layer qualitatively reproduces the main flash-lag findings, including the flash-initiated and flash-terminated findings

(Eagleman & Sejnowski, 2000; Khurana & Nijhawan, 1995; Nijhawan, 1992), the dependency on relative stimulus intensity (Purushothaman et al., 1998) and the influence of cuing of the first motion position (Whitney & Cavanagh, 2000a). On the other hand, the findings are too general to be quantitatively compared to experimental data. It is not clear if the model produces a forward shift great enough to account for the perceptual mislocalisation.

### *Kalman filter models*

As mentioned in section A.2.1.7 the Kalman filter (Kalman, 1960) is a computational principle frequently used in engineering to solve measurement problems. In estimating a time series (like subsequent positions of an object in motion) the Kalman filter uses an internal model to predict the future state of the system to be measured to reduce measurement errors in the presence of noise. In principle this is achieved in a similar way by the neural network architecture proposed by Erlhagen (2003). As described before, Rao et al. (2001) used an extended Kalman filter model to simulate the direction reversal experiments by Whitney and Murakami (1998). Similar ideas have been used by Grush (2005) to explain several temporal phenomena in perception. One basic distinction in the assessment of models of this kind is the time scale of data the computation process has access. Rao et al.'s model simulation uses data from up to 80 ms into the future, arguing for the 'postdictive' nature of perception (Eagleman & Sejnowski, 2000) and a general delay of all percepts by at least 80 ms from the time the corresponding physical event occurred.

### *Bayesian models*

Another class of models that have increasingly been used in neuroscience and visual science are models based on Bayes' theorem. Somewhat surprisingly a full-scale

simulation of the flash-lag paradigm in a Bayesian framework has so far not been published in the literature.

One Bayesian model attempts a far-reaching description of activity in the visual cortex (Rao & Ballard, 1999; Rao, 1999). In this model higher layers of the processing hierarchy build up internal models that try to predict activity in the preceding layer. This activity gets fed back to earlier layers, where it is compared to bottom-up stimulation. The residual error of this comparison is used in shaping the prediction of the next time step in the higher layer. In principle this model is similar to the multi-layered architecture by Erlhagen (2003) and would possibly be able to simulate most flash-lag findings.

#### **A.2.1.9 Conclusion**

As this chapter demonstrates there has been considerable debate about the origins and underlying mechanisms of the flash-lag effect. Several theories have been discussed in the literature, but each attempt faces a few shortcomings or inconsistencies with the experimental evidence. Despite fourteen years of research since Nijhawan's (1994) rediscovery of the phenomenon, there does not seem to be a generally accepted consensus by researchers in the field. This thesis is in large parts an attempt to reconcile the original motion extrapolation theory with some of the later experimental findings on the flash-terminated flash-lag display.

#### **A.2.2 The Representational Momentum Debate**

Another visual phenomenon related to the last visible position of a moving object is called *representational momentum* (Freyd & Finke, 1984). This section will review

some of the literature on representational momentum with special emphasis on the case of smoothly moving objects, as this is most relevant to the scope of this thesis.

#### *A.2.2.1 Original experiments*

In the 1980s Jennifer Freyd conducted several studies into dynamic representations for visual scenes. Her main hypothesis was that static images of scenes implying motion trigger dynamic representations in the mind, and therefore produce systematic errors in, for example, judging positions of objects in static depictions of a dynamic scene, such as an image of a person jumping off a wall. In one study she showed that observers were slower to identify a static test image of a dynamic scene as ‘different’ from an earlier presented image of the same scene, if the test image depicted the scene at an advanced time point rather than an earlier time point (Freyd, 1983). Freyd concluded that observers formed a ‘dynamic mental representation’ of the scene, in which dynamic objects are represented as being in motion.

This is the case not only for ‘natural’ motion, as in the photographs used by Freyd (1983), but also for arbitrary motion implied by simple geometric shapes. In a seminal study Freyd and Finke (1984) presented a sequence of three rectangular shapes in different orientations, with the presentation order either being random or consistent with rotation in one direction. A relatively long inter-stimulus interval (ISI) of 250 ms was used to prevent the perception of apparent motion or motion after effects. After the sequence a test rectangle was presented that could be identical to the last rectangle of the sequence, or rotated slightly forward or backward. Observers were again slower and more error-prone in identifying the forward rotated shape as different, when it was presented after the sequence implying coherent motion. This effect has been termed “Representational Momentum” (Freyd & Finke, 1984). Freyd argued that the dynamic

mental representation of the rectangle has *momentum*, similar to the physical momentum of moving objects. The moving mental representation of an object cannot be abruptly stopped, but continues to move on for a while, and hence leads to the forward bias in memory.

This forward displacement of the last position of a moving object is speed dependent, with higher speeds leading to a larger forward bias in memory (Freyd & Finke, 1985). The displacement also depends on the retention interval, with—at least for relatively short intervals—longer retention causing larger forward bias (Freyd & Johnson, 1987). Both these findings are predicted by the analogy to physical momentum. Extending the idea of internal representations mimicking physical laws, other studies have predicted and presented evidence for similar effects incorporating other physical laws, or ‘environmental invariants’, like gravity, friction, or centripetal forces (reviewed by Hubbard, 1995).

#### **A.2.2.2 *Representational momentum for smoothly moving objects***

Freyd and Finke (1984) originally used what they called ‘implied motion’, subsequent presentation of snapshots of a rotating object at long ISIs, to prevent the perception of apparent motion or motion after effects that could influence the localisation of the object in their task. Only later Hubbard and Bharucha (1988) reported a representational momentum effect for smoothly moving stimuli. They presented a moving target on a straight horizontal or vertical trajectory and asked observers to indicate the last perceived position of the moving object by pointing a computer mouse pointer to the remembered position. Their results showed that the remembered position was usually displaced forward in the direction of motion, with higher velocities leading to larger displacements. Furthermore, observers showed a small bias to remember

horizontally moving targets as disappearing further down on the screen as they actually did, and also showed greater forward displacements for vertical downward motion compared to upward motion (Hubbard & Bharucha, 1988). This finding is consistent with an internalised model of gravity exhibiting an influence on the dynamic representation for the moving object (Hubbard, 1995).

In an additional condition Hubbard and Bharucha (1988) presented a moving target that changed direction when reaching a static visual barrier, as if the target was a ball bouncing off a wall. When the target abruptly disappeared at the static barrier, the memory displacement of the target was in the direction of anticipated motion, i.e., away from the barrier. This result speaks for the hypothesis that the visual system comprises an implicit model of the environment (Hubbard, 1995).

#### ***A.2.2.3 Representational momentum and eye movements***

The early studies on representational momentum did not control for eye movements or even give explicit instructions regarding observers' eye gaze. It is likely that observers were tracking the target with pursuit eye movements, as generally there is a tendency to track moving objects in the visual field. A simple alternative explanation of the representational momentum effect would be as follows. When the object disappears, the eyes and thus the point of fixation keep moving in the same direction for a while, due to neural delays in the control of eye muscles or due to physical inertia of the eyeball. The representational momentum effect occurs, because observers confuse the last position of the moving object with the position of their eye gaze.

This alternative explanation has been argued against on the grounds that the representational momentum effect similarly occurs when multiple targets in implied

motion are presented simultaneously (Finke, Freyd, & Shyi, 1986) and thus eye gaze tracking of targets is not possible. Also, the finding that targets perceived as ‘bouncing’ off an obstacle (Hubbard & Bharucha, 1988) are mislocalised in the anticipated direction, opposite to the previous motion, is difficult to explain with a simple effect of eye movements (Hubbard, 1995).

Investigating the eye movement hypothesis, Kerzel and colleagues (Kerzel, 2000; Kerzel, Jordan, & Müsseler, 2001) replicated Hubbard and Bharucha’s (1988) findings, but found largely reduced or no forward displacement of the target’s final position, when observers were instructed to maintain steady fixation. Furthermore, using temporal order judgements a long perceptual persistence (~59 ms) of a moving object after its abrupt disappearance was derived. Kerzel (2000) concluded that visual persistence plus ‘overtracking’ of the final position by smooth pursuit eye movements (Mitrani & Dimitrov, 1978) explains the representational momentum effect for smoothly moving objects (Hubbard & Bharucha, 1988).

Stork and Müsseler (2004) introduced another manipulation: The target could either disappear randomly under control of experimental software, or when observers pressed a key. They found that perceptual forward displacements are larger in the random offset condition, coinciding with larger ‘overtracking’ of the moving object’s last position, as measured with an eye tracker (Stork & Müsseler, 2004). When observers triggered the disappearance of the target themselves, overtracking and the forward displacement of the final position were largely reduced. This result clearly speaks for a contribution of eye movements to the representational momentum effect, at least for smoothly moving objects. More generally, although a cognitive explanation for

representational momentum involving higher-level processes seems to be prevalent in the literature, low-level perceptual contributions to the effect do play a role and cannot be ruled out completely (Kerzel et al., 2001).

#### ***A.2.2.4 Representational momentum and the flash-lag effect***

If we consider the representational momentum effect a perceptual phenomenon, rather than a cognitive effect in visual short-term memory, the stimulus shares some strong similarities with the flash-terminated flash-lag display. The final position of a moving object is judged, either in comparison to a brief flash (flash-lag effect), in comparison to a subsequently presented probe target (Kerzel, 2000) or by pointing a cursor to the final position (Hubbard & Bharucha, 1988). In both effects, representational momentum and flash-lag, the position of a moving object is perceived as displaced forward, however, the specific circumstances are rather different. The forward displacement of the last perceived position in representational momentum depends on smooth pursuit eye movements (Kerzel, 2000; Kerzel et al., 2001), whereas the standard flash-lag effect is abolished when the moving object is tracked with eye movements (Nijhawan, 2001). The data agree in the case of flash-terminated flash-lag and representational momentum displays, when observers maintain static fixation: In both cases, no forward displacement is observed (Eagleman & Sejnowski, 2000; Kerzel, 2000; Kerzel et al., 2001).

In a set of experiments Müsseler, Stork and Kerzel (2002) tried to directly compare the two phenomena and the Fröhlich effect, with somewhat unexpected findings. For the flash-terminated flash-lag display they found a small perceptual *undershoot* of the moving object, but an overshoot when the flash was absent (representational momentum). This is at odds with other findings by Kerzel and

colleagues showing the absence of representational momentum under steady fixation conditions (Kerzel, 2000; Kerzel et al., 2001). Conversely, Munger and Owens (2004) found an increase in the size of a representational momentum effect, when they added flashes to the stimulus display. More recently Roulston et al. (2006) found undershoots for the final position of a moving object with and without accompanying flashes (termed ‘flash-lead effect’ and ‘reverse representational momentum’, respectively). Despite the contradictions in their results, Müsseler et al. (2002) proposed that an asymmetric spread of activity as proposed by others (Erlhagen & Jancke, 1999; Kirschfeld & Kammer, 1999) could be the underlying cause for all phenomena, the Fröhlich and the flash-lag effects and representational momentum.

However, most recent studies agree that representational momentum does not exist for smoothly moving objects under steady fixation. The earlier findings of representational momentum for implied motion or static images of dynamic scenes seem to be best explained by higher-level cognitive effects in visual short-term memory. What remains to be explained is the absence of an overshoot of a moving object beyond its final position in the representational momentum paradigm and in the flash-terminated flash-lag effect, as some of the theories attempting to explain the localisation of moving objects by the visual system would predict such an effect (see section A.2.1). This thesis offers a new hypothesis based on an interplay of motion extrapolation and backward masking by visual transients.

### A.2.3 Other mislocalisation illusions

#### A.2.3.1 Position shift in the motion aftereffect

Adapting to visual motion in one direction causes a motion aftereffect: If after prolonged exposure to visual motion in one direction a stationary test pattern is presented, it will be perceived to move in the opposite direction of the adapting motion (reviewed in Mather, Verstraten, & Anstis, 1998). This phenomenon has traditionally been thought to demonstrate that perceived motion and position are independent. Although physical motion is defined as a change of position over time, in the motion aftereffect motion is perceived without a change of position. This demonstrates that motion and position are processed in independent pathways in the brain.

Although this observation remains true, motion and position interact in more complex ways. In the motion aftereffect the perceived motion can actually lead to a perceived position shift of the test pattern (Snowden, 1998). When observers adapt to two gratings drifting in opposite directions in separate positions of the visual field, subsequently presented aligned test gratings are seen to be misaligned. Each one appears shifted in the direction opposite of the adapting motion at its presentation position, i.e. in the direction of the motion aftereffect. This effect is thought to be based on activity in cortical motion area MT/V5, as transcranial magnetic stimulation (TMS) of MT/V5 greatly reduces this perceived position shift (McGraw, Walsh, & Barrett, 2004).

#### A.2.3.2 Position shift of motion in stationary windows

Two seminal papers showed that motion within a stationary object can shift the perceived position of the whole object in the direction of the motion (De Valois & De

Valois, 1991; Ramachandran & Anstis, 1990). Ramachandran and Anstis (1990) presented drifting random dots within stationary squares on a background of stationary random dots. The ‘kinetic edges’ of these squares were defined only by the motion of the dots within the squares; when the motion was stopped the squares became invisible. When four of these squares were arranged in a square pattern, whereby the upper two squares contained inward moving dots and the lower two squares outward moving dots, a trapezoid pattern was perceived. All squares appeared shifted in the direction of their contained motion; therefore the distance between the upper squares appeared smaller than between the lower squares. As an explanation Ramachandran and Anstis (1990) offered ‘motion capture’: the kinetic edges of the squares were captured by the motion of dots within the squares. The perceived position of the edge might then be shifted forward in the direction of the motion to an anticipated position, as a way of compensating for some of the processing delays in the visual pathway (Ramachandran & Anstis, 1990). This is in principle an early example of the motion extrapolation hypothesis later formulated by Nijhawan (1994).

Similarly De Valois and De Valois (1991) presented Gabor patches in a vernier task, where observers had to judge the alignment of three vertically arranged patches. The Gaussian envelope of the patches was stationary, however, the cosine of the middle Gabor patch drifted laterally. Consistent with Ramachandran and Anstis’ (1990) findings, the middle patch was perceived to be shifted in the direction of the contained motion. De Valois and De Valois (1991) equally appeal to a mechanism compensating for processing delays in the visual system. Later studies showed that the forward shift seems to be in fact a shift of the centre of mass of the Gabor, rather than a shift of the

complete envelope, as the shift comes together with an increased size of the patch (Tsui, Khuu, & Hayes, 2007).

Whitney and colleagues used similar drifting Gabor stimuli in an fMRI experiment, which revealed somewhat counterintuitive results (Whitney et al., 2003). Four stationary Gabor patches contained motion either drifting towards or away from the fixation point. The inward drifting Gabors were perceived as closer to the fovea than the outward drifting Gabors. Activity in visual cortex, however, exhibited the opposite pattern: Inward drifting stimuli were represented more anterior, outward drifting stimuli closer to the foveal representation at the occipital pole. Whitney et al. (2003) conclude that the differential activity measured in fMRI in response to the moving stimuli reflects inhibitory processes at the ‘trailing’ part of the stimulus. Such inhibitory activity has been proposed to serve the deblurring of a moving stimulus (Burr, 1980; Kirschfeld & Kammer, 1999).

#### ***A.2.3.3 Position shift of stationary flashes due to visual motion***

Not only moving objects themselves (or stationary objects containing internal motion; see above) can be mislocalised by visual motion. Whitney and Cavanagh (2000a) showed convincingly that stationary flashes can be ‘dragged’ along by the motion of adjacently presented moving gratings and mislocalised in the direction of nearby motion. This effect extends over considerable amounts of visual space and occurs for radial as well as linear moving gratings. A crucial difference between the effect and other mislocalisation phenomena discussed in sections above is that in this case the mislocalised object is not moving, but physically and perceptually stationary. The mislocalisation is, however, not specific to stationary flashes; the first or final position of moving objects are also influenced by nearby moving gratings (Whitney &

Cavanagh, 2002), i.e. nearby motion influences the Fröhlich effect and representational momentum. Preliminary findings have shown that the illusory displacement of flashes can also be achieved crossmodally: When a human observer actively moves her hands in complete darkness and is asked to localise visual flashes projected into the same spatial plane as the hands, the flashes are mislocalised in the direction of hand movements (Nijhawan & Maus, 2006).

The mislocalisation of flashes due to surrounding motion is small, compared to mislocalisations measured in the flash-lag effect (Whitney & Cavanagh, 2000a). Nevertheless, this mislocalisation might influence the relative localisation of moving and flashed objects in the flash-lag illusion. Indeed, several researchers have investigated this and found that the dependency of the flash-lag effect on the spatial separation between flash and moving object (Linares et al., 2007) or directional anisotropies in the flash-lag effect (Shi & Nijhawan, 2007) can be explained by a combination of motion-induced mislocalisations for both the flash and the moving object. Eagleman and Sejnowski (2007) recently argued that a common mechanism might underlie both mislocalisation effects (see above).

#### *A.2.3.4 Apparent motion*

In apparent motion subsequent presentation of a static object in distinct locations leads to the perception of the object in motion, travelling from the first to the second presentation position (Wertheimer, 1912). Interestingly, even the object at the first presentation position is perceived as moving, although the visual system does not have information about the alleged motion before the object is presented in its second position. This has been cited as a clear example of a ‘postdictive’ or retroactive effect in perception (Eagleman & Sejnowski, 2000). When an apparent motion stimulus is

presented repeatedly in a loop, i.e. two squares are flickering in counterphase, a square is perceived to move back and forth continuously. In this case it is thought that the perceived motion is computed in ‘real time’, i.e., it is not anymore postdictive, but predictive (Kolers, 1972). In a recent study it has been shown that when a low-contrast ‘token’ of the apparent motion-inducing square is presented in a position on the path of apparent motion, it is more likely to be detected, when it is ‘in phase’, i.e. when it matches the spatiotemporal prediction of a coherently moving object (Schwiedrzik, Alink, Kohler, Singer, & Muckli, 2007). This can be interpreted as an instance of low-level input matching a neural prediction.

Several neuroimaging studies have recently investigated what cortical areas are involved in the perception of apparent motion (Larsen, Madsen, Lund, & Bundesen, 2006; Liu, Slotnick, & Yantis, 2004; Muckli, Kohler, Kriegeskorte, & Singer, 2005; Muckli et al., 2002; Sterzer, Haynes, & Rees, 2006). Activity in area MT+/V5 correlates with the motion percept in a bistable apparent motion stimulus that exhibits switches between the perception of two stationary squares and one square in motion (Muckli et al., 2002). Activity in area MT/V5 has also been shown in retinotopic areas representing the unstimulated path of the apparent motion (Liu et al., 2004). This study did not find activity in earlier retinotopic areas, particularly in primary visual cortex. Conversely, two later studies with more sensitive methods did show activity in retinotopic parts of V1 that lay on the path of apparent motion, but had not been visually stimulated (Muckli et al., 2005; Sterzer et al., 2006). The authors argue that feedback from motion-sensitive areas to V1 might be the underlying cause of this activity, although local lateral interactions within V1 could not be excluded.

A phenomenon very similar to apparent motion is the line-motion illusion (Hikosaka et al., 1993; Wertheimer, 1912): When a square and subsequently a line overlapping the square are presented, the line is perceived to emanate from the square. This motion illusion is explained by focal visual attention around the cue stimulus, the square, which causes parts of the line close to the square to be processed with shorter latency (Hikosaka et al., 1993). Neurophysiological and optical recordings of cat primary visual cortex showed that the neural response to the line, in close correlation to the percept, spreads from the position of the square in a cortical wave of activity (Jancke, Chavane, Naaman, & Grinvald, 2004a). This seems to be a purely local effect within the retinotopic map of V1, although here top-down effects of feedback from motion-sensitive areas cannot be excluded. In contrast to long-range apparent motion as presented above, the line-motion illusion works on a smaller spatial scale, which is more readily explained by lateral spread of activity within the retinotopic map of V1. The relatively small receptive fields of neurons in V1, however, make it unlikely that long-range apparent motion can be explained by the same mechanism. In this case, it seems, feedback from higher motion-sensitive areas is necessary (Muckli et al., 2005; Sterzer et al., 2006).

#### ***A.2.3.5 Position shift of odd-coloured flashes in apparent motion***

An interesting mislocalisation illusion involving moving objects has been presented by Cai and Schlag (2001). A bar is shown on an apparent motion trajectory, while also changing size. If in one presentation position the bar is shown in a different colour, the odd-coloured bar is perceived to be further along the trajectory and a different size than the physically presented odd-coloured bar. The authors argue that an illusory conjunction of the odd colour feature with the position and size of a bar further along the trajectory explains this illusion. However, similar forward mislocalisations

also occur, when no other bar is presented that the odd colour could be bound to. When there is a gap in the trajectory just after the sudden colour change, the odd coloured bar is perceived to lie within the gap (Cai & Cavanagh, 2002). Similarly, when a single long bar amongst a sequence of short bars is presented just before the blind spot boundary, it is perceived to lie within the blind spot (Cai & Cavanagh, 2002). Here the authors argue that the odd feature gets assigned to an interpolated motion position.

The same illusion as presented above (Cai & Schlag, 2001) has been used in intracortical recordings of macaque monkeys to investigate, whether the neural representation of the odd-coloured bar is shifted in retinotopic space (Sundberg, Fallah, & Reynolds, 2006). Single neurons in area V4 showed a spatial shift of their receptive fields in the opposite direction of motion. Neurons selective to the odd-coloured bar responded when the bar was moving towards their receptive field, but still occupied positions outside of the receptive field. Interestingly, this shift occurred even when the odd-coloured bar was the last presentation of the bar in apparent motion and human observers did not show a perceptual shift of the perceived position (Sundberg et al., 2006). This finding indicates that activity in V4 might contribute to the perceptual mislocalisation in this illusion, but is not sufficient to explain perceptual localisation as a whole.

#### **A.2.4 Visual Masking**

In visual masking a target stimulus, which is perfectly visible when presented on its own, can be rendered harder to detect or even completely invisible by the presentation of another stimulus, the mask. Many target-mask configurations are known to produce visual masking (reviewed in Breitmeyer, 1984). Masking phenomena can be

classified into several classes. One main distinction is between forward masking, where the mask is presented in time before the target, and backward masking, where the mask is presented after the target. Other distinctions in visual masking depend on the nature of the mask being used: masking by light uses large luminous fields as masks that spatially overlap the target; masking by noise uses random dot patterns, masking by structure uses masks sharing features with the target, like orientation of lines or curvature. In metacontrast masking, the mask does not overlap the target, but consists of adjacent stimuli. Furthermore, types of masking can be distinguished by the dependence of the magnitude of masking on stimulus onset asynchronies (SOAs) between mask and target. Type A masking functions have maximum masking effects at an SOA of zero, that is when mask and target are presented simultaneously, and decrease monotonically in both directions. Type B masking functions, also called U-shaped masking functions, are typically found in metacontrast backward masking and have maximum masking effects at an SOA of about 100 ms (Breitmeyer, 1984; Breitmeyer & Ganz, 1976). This section will focus on backward metacontrast masking only and present some of the relevant literature.

#### ***A.2.4.1 Metacontrast masking***

Metacontrast occurs when a briefly presented visual target stimulus is succeeded by a non-overlapping adjacent mask stimulus (Stigler, 1910). When rating the perceived brightness of the target, observers rate the target to be far weaker or even completely invisible. This effect occurs for a wide range of stimuli; commonly used are simple bars or ring-disc configurations. The perceived brightness of the target is a function of the SOA between the target and the mask. Typically a U-shaped function is found, with a maximum decrease in perceived brightness, when the mask is presented about 100 ms after the target (Alpern, 1953). When target and mask are presented simultaneously

(SOA = 0 ms) or the target precedes the mask by more than  $\sim 250$  ms, no reduction in brightness is measured. This U-shaped function is referred to as Type B visual masking (Breitmeyer, 1984; Breitmeyer & Ganz, 1976). Although originally it was maintained that metacontrast masking can only be achieved under monoptic viewing conditions (Alpern, 1953; Stigler, 1910), later studies have revealed that metacontrast is also obtained under dichoptic viewing, when the mask and the target are presented to different eyes (Breitmeyer, 1984). This indicates that the neural site of interaction between the representations of target and mask must be cortical.

### *Metacontrast and apparent motion*

Following from observations that metacontrast and apparent motion stimuli share a lot of similarities, Kahneman (1967) suggested that metacontrast may be a case of “impossible apparent motion”. When a test square is subsequently presented in two adjacent positions, this gives rise to apparent motion. Interestingly the first square is often seen darker as the second square (Wertheimer, 1912). This reduction in contrast is probably due to inhibitory influences inflicted by the second square. Similarly metacontrast has been used to explain the invisibility of the first position of smoothly moving objects in the Fröhlich effect (Kirschfeld & Kammer, 1999). When two squares are presented adjoining two sides of a previously presented target square, this gives rise to metacontrast, and the visibility of the target square is reduced. Often the squares of the mask are perceived to be moving outwards. Both effects similarly depend on stimulus timing (Kahneman, 1967). According to Kahneman, the inhibitory processes inherent in apparent motion are the underlying cause of metacontrast masking. However, because apparent motion can be perceived on spatial scales far greater than metacontrast, this explanation has remained controversial (Breitmeyer, Love, & Wepman, 1974; Weisstein & Grawney, 1969).

#### **A.2.4.2 Masking by stimulus offsets**

The abrupt offset of a mask stimulus can be sufficient to produce metacontrast masking. Breitmeyer and Kersey (1981) presented a disc target surrounded by a ring mask. The mask was presented for 2 s, then the target disc was flashed for 50 ms, and the mask was turned off at target onset-mask offset asynchronies varying from 50 to 250 ms. Observers had to rate contrast of the target, and a typical U-shaped metacontrast masking function was found (Breitmeyer & Kersey, 1981). The stimuli in this experiment were presented dichoptically, with the target and the mask presented to opposite eyes, arguing for a cortical mechanism as the source for the masking.

The combination of masking by onsets and offsets can lead to continuous suppression of the visibility of a target, a ‘standing wave of invisibility’ (Macknik, Martinez-Conde, & Haglund, 2000). When a target bar and two non-overlapping flanker bars are flickering in counterphase with each other, a complete and ongoing suppression of the visibility of the target bar can be observed. In physiological measurements it has been shown that both the onset and the offset of a mask exhibit strong inhibitory influences on neighbouring neurons representing the target (Macknik et al., 2000). Furthermore, both the onset and offset of a target stimulus seem to be important in its visibility, and masking either of these by appropriate mask onsets or offsets results in reduced visibility of the target (Macknik & Livingstone, 1998).

#### **A.2.4.3 Models of masking**

##### *Sustained and transient channels*

One influential model of visual masking has been the *sustained-transient dual channel* theory (Breitmeyer & Ganz, 1976). This theory proposes that masking comes

about due to an interaction between the transient magnocellular (M-) pathway and the sustained parvocellular (P-) pathway. Put simply, visual awareness of a stimulus including perception of feature-rich objects requires information from the slow P-pathway. The sudden onset (or offset) of the mask stimulus, however, is processed in the faster M-pathway. Transient activity in the M-pathway can inhibit sustained activity of the P-pathway and thus interfere with the perception of the target and produce masking effects. Due to the differential latencies in M- and P-pathways, U-shaped masking functions of SOA are obtained. This approach and its application to experimental data have been discussed in detail (Breitmeyer, 1984; Breitmeyer & Ogmen, 2000).

### *Neural Competition*

Keysers and Perrett (2002) proposed that a simple concept of neural competition could explain many masking effects, as well as other visual phenomena such as the attentional blink and bistable perception. Neural representations for objects in visual cortex persist after physical stimulation ceases. If another object is presented in the spatiotemporal vicinity, neural activity in the cortex represents two objects at the same time. As two objects usually cannot occupy the same space simultaneously, the visual system tries to resolve this conflict between two object representations by a neural competition process (Keysers & Perrett, 2002). The ‘stronger’ representation usually wins this competition and is perceived. A representation might be stronger due to recency or higher stimulus intensity. This proposal has been criticised for being oversimplistic and disregarding much of the masking literature (Enns & Di Lollo, 2002). To be able to account for masking effects and make behavioural predictions, the competition model would have to be formalised more stringently. A similar proposal

invokes neural competition processes in the context of spatial attention (Desimone, 1998).

#### *Wilson-Cowan type neural networks*

More recently a two-layer neural network model based on the Wilson-Cowan architecture (Wilson & Cowan, 1973) has been used to model some spatial and temporal aspects of metacontrast masking (Hermens, Luksys, Gerstner, Herzog, & Ernst, 2008; Herzog et al., 2003). The basic properties of this network architecture are described above (section A.2.1.8). Rather than relying on different processing speeds for signals in two distinct channels, this model uses local interactions at the level of a retinotopic representation, namely lateral excitation and inhibitory feedback, to explain backward masking effects. These mechanisms might well be underlying a ‘neural competition’ as posited by Keysers and Perrett (2002). As well as reproducing A-type and B-type masking functions (Hermens et al., 2008), one major advantage of this model is that it also makes specific predictions for the effect of different spatial mask layouts, like in the ‘shine through effect’ (Herzog & Koch, 2001; Herzog, Koch, & Fahle, 2001).

### **A.3 Aims and Hypotheses**

As section A.2 has shown there is considerable debate in the literature about how the visual system localises objects in motion. Several visual illusions are known in which moving objects are mislocalised in the direction of motion. These illusions include the flash-lag effect, representational momentum and motion-induced position shifts of stationary apertures or flashes (see above). Several theories have been brought forward to explain these illusions. Temporal theories state that the integration of positions over time or differential processing latencies for moving and flashed objects

can explain these mislocalisation phenomena. Spatial theories generally claim that the mechanism underlying these mislocalisations works spatially. One such spatial theory proposes a predictive motion extrapolation mechanism that uses information from the trajectory of a moving object to shift the moving object forward in space (Nijhawan, 1994; in press). This forward shift compensates for neural processing delays in the visual pathways and facilitates the accurate perception of positions of a moving object, which would otherwise lag behind their true physical positions. This theory has been criticised for the lack of an explanation for findings in the flash-terminated and motion-reversed versions of the flash-lag effect (see A.2.1.3). Motion extrapolation would predict a perceived overshoot of a moving object beyond its final position, or beyond the point at which it reverses direction, which most experiments do not find.

Other theories have their shortcomings, too. As reviewed above, the differential latencies account for example lacks general physiological support. Postdiction is metaphysically problematic, as it proposes a general lag of all perception after physical events and reduces it to an epiphenomenon without behavioural consequences. From an evolutionary viewpoint it makes a lot of sense to assume that organisms benefit from the ability to accurately, in terms of both space *and* time, represent the positions of objects in the environment. The proposal below shows how findings from the flash-terminated flash-lag effect can be reconciled with a predictive explanation of the flash-lag effect.

All prediction is prone to errors, when abrupt changes occur and violate predictions. The nervous system, however, has evolved mechanisms geared specially to represent such abrupt changes. As abrupt events cannot be predicted or modelled by the

perceptual system in the same way as sustained input or predictable movement of an object, transient signals in efferent pathways associated with abrupt events can cause retroactive changes of the content of perceptual awareness. In backward masking (reviewed in A.2.4) transients can render a target stimulus invisible, although the transients occur after the presentation of the target. This has important implications for the apparent inability of predictive theories to explain the flash-terminated flash-lag effect (Nijhawan, 2002). It is possible that the transient signals associated with the abrupt disappearance of the moving object in the flash-terminated flash-lag display act as a mask to extrapolated positions. The object would normally be perceived in extrapolated positions beyond the final presentation position, but the transient signal overrides this prediction and thus corrects the prediction error. Other abrupt changes to the moving object's trajectory, like abrupt direction changes, might involve similar transient signals (see below).

In this thesis I argue that a two-process mechanism underlies the perceptual localisation of objects in motion: 1) A motion extrapolation mechanism provides a visual prediction for the position of a coherently moving object, and 2) this predicted position can be corrected by a retroactive mechanism based on transient signals associated with sudden events that make the prediction invalid. Previous literature provides lots of evidence for the existence of each of these mechanisms independently, as shown in the following two sections. The experimental work in this thesis (introduced in section A.3.3) will evaluate the above proposal and provide evidence that the perceived positions of moving objects can indeed be explained by this two-process mechanism.

### A.3.1 Visual prediction

It is a given fact that at some point in neural processing prediction has to take place, otherwise interaction with moving objects in a highly dynamical environment would be impossible. The motor output of an organism has to be ‘up to date’, otherwise it would miss the target of the action. An analysis of high-speed ball games, for example, provides evidence for the remarkable predictive accuracy that motor output can achieve (Land & McLeod, 2000). It is more controversial, whether earlier stages of processing achieve similar accuracy. Is all compensation for delays performed in the motor branch of the nervous system, or is perception equally predictive? Visual prediction posits that the content of perceptual awareness is already a prediction performed in the sensory system (Nijhawan, 1994; in press).

Visual prediction of positions of moving objects has been proposed in the context of the flash-lag effect (Nijhawan, 1994) and has since been highly debated, as presented above. In other contexts predictive effects in vision seem to be more established. A general predictive coding mechanism has been suggested as a unifying principle for over 50 visual illusions (Changizi, Hsieh, Nijhawan, Kanai, & Shimojo, in press). One commonly cited phenomenon is the motion-induced position shift for stationary apertures containing motion (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). In both articles describing this phenomenon the authors suggest that a predictive mechanism causes the perceived position shift in the direction of motion.

#### A.3.1.1 Neural mechanisms of visual prediction

Primate brains have evolved specialised mechanisms for the detection of motion. At many stages of visual processing there is evidence for a predictive coding of positions of moving objects to some degree.

### *Retina*

The earliest stage of neural processing of visual information is in the retina itself. Interestingly, already in retinal ganglion cells, which form the output layer of the retina, prediction can be found. In response to a moving stimulus, the peak firing rate in the ganglion cell population is found to be at or even ahead of the leading edge of the stimulus (Berry et al., 1999). There is no anatomical input from higher areas in the pathway back to the retina, so this predictive forward shift of the neural representation comes about by local interactions in the retina. Computationally the response properties of retinal ganglion cells can be modelled with spatiotemporal filters and a contrast gain control mechanism (see section A.2.1.8).

### *Thalamus*

The lateral geniculate nucleus (LGN) of the thalamus receives input from the retina and relays it to the primary visual cortex (V1). Or at least this is the traditional view. Neural activity in LGN is highly shaped by cortical feedback. In fact, only ~10% of synaptic input into LGN cells stems from the retina, far more – about 30% – stems from cells in layer 6 of V1, which in turn receives fast feedback from motion area MT/V5 (Sillito, Cudeiro, & Jones, 2006). Anatomically, the feedback from V1 to the LGN is local, but it also spreads to nearby retinotopic locations along the orientation of the receptive field and in the direction of motion selectivity of the V1 cell. The spread of feedback to other retinotopic locations in the LGN possibly causes a shift in the retinotopic position of activity towards future stimulus positions. In experiments manipulating the responsiveness of MT/V5 by local drug application in macaque cortex significant changes in the response properties of cells in V1 and the LGN could be shown (Sillito & Jones, 2002). This feedback loop from MT/V5 via V1 to the LGN has

been interpreted to “enable predictive modulation of circuitry at earlier levels, even before the input arrives” (Sillito et al., 2006, p. 307).

### *Cortex*

Direction-selective neurons that respond maximally to stimuli moving in one direction exist in V1 and throughout visual cortex. A few studies have shown position shifts in the neural activity in retinotopic maps that could underlie predictive mislocalisation phenomena. When internal motion shifts the perceived position of a static Gabor patch (De Valois & De Valois, 1991), the retinotopic representation in V1 is surprisingly shifted in the opposite direction (Whitney et al., 2003). This finding is thought to be based on inhibitory activity at the trailing edge of the stimulus.

Sundberg et al. (2006) convincingly showed a distortion of retinotopy in macaque area V4 for stimuli that involved a colour singleton in an apparent motion sequence (Cai & Schlag, 2001). Neurons responded to an odd-coloured ‘flash’ even before it entered the neuron’s receptive field. Interestingly, this shift of the receptive field occurred also, when the odd-coloured flash was the last presentation of the bar in apparent motion and human observers did not show a perceptual shift of the perceived position (Sundberg et al., 2006). This finding is consistent with separate position representations being maintained in the visual system, and the perceived position being determined by an interplay between different position representations.

It has been hypothesised that in mislocalisation illusions, feedback from motion sensitive areas with large receptive fields can add a spatial bias to activity in lower areas that represent positions on a finer scale (Muckli et al., 2005; Sterzer et al., 2006). Although it might be argued that re-entrant feedback from higher areas to primary

visual cortex is too slow to bring about a time-critical prediction mechanism, it has to be noted that area MT/V5 shows some of the shortest response latencies to visual stimuli in the primate cortex (Schmolesky et al., 1998). There is also evidence that MT/V5 receives direct anatomical input from the LGN (Sincich, Park, Wohlgemuth, & Horton, 2004), which would actually put MT/V5 on the same level of the hierarchy as V1.

A more general framework of computations in visual cortex posits that higher cortical areas in principle try to predict activity from lower areas in the hierarchy and feed this prediction back to earlier layers (Rao & Ballard, 1999). In this model the feed-forward stream effectively only communicates the error of the prediction to the higher layers.

### **A.3.2 Correction by transients**

In visual backward masking the presentation of a mask at optimal SOAs after a target can render the target less visible or even invisible (Breitmeyer, 1984). The relevant literature on this effect is reviewed in section A.2.4. The influence of the mask could be interpreted as a ‘correction’ of perceptual content. In most cases the target is only presented briefly, but would clearly be perceived without the presentation of the mask. The subsequent presentation of the mask, however, gives a new context to the target that makes it less salient. In a way the mask overrides the perception of the target and corrects it with an alternative percept.

Analogously to masking as described above is the ‘correction by transients’ mechanism proposed in this thesis and earlier (Nijhawan, 2002). In the flash-terminated flash-lag display a retinal Off-transient signals that the moving object has disappeared

in one particular location. A visual prediction mechanism maintains a representation that positions the moving object further ahead, but the transient signal contradicts this prediction and is able to override it with an alternative percept — the disappearance of the object in its real offset position.

It is indeed the transients of a mask, both at the onset and the offset, that cause most of the inhibitory influences on the target (Macknik et al., 2000). Interestingly, it has been shown that response offsets of neurons in the LGN and visual cortex occur faster than response onsets (Bair, Cavanaugh, Smith, & Movshon, 2002). Recently, synchronised bursts of firing from retinal ganglion cells have been found in response to direction changes of moving stimuli (Schwartz, Taylor, Fisher, Harris, & Berry, 2007). Although the experiments of this thesis focus on the case of abrupt offsets, this recent finding offers the possibility that masking effects by transient signals similarly occur for the case of abrupt direction changes (Whitney & Murakami, 1998).

Similar to the present ‘correction by transients’ proposal, it has recently been shown that transients can reveal the veridical position of a moving object (Kanai & Verstraten, 2006). In this study a new variant of the ring-disc version of the flash-lag effect was used: The moving object was a disc and the flash was a surrounding ring. When the ring was flashed and the moving disc physically filled out the ring, the moving disc was seen simultaneously in two positions: in a position shifted forward, like in more common flash-lag displays, and additionally in a position filling out the flashed ring. Kanai and Verstraten (2006) argue for a perceptual filling-in mechanism triggered by the transient of the flashed ring that reveals the moving object in its veridical position. A related phenomenon can be shown with transcranial magnetic

stimulation (TMS). When TMS pulses are delivered to occipital areas, a moving object can be seen in two simultaneous positions (Wu & Shimojo, 2002). One position corresponds to the continuously visible moving object, the other lags behind and is interpreted by the authors as “an image from the past” (Wu & Shimojo, 2002). These findings present evidence for the hypothesis that multiple representations of positions are maintained in the visual system. The present proposal states that, similarly, the transient of the abrupt disappearance of the moving object facilitates the perception of its veridical position, while additionally masking the extrapolated position.

### **A.3.3 Outline of Articles**

The proposal above leads to some experimental predictions. These predictions are addressed in experiments presented in the four research articles of this thesis. The specific questions and hypotheses of each article and the main findings are briefly introduced below.

#### *A.3.3.1 Article I – Disappearance without a transient*

The central hypothesis of this thesis states that the final position of a moving object is perceived accurately, because the retinal transient signal of an object’s offset corrects for an overshoot produced by visual prediction. This implies that a moving object that disappears from view without providing a transient signal should lead to an overshoot and be perceived in extrapolated positions beyond the final presentation position. This prediction is tested in Article I.

To make an object disappear without a strong transient we employed a fading moving stimulus that gradually reduced luminance contrast until it went below detection threshold and disappeared from view. The position at which the object became visible

was measured in a two-alternative forced choice (2AFC) task, asking observers whether the moving object was seen to have passed a visually marked position or not. This final perceived position is hypothesised to lie beyond the final presentation position. Clearly, for a fading stimulus the final presentation position is not well defined. Therefore the luminance at the measured final position was compared to the luminance detection threshold for the same object without the same motion history. This comparison resulted in a large difference between the two measurements that is interpreted as a perceptual forward shift of an object disappearing without a transient signal.

#### ***A.3.3.2 Article II – Neural correlates of extrapolation for fading objects***

Using similar stimuli as in Article I, here we asked which cortical areas are involved in the forward shift of the final perceived position of a fading moving object. We measured fMRI signals from observers viewing gradually fading and gradually appearing moving stimuli. As a control condition we also presented motion trajectories with abrupt offsets and onsets. We focused on retinotopic regions of interest (ROIs) just next to one endpoint of the trajectory in several cortical visual areas and compared blood-oxygenation level dependent (BOLD) signals in response to stimuli moving in opposite directions. When the stimulus moving towards the ROI resulted in higher signals than the stimulus moving away from the ROI, this was interpreted as predictive activity.

We found such predictive activity in motion-sensitive area V3A. The predictive activity there was, however, not specific to fading motion; the comparison of stimuli disappearing with a strong offset and stimuli starting motion in the opposite direction with a strong onset showed the same pattern of activity in area V3A. Area V1 showed no significant differences between motion directions, but generally higher activity for

strong motion offsets and onsets. It is concluded that the perceived final position is determined by an interplay of position representations at several cortical processing stages.

#### ***A.3.3.3 Article III – Motion extrapolation into the blind spot***

Another example of visual stimuli disappearing from view without providing a strong offset are objects moving into the retinal blind spot in monocular viewing. No photoreceptors at any retinal location will register the sudden disappearance of the whole object; therefore it should similarly ‘overshoot’ and be perceived in retinally blind areas. This prediction was confirmed.

The experiment presented in this article used two moving objects, one of which moved into the blind spot, and the other disappeared in an abrupt offset on the other side of fixation. Observers performed a temporal order judgement task indicating which object they perceived to disappear first. When the abrupt offset occurred exactly at the mirror position of the blind spot boundary, and both offsets should appear to happen simultaneously, observers always indicated that the bar moving into the blind spot was perceived to disappear later. This again is interpreted as a forward displacement of the final perceived position of a moving object due to the absence of a terminating transient signal.

#### ***A.3.3.4 Article IV – Offset-lag and manipulating the relative strengths of the two processes***

The correction-by-transients hypothesis predicts that the perceived position of an abrupt offset of a moving object should be different from the perceived position of a continuously moving object. If two aligned objects move and one of them disappears

abruptly, the perceived position of the offset should lag behind the other object. This predicted ‘offset-lag effect’ is confirmed in the experiments of Article IV. In Experiment 1 two aligned bars moved across the screen, one of which disappeared in an abrupt offset. Observers were instructed to adjust the remembered positions of the two objects at the time of the disappearance. They consistently placed the offset position in a position lagging the moving object. A more controlled 2AFC method in Experiment 2 gave the same result and revealed a roughly linear relationship between the misalignment effect and the speed of motion. The misalignment is interpreted as a forward shift of the moving object due to a visual prediction mechanism, whereas the offset is localised accurately due to the correcting mechanism based on the transient.

It should be possible to manipulate the perceived position of a moving object by manipulating the relative strengths of the two underlying representations. In Experiment 3 we used a flash-lag task to measure the forward displacement of a moving object that disappeared only for a short time or abruptly reduced luminance contrast to various fractions of the previous contrast. Manipulating the relative strength of the two position representations in this way resulted in intermediate positions being perceived, with weaker motion signals or stronger transients leading to less forward displacement. These findings and their implications for theories of localisation for moving objects are discussed in detail.

## A.4 General Discussion of Findings<sup>1</sup>

### A.4.1 Summary of experimental findings

This thesis presented four research articles with experiments supporting the central hypothesis that the perceptual localisation of moving objects depends on a predictive motion extrapolation mechanism, which can be corrected for in the case of sudden unpredictable events. Transient signals associated with sudden events like an abrupt offset can mask the extrapolated representation from visibility and facilitate the perception of the accurate final position. Article I showed that moving objects disappearing without such transients are seen in positions shifted forward beyond their luminance contrast detection threshold. Article II investigated which cortical areas might contribute to this forward displacement. Despite the lack of specific activity clearly correlated with the illusory percept, it can be concluded that motion-sensitive area V3A maintains a representation of the moving object in positions shifted forward in the direction of motion.

Visual objects moving into the retinal blind spot are seen as disappearing well inside the blind area, another clear example of a spatial shift of the final perceived position of a moving object, presented in Article III. Finally, Article IV presented a new visual illusion predicted by the hypothesis. A moving object that suddenly disappears is perceived to lag behind an aligned moving object that continues to move. In further experiments of Article IV it is shown how changing the relative strengths of the two

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<sup>1</sup> It is recommended to make yourself familiar with the articles in chapters B to E before reading this section.

involved mechanisms changes the perceived position of a moving object in a flash-lag task.

#### *A.4.1.1 Comparison of effect sizes*

The effects reported in this thesis show somewhat varying effect sizes. Typically cited values for forward displacements in the flash-lag and the Fröhlich effects are in the range of about 40 to 120 ms (Kirschfeld & Kammer, 1999; Nijhawan, 1994; Whitney & Murakami, 1998). The forward displacement effect measured in the fading study of Article I amounts to  $\sim$ 128 – 175 ms, depending on which of the control conditions is used for comparison. This effect is unusually large compared to other effect sizes reported in the literature. It is therefore likely that some additional effect, for example hysteresis, contributes to the forward displacement.

The forward displacement of objects into the blind spot in Article III is on average 51 ms. This measurement is based on a temporal order judgement task on the time of disappearance of two separate objects: One object disappearing abruptly and the other disappearing in the blind spot. The accuracy of localisation performance for the abrupt offset has not been verified in the same experiment, but other studies in the literature (Kerzel, 2000; Stork & Müsseler, 2004) and findings of Experiment 2B in Article IV show that the position of an abrupt offset is perceived accurately, with sometimes a small undershoot. The small undershoot could lead to an overestimation of the effect. However, the method used in Article III for the measurement of the blind spot boundary results in a lower bound estimate of the blind area. If we assume that the blind spot is actually slightly larger, this would reduce the effect size and probably counteract any overestimation due to undershoots of abrupt offsets as mentioned above. In Article IV

the offset-lag effect amounts to  $\sim 66 - 76$  ms. The baseline flash-lag effect measured in Experiments 3A and 3B is about  $42 - 45$  ms.

In summary the effect sizes of the present experiments with the exception of the fading effect in Article I are in the typical range of forward displacement effects found in the literature. It remains an interesting question what causes the different effect sizes between different experiments and also between different observers. Are there genetic influences or effects of experience on perceived forward displacements? Will professional players of high-speed ball games show larger prediction effects than untrained individuals? These questions might be interesting to pursue in the future.

#### **A.4.2 Re-evaluation of theories of flash-lag**

The experiments in this thesis try to argue for the motion extrapolation account of the flash-lag effect (Nijhawan, 1994). The biggest shortcoming of this account is its apparent inability to explain the lack of a forward displacement in the flash-terminated (Eagleman & Sejnowski, 2000) or motion-reversed (Whitney & Murakami, 1998) flash-lag displays. The proposal of this thesis shows how this shortcoming can be overcome, when an additional mechanism is assumed that corrects for prediction errors in the event of sudden changes to the motion trajectory. While the findings from experiments in this thesis are generally consistent with this proposal, they also provide evidence against some of the alternative theories to explain the flash-lag effect.

Temporal integration theories state that positions of an object are sampled over an extended period of time and averaged to yield a perceived position (Brenner & Smeets, 2000; Krekelberg & Lappe, 1999; Roulston et al., 2006). This theory has difficulties to

explain some of our findings. Articles I and III show that a moving object is visible in locations that are subliminally stimulated, or not stimulated at all. Obviously these positions cannot contribute to any averaging process. It seems that a spatial mechanism is necessary to explain these findings. The offset-lag effect in Article IV seems to be generally consistent with the idea of a temporal averaging mechanism. However, a detailed analysis of the findings of Experiment 3 in Article IV provides evidence against a temporal integration account (discussed in E.7.2.2). When a moving object is blanked for a brief amount of time, say 40 ms, which is usually thought to be shorter than the integration time, the positions that would be occupied during these 40 ms do not contribute to the average. The outcome of the averaging process in this case should be shifted in the direction of motion. The experiments revealed the opposite finding, a decrease of the perceived forward shift, which is well explained by the increasing influence of the Off-transient over the extrapolated position representation.

Regarding the experiments of Articles I and III, the same reasoning as above applies to the differential latencies account of the flash-lag effect (Ogmen et al., 2004; Purushothaman et al., 1998; Whitney & Murakami, 1998). Different processing latencies for moving versus flashed stimuli cannot explain the visibility of a moving object in positions stimulated below threshold or in the retinal blind spot. In fact, the experiments in Articles I to III did not employ flashes at all. In Experiments 1 and 2 of Article IV the perceived final position of a moving object is compared with the instantaneous position of a continuously visible moving object. It is unclear how a differential processing latency can explain the spatial gap between the two positions measured there (detailed discussion in E.7.2.1). One important fact to note is that a visual prediction mechanism shifting the perceived position of a moving object forward

will also lead to measurements of shortened processing latencies for the moving object compared to flashes. Most experiments on the flash-lag effect do actually not allow to distinguish between the two accounts. The present experiments, however, provide clear evidence for a spatial mechanism at work.

Another possible spatial account of the flash-lag effect and other illusions has recently been proposed by Eagleman and Sejnowski (2007). While their earlier proposal (Eagleman & Sejnowski, 2000) was in essence a temporal integration account with the added feature of a postdictive assignment of the outcome of integration to an earlier point in time, the new account proposes a spatial shift of perceived positions. What remains the same as in the earlier version is the proposed postdictive nature of the mechanism. The new proposal claims that a position is computed and the “result is biased in the direction of motion signals that stream in over the next ~80 ms” (Eagleman & Sejnowski, 2007, p. 2). This “motion biasing will normally push objects closer to their true location in the world” (p. 9). While it is true that such a mechanism might reduce the spatial error that would normally be caused by neural delays in the visual pathway, it does not produce a spatially accurate localisation online, but only after an additional delay (the delay invoked by waiting for new motion signals plus the time it takes for them to be processed). Why such a mechanism that produces accurate localisation judgements only after considerable delay should be beneficial, remains to be answered. Admittedly, most of the findings of Article IV can well be explained by the motion biasing account. The proposal is, however, unable to explain the findings presented in Articles I and III. In the case of a moving object disappearing in the blind spot, no motion signals are available from after the object passed the blind spot

boundary. The shift of the perceived position into the blind area is necessarily caused by earlier motion signals.

#### **A.4.3 Computational model**

The proposal of this thesis remains on a qualitative, descriptive level. To assess its feasibility it would help to have an implementation of a computational model to actually make predictions for real behavioural experiments. The two components of the mechanism described, a motion extrapolation mechanism to predict the positions of moving objects and a masking mechanism based on transient signals, have both separately been modelled by surprisingly similar neural network architectures. Networks of the Wilson-Cowan type (Wilson & Cowan, 1973) that are designed to implement some basic features of cortical processing have successfully been used to implement both motion extrapolation mechanisms (Erlhagen, 2003) and backward masking mechanisms (Hermens et al., 2008; Herzog et al., 2003). It would be a worthwhile enterprise to investigate if one set of network parameters is able to implement both processes, as needed for the current proposal. Some preliminary investigations (data not reported) hint that this is difficult, as extrapolation on the one hand relies on the excitatory spread of activity, and masking on the other hand on the inhibitory effects in the network. Parameter values that produce large enough extrapolation to account for the flash-lag effect are unlikely to exhibit sufficient inhibition to account for masking, and vice versa. A multi-layered architecture as proposed by Erlhagen (2003) with different parameter regimes in different layers is most likely needed.

#### A.4.4 Limitations and future work

One major limitation of the experiments in this thesis is that they focus on the case of abrupt offsets of moving objects. As mentioned in various places throughout the thesis (A.2.1.3, B.4, E.7.5) abrupt reversals of the motion direction of a moving object also do not cause overshoots of the moving object. In fact, the moving object is not perceived in the extreme position at all, but perceptually reverses even before reaching the point of physical reversal (Whitney & Murakami, 1998; Figure A.2). Direction reversals produce strong neural signals at higher stages of the visual system (Clarke, 1972; Hoffmann, Unsold, & Bach, 2001; Pazo-Alvarez, Amenedo, & Cadaveira, 2004). Recently, electrophysiological recordings from isolated retinae have shown synchronised burst activity in response to direction reversals (Schwartz et al., 2007). It is known that the position of a moving object is to some extent anticipated by ganglion cells (Berry et al., 1999), so this recent finding has been described as “the retina trumpets its failed predictions” (Holy, 2007). I have proposed that these signals could have masking effects on extrapolated position representations, analogously to the proposal of Off-transients. Even with this proposal some open questions remain. Why, for example, is an object changing direction not seen in the physical reversal position? It could be that ‘direction change signals’, as proposed above, mask extrapolated positions and thus prevent an overshoot from being perceived. Then the motion in the new direction quickly gains influence and the perceived position is shifted in the new direction. An interesting avenue of research would be to employ stimuli that (analogously to the fading stimuli of Article I) do not change direction abruptly, but gradually by decelerating. Variations on this experiment could use speed changes following laws of motion applying to biological or physical motion (e.g. Zago et al., 2004).

Article II found predictive activity in area V3A that represented a moving object ahead of its physical position. Other studies have suggested that feedback from motion-sensitive area MT/V5 plays a role in the perception of motion illusions (McGraw et al., 2004; Muckli et al., 2005; Sterzer et al., 2006). Direct evidence for the involvement of feedback in illusions such as the flash-lag effect, Fröhlich effect, or motion-induced position shifts is to date not available. Many studies have used TMS over area MT/V5 to disrupt activity and investigate the effects on several motion perception tasks (Laycock, Crewther, Fitzgerald, & Crewther, 2007; Sack, Kohler, Linden, Goebel, & Muckli, 2006; Silvanto, Cowey, Lavie, & Walsh, 2005a; Silvanto, Lavie, & Walsh, 2005b; Walsh, Ellison, Battelli, & Cowey, 1998). TMS stimulation of area V5/MT in experiments using a flash-lag paradigm should provide valuable insight into the role of feedback for these mislocalisations. Neuronavigated TMS methods, where the area to be targeted is first identified in functional MRI scans (Sack et al., 2006), might also make it possible to target area V3A, the area implied by the results of Article II.

## A.5 Conclusion

The experimental findings of this thesis showed that moving objects disappearing without eliciting a strong retinal transient signal are perceived in positions shifted forward from the last detected retinal presentation position (Articles I and III). Abrupt offsets of moving objects however, are perceived accurately and lagging behind the position of a continuously moving object (Article IV). These findings present evidence for a two-process mechanism for the perceptual localisation of moving objects: The visual system predicts positions of moving objects and shifts perceived positions forward to counteract neural processing delays in the visual pathways. In the case of

unpredictable events like sudden offsets, a second mechanism based on transient signals is able to correct the prediction and facilitate accurate localisation of final positions.

Several cortical areas are most likely involved in this two-process mechanisms. Article II showed that area V3A maintains predicted position representations for moving objects. Extrapolated position representations in higher motion-sensitive areas are possibly fed back to primary visual cortex to bias the fine-grained retinotopic representation of objects there towards the direction of motion. Accurately localised bottom-up transients from the retina however are able to override these biases.

The perceptual outcome of the localisation process depends on the relative strengths between these two different position representations. Article IV showed that it is possible to influence position judgements by manipulating the strength of the motion representation or the strength of the transient signal. Weaker support for the motion representation and stronger transients both lead to smaller forward displacements of perceived positions.

This two-process mechanism for the localisation of moving objects might present an optimal trade-off between the requirements of accuracy and timeliness. Objects on predictable trajectories are perceived accurately in time and space, whereas unpredictable offsets are perceived spatially accurate with the inevitable delay of neural processing latencies. This architecture optimally reduces spatiotemporal localisation errors for objects in motion.

## B Article I

# **Forward displacements of fading objects in motion: The role of transient signals in perceiving position<sup>2</sup>**

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### **Abstract**

Visual motion causes mislocalisation phenomena in a variety of experimental paradigms. For many displays objects are perceived as displaced ‘forward’ in the direction of motion. However, in some cases involving the abrupt stopping or reversal of motion the forward displacements are not observed. We propose that the transient neural signals at the offset of a moving object play a crucial role in accurate localisation. In the present study we eliminated the transient signals at motion offset by gradually reducing the luminance of the moving object. Our results show that the ‘disappearance threshold’ for a moving object is lower than the detection threshold for the same object without a motion history. In units of time this manipulation led to a forward displacement of the disappearance point by 175 ms. We propose an explanation of our results in terms of two processes: Forward displacements are caused by internal models predicting positions of moving objects. The usually observed correct localisation of stopping positions, however, is based on transient inputs that retroactively attenuate errors that internal models might otherwise cause. Both processes are geared to reducing localisation errors for moving objects.

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<sup>2</sup> An earlier version of this article has been published in *Vision Research* (Maus & Nijhawan, 2006).

## B.1 Introduction

Visual motion can influence the perceived position of objects as shown in various experimental paradigms. In representational momentum observers perceive the final position of a moving object as shifted in the direction of motion (Freyd & Finke, 1984; Hubbard, 1995). In the Fröhlich effect the position of the sudden onset of a moving object is misperceived; the object seems to appear at a later point of the trajectory (Fröhlich, 1923; Kirschfeld & Kammer, 1999). When observers view moving elements contained within the boundaries of static windows, a motion-induced positional bias is observed such that the windows appear displaced in the direction of motion (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). Flashes can be mislocalised in the direction of motion when they are presented near a moving object (Whitney & Cavanagh, 2000a). In the flash-lag effect a moving object is perceived to be ahead of a flashed stationary object, although both are physically aligned in space (Metzger, 1932; Nijhawan, 1994). A common feature in all these studies is that motion causes a mislocalisation in the ‘forward’ direction; i.e. the displacement occurs in the direction of future positions of the moving object.

Given these findings it is surprising to find some displays in which this expected forward shift is not observed. These displays involve unpredictable events such as moving objects abruptly stopping, changing direction and/or speed. When a moving object unpredictably stops, it does not appear to overshoot its final position. This has been observed in experiments using flashes for the relative judgement of the stopping position (Eagleman & Sejnowski, 2000; Nijhawan, 1992), using pointing movements (Kerzel, 2000) and static probe stimuli (Kerzel et al., 2001). When a moving object abruptly changes direction, then the perceived position at which the object reverses is

not displaced forward (Whitney & Murakami, 1998). However, recently some conditions have been found, in which similar stimuli do produce ‘overshoots’. If abruptly stopped moving objects are blurred (Fu et al., 2001) or presented in the retinal periphery (Kanai et al., 2004) a forward displacement is reported.

Why is the forward displacement of abruptly stopped moving objects sometimes not observed? We suggest that whether a given stimulus will produce the forward displacement or not depends on the relative operational strength of two opposing mechanisms. The first mechanism uses information from the earlier part of the moving object’s trajectory to accurately predict its position, possibly to compensate for the spatial lag in position that would otherwise be expected due to delays in the neural processing between the photoreceptors and higher visual areas. When abrupt events cause transient neural signals, strongly stimulating the visual system, a second mechanism is engaged that acts like a ‘correction’ overriding the output of the first mechanism.

Our thesis is based on well known psychophysical and physiological facts. Events occurring later in time can change the perception of earlier events (Breitmeyer, 1984; Dennett & Kinsbourne, 1995; Kolers, 1972; Libet, 1981; Ross, 1972; van der Waals & Roelofs, 1931). For example, in backward masking a briefly presented visual stimulus can be rendered invisible, if it is followed by another stimulus nearby (Alpern, 1953; Breitmeyer, 1984). More importantly for the present experiments, stimulus offsets per se can reduce the visibility of a previously presented target (Breitmeyer & Kersey, 1981). Temporal transients like stimulus onsets and offsets elicit strong neural responses, both excitatory and inhibitory, that can suppress the perception of other

stimuli (Macknik et al., 2000). Here we explore the possibility that the strong transient neural signal associated with the disappearance of a moving stimulus provides the visual system with a cue that allows for the localisation of the vanishing position without a forward displacement. Analogously to backward masking this transient might influence perception retroactively and facilitate the perception of the correct vanishing position (Nijhawan, 2002).

In this study we test our thesis by manipulating the transient at the offset of a moving object. We employed a *gradually fading* moving object that initially appeared bright and then disappeared for the observer without a strong transient. Does this object disappear at the position in its trajectory where its luminance is at detection threshold, or does it overshoot this point and will be visible in positions where retinal input per se can no longer sustain perception of the object?

## B.2 Experiment 1

The purpose of this experiment was to measure the luminance at which a fading moving object is seen as disappearing by the observer, and determine whether this luminance is above or below detection threshold for the same moving object without the same motion history. We used two conditions: In the ‘long-trajectory motion’ condition a small dot moved on a circular trajectory while continuously becoming dimmer. Observers judged whether the dot disappeared before or after a radial reference line presented adjacent to the moving dot (Figure B.1C). In the ‘short-segment motion’ condition the same dot was presented moving for only a short trajectory at different luminances. The observers reported whether they perceived the dot or not. We predicted

that the long-trajectory dot would perceptually disappear in a forward-displaced position, i.e. at luminance levels where the short-segment dot was not detectable.

### **B.2.1 Methods**

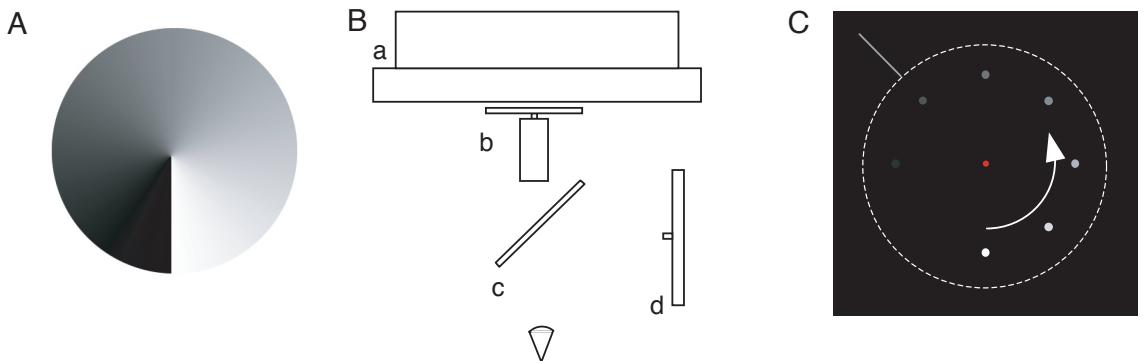
#### ***B.2.1.1 Participants***

Eight observers participated in the experiment. Two observers (including author GM) were informed, while six were naïve about the hypothesis. All had normal or corrected to normal visual acuity.

#### ***B.2.1.2 Apparatus and Stimuli***

The stimuli were shown in a dimly lit room on a CRT computer monitor (Sony CPD-E500) at 1280 x 1024 pixel resolution and 85 Hz refresh rate. Stimuli were generated using Matlab and the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The observer viewed the screen from a distance of 80 cm with the head stabilised by a chin rest. The stimulus consisted of a small white dot (3 x 3 pixels, 0.06° x 0.06°) moving counter-clockwise on a circle (radius 2.8°). Analogue fading of the dot was achieved by hardware: a variable neutral density filter (Edmund Optics Inc.; range of neutral density 0 – 4; range of transmission 1 – 0.0001; see Figure B.1A) was mounted between the observer and the screen. In this experiment the filter was fixed in the position shown in Figure B.1A. A fixation LED was presented at the centre of the circular trajectory using a beam splitter (Figure B.1B). To the observers the dot appeared to fade as it moved (see Figure B.1C). Using this physical setup rather than changing the dot's luminance in the software had several advantages. In software luminance can only be changed in steps of finite size. This confines experimenters'

control over stimuli, especially for luminance contrasts close to the detection threshold<sup>3</sup>. This method also makes correction for non-linearities in the monitor's luminance function unnecessary.



**Figure B.1** (A) The variable neutral density filter that was mounted between observers and the screen. (B) The apparatus: In front of the computer screen (a) the neutral density filter was mounted on a rod (a micro stepper motor in Experiment 2; b). A beam splitter (c) was used to present a fixation LED (d) in the plane of the screen. (C) Stimulus in the ‘long-trajectory motion’ condition: observers viewed a white dot moving behind the filter on a counterclockwise trajectory starting at 0° (6 o’clock position). The dot appeared to fade as it moved until it disappeared at around 220°. The dotted line depicts the outline of the filter disc in front of the screen. A grey radial line was presented at different positions.

#### B.2.1.3 Procedure

This experiment consisted of two conditions. In the ‘short-segment motion’ condition we measured the dot luminance, at which observers were able to detect the dot’s presence with 50% probability. In the ‘long-trajectory motion’ condition we measured the luminance at which the same fading moving dot was seen as disappearing.

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<sup>3</sup> The ability to rotate the filter with a micro stepper motor (see Experiment 2) also enables us to change the luminance of a moving object with any continuous function.

Note that different luminances of the dot were achieved by presenting the dot behind different regions of the filter, therefore larger angular positions directly correspond to lower luminances. All analysis was carried out in terms of positions.

The stimulus in the short-segment motion condition consisted of five screen refresh frames (58.8 ms at 85 Hz refresh rate), during which the dot rotated for about 12° (arc distance 0.6° visual angle) at an angular velocity of 204 °s<sup>-1</sup> (tangential velocity 10.4 °s<sup>-1</sup> visual angle). During this motion, the dot's luminance decreased by a factor<sup>4</sup> of 0.7. To achieve different intensity levels the stimulus was presented at one of ten different positions behind the filter. A radial line (length 1.6°) presented adjacent to the filter precued the starting position of the dot. At the starting position of each trial the dot appeared brightest, so this position and luminance were used to work out the actual detection performance. Trials were structured as follows: First the cue line appeared, 400 ms later the stimulus was presented for 58.8 ms. After another 300 ms the cue line was turned off and the observer was prompted to press one of two keys to report whether they saw the stimulus or not. To counteract observers simply learning the position where the stimulus was visible, on 20% of the trials the cue line was presented, but was not followed by the stimulus. Observers were not informed about the presence of these 'catch' trials.

In the long-trajectory motion condition the dot started moving from the 6 o'clock position (0°), where the filter's transmission was 1, and moved counterclockwise into the darker parts of the filter. The dot's velocity was the same as in the short-trajectory

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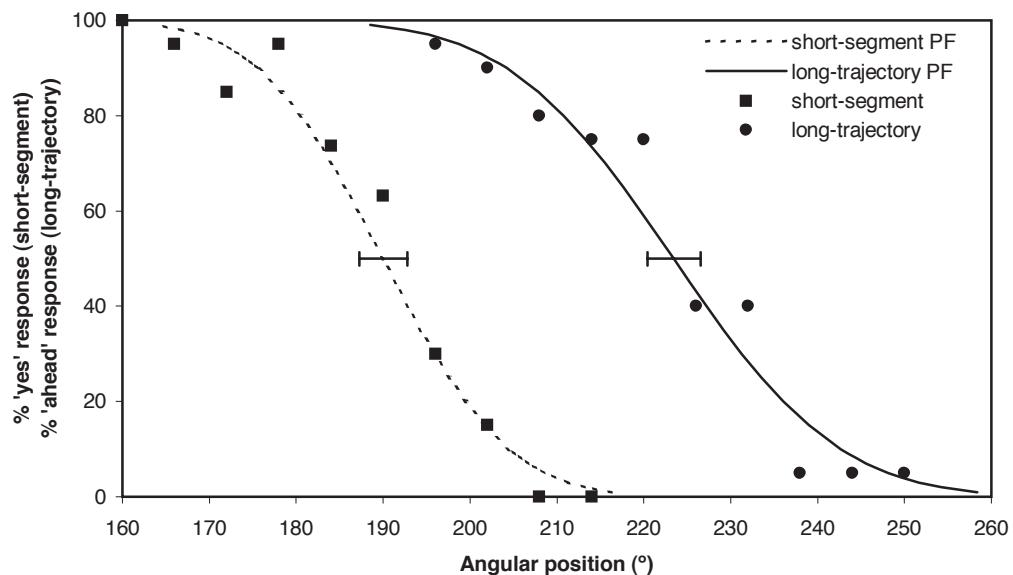
<sup>4</sup> factor =  $\frac{\text{luminance in last frame}}{\text{luminance in first frame}}$

motion ( $204^{\circ}\text{s}^{-1}$ ;  $10.4^{\circ}\text{s}^{-1}$  visual angle). Although the dot on the screen completed a whole circular trajectory, it was typically perceived to disappear at about  $220^{\circ}$  (Figure B.1C). While the dot was moving a radial reference line was shown adjacent to the filter, randomly at one of ten different positions. Observers pressed one of two keys, indicating whether they saw the dot disappear ‘ahead of’ or ‘before’ the line. On 20% of the trials the dot actually vanished from the screen at a position where it was still clearly visible,  $10^{\circ}$  (angular position) before the line. These trials prevented observers from learning about the vanishing positions.

An initial experimental session was used to a) familiarise observers with the stimuli, and b) select the ten positions where the short-segment motion would be presented to each observer because of individual differences in absolute thresholds. Following this each observer performed a block of 250 trials of the short-segment motion condition and 250 trials of the long-trajectory motion condition. Twenty measurements were made for each data point in both conditions (20 trials  $\times$  10 data points + 50 catch trials = 250 trials). In three short breaks the main room lights were turned on to avoid dark adaptation of the observers. Psychometric functions were fitted to the data using probit analysis (Finney, 1971; McKee, Klein, & Teller, 1985) to obtain 50%-thresholds. Confidence intervals for these thresholds were computed using a bootstrap method (Foster & Bischof, 1991). Responses on the catch trials in both conditions were used to measure ‘false alarm’ rates and to compute a bias measure  $c$  (Macmillan & Creelman, 1991). Observers that showed a response bias in their decisions on the catch trials of  $abs(c) > 1$  (standard deviation units) in either direction were excluded from the analysis.

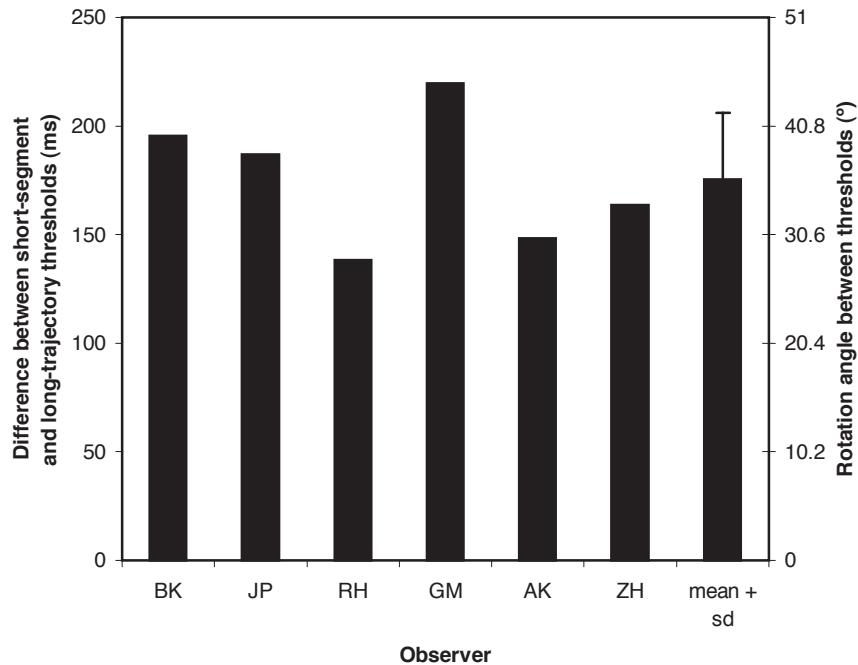
### B.2.2 Results

All observers reliably reported that the moving dot in the long-trajectory motion condition was visible at luminances, at which they were unable to detect the short-segment motion dot. However, two observers were excluded from the analysis because of large biases in their responses on the catch trials. These observers were unable to reliably detect the disappearance of the dot even at relatively high luminances. For the remaining six observers biases were smaller than one standard deviation.



**Figure B.2** Raw data and fitted psychometric functions from Experiment 1 for naïve observer ZH. The abscissa denotes the angular position of the reference line where the dot was presented (short-segment motion) or where observers made the decision ('dot disappeared ahead of/before the line'). Higher angular positions correspond to lower stimulus luminances. The ordinate denotes percent 'yes' responses (short-segment motion) and percent 'ahead' responses (long-trajectory motion). The horizontal error bars represent 95%-confidence intervals for the 50%-thresholds.

The difference between the two thresholds in every single remaining observer was at least four times the size of the 95%-confidence intervals for the thresholds. The raw data and fitted psychometric functions for one naïve observer are shown in Figure B.2. The average rotation angle between thresholds across all observers was  $35.8^\circ$  ( $sd = 6.3^\circ$ ; arc distance  $1.8^\circ$  visual angle,  $sd = 0.3^\circ$ ). The distance measure was translated into a time measure, describing for how long the dot was visible after it passed the detection threshold measured in the short-segment motion condition. On average this time was 175.4 ms ( $sd = 30.8$  ms). Figure B.3 shows the threshold differences for all six observers and the group mean. The slopes of all psychometric functions were similar and showed no significant differences between conditions (dependent test:  $t(5) = 2.32$ ,  $p = 0.068$ ; data not shown).



**Figure B.3** Difference (in units of time and rotation) between the thresholds for the long-trajectory motion and the short-segment motion conditions for each of the 6 observers and the group average (with standard deviation).

### B.2.3 Discussion

All observers showed a robust difference between the thresholds for the long-trajectory motion and the short-segment motion conditions. Observers were unable to detect the short-segment dot at luminance levels (and positions) at which they still reliably saw the long-trajectory dot. We interpret this as a forward displacement of the dot's vanishing position in the long-trajectory condition. In this condition the dot disappears without providing a strong transient signalling its offset. Therefore the proposed correction mechanism for the perceived final position is not operational, and the dot is visible in positions at which retinal input alone is insufficient to reliably yield a percept, as in the short-segment motion condition.

Two factors unrelated to our hypothesis could have contributed to the results. The visibility of the dot in the short-segment motion condition could be diminished as the dot was presented at different locations. Although the position of the dot was cued, it might be argued that the spatial uncertainty is greater in the short-segment motion condition than in the long-trajectory motion condition. This could allow observers to deploy attention to 'track' the long-trajectory dot, leading to better detection performance. In addition, probability summation might contribute to the better visibility of the long-trajectory stimulus. The short-segment dot is presented for only five refresh frames, whereas the long-trajectory is presented for longer after it passes the reference line. Because more frames are presented in the long-trajectory condition (although in each frame the dot will be dimmer than in the previous one), probability summation predicts better detection of the dot that is presented for more discrete frames. Experiment 2 addresses these *attention* and *probability summation* hypotheses.

## B.3 Experiment 2

This experiment measures the detection threshold for the short-segment motion dot in a different way. Again the dot's luminance was changed from trial to trial, but it was now always presented in the same position. Furthermore, the stimulus was presented repeatedly until the observer gave her response. In a second condition the length of the trajectory was approximately doubled to check if more discrete presentation frames increased the dot's detectability. If the higher detection threshold for the short-segment dot in Experiment 1 is based on observers' uncertainty about its presentation position or attentional disadvantages over the long-trajectory dot, it is expected that these modifications will eliminate the difference in thresholds. Furthermore, if the difference in thresholds in Experiment 1 depended on the longer presentation of the long-trajectory dot at sub-threshold luminances, the extension of the trajectory length in this experiment is expected to lead to significant differences in detection thresholds.

### B.3.1 Methods

#### B.3.1.1 Participants

Four observers from Experiment 1 took part in this study. Three observers were naïve about the purpose of this experiment.

#### B.3.1.2 Apparatus and stimuli

Most of the apparatus was the same as in Experiment 1. A micro-stepper motor (Parker Hannifin Corp.) controlled by the experimental software was used to rotate the filter disc. Now the dot was always presented in the 12 o'clock position, 2.8° above the fixation point. Rotation of the filter changed the dot's luminance. In an additional

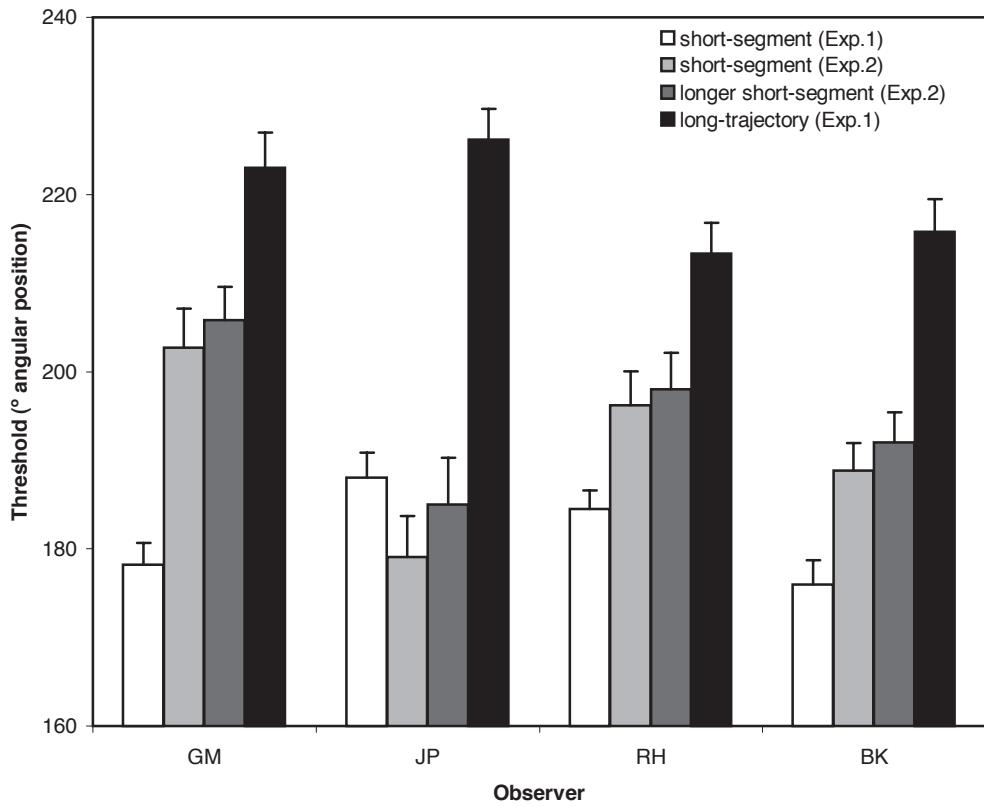
condition the trajectory length of the stimulus was increased from  $12^\circ$  to  $26.4^\circ$  (arc distance  $1.3^\circ$  visual angle; 11 refresh frames, i.e. 129.4 ms at 85 Hz refresh rate). On the extended trajectory the dot's luminance decreased by a factor of 0.45.

### ***B.3.1.3 Procedure***

To alert the observer an acoustic beep signalled the start of a trial. The stimulus was repeatedly presented until the observer made a response. Again the response was a key press, indicating whether the observer saw the stimulus or not. After the response the screen turned black and the motor moved the filter to the next position. For each of the two segment lengths there were 120 trials, ten trials at twelve different luminance levels. The trial order was randomised for each observer for a total of 240 trials.

## **B.3.2 Results**

The thresholds measured for the two motion segment lengths did not differ significantly from each other, as confidence intervals for both thresholds overlap for every single observer. Figure B.4 shows the data of Experiment 1 and Experiment 2. The detection performance improved for three observers compared to the short-segment condition of Experiment 1. However, all four observers still showed a large difference between the new detection thresholds and the disappearance threshold for the dot in the long-trajectory condition of Experiment 1. The differences between the long-trajectory threshold of Experiment 1 and the thresholds of Experiment 2 reduced to  $26.1^\circ$  rotation ( $sd = 11.9^\circ$ ) on average, collapsed over the shorter and longer motion segments. This corresponds to a time shift of 128.0 ms ( $sd = 58.1$  ms).



**Figure B.4** Absolute thresholds from Experiments 1 and 2 for four observers who participated in both experiments (including author GM). Bigger angular position denotes lower luminance of the stimuli. The white bar represents the detection threshold for the short-segment stimulus from Experiment 1; the two grey bars depict thresholds for the two short-segment stimuli in Experiment 2; the black bar shows the disappearance threshold of the long-trajectory stimulus from Experiment 1. Errorbars show 95%-confidence intervals for each threshold.

### B.3.3 Discussion

Probability summation would predict that increasing the trajectory length of the short-segment dot would lead to its greater detectability. Experiment 2 shows that despite a small improvement the longer short-segment stimulus is not detected significantly better than the original stimulus. It can be concluded that probability

summation cannot be the sole contributor to the difference in thresholds measured in Experiment 1.

Experiment 2 eliminated spatial uncertainty for the short-segment stimulus by presenting it repeatedly in the same position. These manipulations did improve detection performance in three out of four observers. Nonetheless there remains a wide gap between the thresholds for short-segment motion (of Experiments 1 and 2) and long-trajectory motion (Experiment 1), amounting to more than 120 ms. We interpret this difference as a forward displacement due to the dot's motion history.

## B.4 General Discussion

Close examination of the studies that do not show a forward displacement for moving objects (Eagleman & Sejnowski, 2000; Kerzel, 2000; Nijhawan, 1992; Whitney & Murakami, 1998) points to one potential common denominator for correct object localisation: a strong transient signalling an abrupt change in the moving object. We hypothesised that this transient carries accurate positional information, which is used by the visual system to enable the perception of the correct position (Nijhawan, 2002).

Although this transient arrives at relevant cortical areas after a significant delay following retinal stimulation, the transient is able to influence the perceived position of the object in a retroactive manner. Similar retroactive effects are evident in backward masking and other phenomena (Breitmeyer, 1984; Dennett & Kinsbourne, 1995; Kolers, 1972; Libet, 1981; Ross, 1972; van der Waals & Roelofs, 1931).

In the present experiments we tested this hypothesis by removing the retinal transient elicited by the moving object's offset. This was achieved by using a gradually

fading object (Experiment 1). We expected that a fading moving object that does not provide a transient signal would show a forward displacement; i.e. it would be visible at luminances lower than the detection threshold for motion over short segments. Experiment 1 confirmed this expectation. In Experiment 2 we confirmed that this result cannot be attributed solely to probability summation depending on the length of the motion sample or to greater deployment of spatial attention in the long-trajectory motion condition.

Our results are particularly noteworthy, as similar non-fading stimuli, where a transient does signal the abrupt offset, have previously been shown to be localised correctly or mislocalised in the opposite direction (Kerzel, 2000; Stork & Müsseler, 2004). Kanai, Sheth, and Shimojo (2004) described a set of conditions where an overshoot of the moving object can be found with abrupt offsets. One of these conditions used a very low-contrast moving object. The Off-transient of a low-contrast object is weaker than of a high-contrast object. Our interpretation of their finding would be that the weak transient signal is not able to trigger the correction mechanism described here; therefore the moving object is perceived to overshoot.

The present study manipulated the transient related to the offset of a moving object. To apply to experimental paradigms where there is an abrupt change in the direction of motion (Whitney & Murakami, 1998) our findings have to be extended to transients related to direction changes. It is known that the visual system responds strongly to such unpredictable events. For example, EEG studies have shown event-related potentials in response to the onset of motion and changes in the direction of motion (Clarke, 1972; Hoffmann et al., 2001; Pazo-Alvarez et al., 2004). These signals

seem to originate from higher visual areas, and may signal the change of the direction of motion to areas coding for object position. More recently synchronised firing of retinal ganglion cells in response to a direction reversal of a moving stimulus has been demonstrated in neurophysiological measurements (Schwartz et al., 2007). These signals might contribute to the localisation of direction changes and extend our hypothesis to explain the lack of a perceptual overshoot in paradigms where moving objects stop without disappearing (Eagleman & Sejnowski, 2000) or abruptly change direction (Whitney & Murakami, 1998).

Hysteresis is the well-known effect that descending staircases of stimulus contrast lead to lower threshold estimates than ascending staircase (e.g. Palmer, 1999). Given the unusually large magnitude of the effect presented here (128 – 175 ms) compared to usually measured effect sizes in the flash-lag effect (~80 ms), it is likely that hysteresis contributes to the effect. Whether hysteresis for contrast change alone can explain the large effect size remains to be tested. However, whatever neural mechanism is the underlying cause for hysteresis, the same mechanism might also be involved in motion extrapolation. A recurrent network architecture identified by Wilson and Cowan (1973) has been used to explain hysteresis effects in binocular vision and in the perception of motion direction (Williams, Phillips, & Sekuler, 1986). Indeed, a very similar architecture is also shown to produce motion extrapolation effects for moving objects (Erlhagen, 2003, see below).

Our interpretation of the forward displacement for moving objects found in the present study and in the various other paradigms is as follows. There are non-trivial neural delays in the transduction, transmission and processing of information within the

nervous system. It has been suggested that there are mechanisms to compensate for these delays, otherwise it would not be possible to successfully interact with a dynamic environment (De Valois & De Valois, 1991; Ghez & Krakauer, 2000; Lacquaniti & Maioli, 1989; Nijhawan, 1994; Wolpert et al., 1995). Especially the interaction with moving objects would pose a severe problem, because the position information available to the system would always lag behind the position the object presently occupies. Possible neural mechanisms for the anticipation of moving objects in the visual system have been identified, including local lateral interactions in the retina (Berry et al., 1999) and later levels (Baldo & Caticha, 2005; Jancke et al., 2004b; Kanai et al., 2004; Kirschfeld & Kammer, 1999), and/or internal models that facilitate extrapolation by top-down influences on early cortical representations. Internal forward models have been proposed previously to account for forward displacements found in experiments involving limb movements (Miall & Wolpert, 1996; Wolpert et al., 1995). The visual system might generate an analogous internal model for the processing of moving visual stimuli (Erlhagen, 2003; Miall & Wolpert, 1996; Nijhawan & Kirschfeld, 2003).

Our present findings suggest that neural processes underlying the perception of a moving object can be maintained with weaker neural activity due to an internal model. The perceived position is to some degree independent from bottom-up stimulation. Motion in the model cannot be stopped instantaneously. However, when motion in the outside world is stopped with a strong transient this generates a strong neural response, which carries accurate position information. This transient overrides the neural activity that is otherwise maintained by the internal model. When the transient input is

weakened (for example due to gradual fading) the internal model runs unhampered for longer.

It seems to be necessary that the correcting transient stems from the moving object itself and not from neighbouring objects. Other transients (like flashes nearby) do not usually reset the predicted position of a moving object, but lead to a spatial offset between moving object and flashes (the flash-lag effect). However, recently conditions have been found, in which flashes can lead to a reconstruction of the veridical position of the moving object. Kanai and Verstraten (2006) observed that, additionally to the forward displaced position of a moving object, a second instance of the same object in its veridical position can be seen when flashes are positioned suitably to trigger filling-in processes.

In contrast to our view described above, Eagleman and Sejnowski (2000) proposed that in the flash-lag effect “the flash resets motion integration” (p. 2037), and later the newly integrated position of the moving object is “postdicted to the time of the flash” (p. 2038). The general principle of a subsequent event influencing the perceived position is compatible with our proposed retroactive correction mechanism. However, Eagleman and Sejnowski claimed that the flash-lag effect is caused exclusively by retroactive (or ‘postdictive’) mechanisms. Our interpretation of the flash-lag effect would be different: The position of the moving object is constantly predicted by an internal model to compensate for delays in the neural pathways (Nijhawan, 1994). The flash does not interfere with this prediction, therefore an offset between the moving object and the flash is perceived in standard flash-lag displays. In the case of the abrupt stopping of motion (e.g. the flash-terminated flash-lag display) the transient signal

associated with this abrupt event does interfere with ongoing motion processing and retroactively influences the perceived position of the moving object. We use both predictive and retroactive mechanisms in this explanation, which might at first seem unparsimonious. However, we assume that whenever the brain can use predictive mechanisms, it will do so to benefit from a more ‘up to date’ world model. Confronted with unpredictable, sudden events, the brain will employ retroactive mechanisms to come up with the most reasonable interpretation of the sensory input. This interaction of two opposing mechanisms is advantageous to an animal because it maximally reduces localisation errors of moving objects.

**C Article II****Neural correlates of motion extrapolation in early visual cortex: An fMRI-study****Abstract**

A gradually fading moving object is perceived to disappear at positions beyond its luminance detection threshold, whereas abrupt offsets are usually localised accurately. What cortical areas are involved in this motion extrapolation of fading objects? Using fMRI, we localised regions of interest (ROIs) in retinotopic maps abutting the trajectory endpoint of a bar moving either towards or away from this position while gradually decreasing or increasing in luminance. Area V3A showed predictive activity, with stronger BOLD responses for motion towards versus away from the ROI. This effect was independent of the change in luminance. In Area V1 we found higher activity for high-contrast onsets and offsets near the ROI, but no significant differences between motion directions. We suggest that perceived final positions are based on an interplay of motion-sensitive and primary retinotopic representations. In the absence of high-contrast offset transients indicating final positions, predictive overshoots are perceived.

## C.1 Introduction

Signals in the brain do not travel at the speed of light. For example, in the visual system all processes involved in the build-up of a percept—from phototransduction in the receptor cells and synaptic transmission in the retina, via the conduction of action potentials along the optic nerve and more synapses in the LGN to processing in the occipital cortex—require significant processing times. Usually cited latency values for the first neural response in visual cortex from the time light hit the eye range from 34 to 100 milliseconds (Schmolesky et al., 1998). For an acting organism in a dynamic environment these delays can cause severe problems. For the case of a moving object for example, these delays mean that the perceptual systems in the brain do not have access to the true position of the object at any time, but will always have delayed information. For interaction with a moving object accurate localisation by the perceptual system is advantageous, as it reduces computational cost in the motor system, which additionally has to deal with delays in efferent pathways and muscles (Wolpert et al., 1995).

It has been proposed that perceptual systems comprise an extrapolation mechanism for coherently moving objects that helps to overcome the consequences of neural delays in the sensory pathways (Nijhawan, 1994). This mechanism supposedly becomes apparent in the flash-lag effect, where a moving object is seen ahead of a flashed object, although both are physically aligned at the time of the flash (Krekelberg & Lappe, 2001; Nijhawan, 1994, 2002). These findings have sparked an ongoing debate about how moving objects are localised by the visual system. Alternative accounts to motion extrapolation include differential latencies, temporal integration, and

postdiction. Differential latency accounts of the flash-lag effect propose that moving objects are generally processed faster than flashes in the visual system, thereby leading to the perceived spatial lag between physically aligned stimuli (Purushothaman et al., 1998; Whitney & Murakami, 1998). Temporal integration accounts claim that positions of a moving object are sampled over an extended time window and then integrated to yield the perceived position (Krekelberg & Lappe, 2000; Roulston et al., 2006). For a flash or a static object only one position enters this integration process, so these stimuli are accurately localised, whereas a moving object is perceived with a spatial bias towards the direction of motion. Eagleman and Sejnowski (2000) additionally proposed that a flash resets the integration of motion, and the subsequently re-sampled motion position is then reassigned, or ‘postdicted’, to the time of the flash.

In particular, the absence of a perceived misalignment in the so-called flash-terminated display, when the moving object disappears abruptly at the time of the flash, has been used to argue against the original spatial extrapolation account (Eagleman & Sejnowski, 2000). Motion extrapolation would predict that a moving object that disappears or stops abruptly perceptually overshoots its final presentation position. Alternatively, temporal integration theories can explain the absence of said overshoot readily, as no positions beyond the end of the trajectory contribute to the integration process. However, recently Maus and Nijhawan (2006, Article I; in press, Article IV) argued that the abrupt offset of a moving object supplies a strong accurately localised transient signal that masks any extrapolated representation of the object and thus determines the object’s perceived final position. When a moving object disappears without providing such a strong transient signal, the object is seen disappearing in an extrapolated position. Maus and Nijhawan (2006, Article I) employed a gradually

fading moving object and showed that it is perceived to disappear at luminance contrasts below the detection threshold. They argued that the final part of the perceived trajectory of these fading objects is not based on retinal input, but on an internal model entailing the extrapolated position.

Here we ask what cortical areas might be involved in this particular kind of motion extrapolation. Possible mechanisms for spatial extrapolation include lateral spread of activity within a retinotopic map (Erlhagen, 2003; Jancke et al., 2004a; Sundberg et al., 2006) and feedback from motion-sensitive areas to earlier retinotopic areas. Especially area MT+ (V5) plays a pivotal role in motion perception (Pascual-Leone & Walsh, 2001; Sack et al., 2006; Silvanto et al., 2005b) and prediction of moving objects (Senior, Ward, & David, 2002). Large receptive fields in MT/V5 and reciprocal connections to V1 give rise to the possibility that feedback from motion selective areas can bias the more fine-grained spatial representation in primary visual cortex in the direction of stimulus motion. Other areas selective to visual motion include area V3A in dorsal occipital cortex (Tootell et al., 1997).

Using functional magnetic resonance imaging (fMRI) it has recently been shown that during apparent motion there is activity in primary visual cortex correlated with the illusory motion percept (Larsen et al., 2006; Muckli et al., 2005; Sterzer et al., 2006). This activity is localised retinotopically in the unstimulated path of the illusory motion. Here we similarly measure activity in retinotopic areas corresponding to the illusory part of the trajectory of fading moving objects (Maus & Nijhawan, 2006). While measuring blood oxygenation level dependent (BOLD) signal changes in retinotopic areas of the occipital cortex we presented a moving visual stimulus either gradually

increasing or decreasing in luminance contrast and therefore terminating either with or without a high-contrast transient in its final position. The stimulus gradually fading out is seen moving beyond its last suprathreshold presentation position (Maus & Nijhawan, 2006), whereas the appearing stimulus is only perceived in later positions of the trajectory (Fröhlich, 1923). Focusing on retinotopic areas that maintain stimulus position with relatively high resolution, we compared BOLD responses of gradually fading moving bars to gradually appearing bars to see which areas might be involved in the differential perceptual outcomes in response to physically identical stimulation. We expected to find evidence for neural extrapolation in motion-sensitive areas and hoped to find a neural activation pattern akin to behavioural results in early retinotopic areas.

## C.2 Methods

### C.2.1 Participants

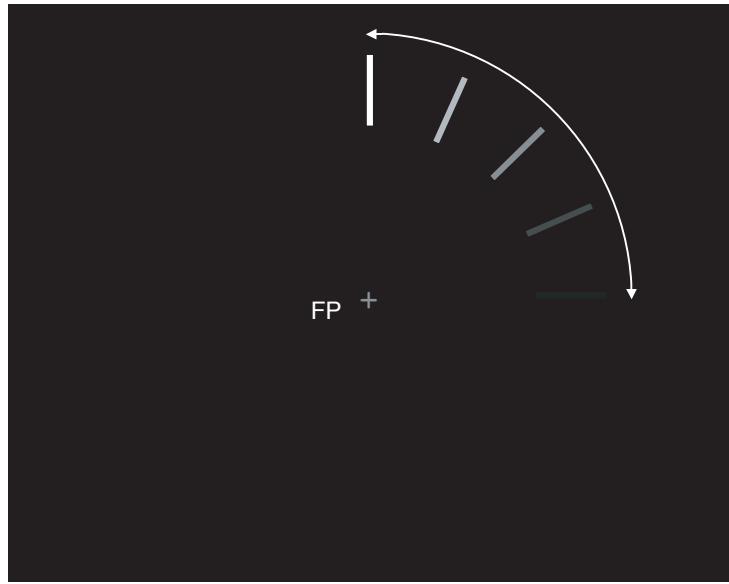
Ten participants (five female, mean age 25.9, standard deviation 4.4 years) took part in the study for monetary compensation. All had normal or corrected to normal visual acuity and gave written consent after being informed about the study and the procedure.

### C.2.2 Apparatus and stimuli

Stimuli were projected with an LCD projector (Sanyo PLC-XP41 with a custom-build zoom lens) onto a frosted screen in the magnet bore. Participants viewed the screen via a mirror mounted onto the head coil. Viewing distance was approximately 30 cm. The stimuli were generated using Matlab and the Psychophysics toolbox extensions (Brainard, 1997; Pelli, 1997).

For the retinotopic localisation of regions of interest (ROIs) we presented flickering checkerboards at a position 7.3° of visual angle to the right of a central fixation cross, i.e., on the horizontal meridian (middle checkerboard, cb-mid), as well as rotated 4° counter-clockwise (upper checkerboard, cb-up) and 4° clockwise (lower checkerboard, cb-low) around the fixation cross. The checkerboards consisted of 2 x 11 alternating black and white squares (0.35° x 1.91° visual angle) and flickered at 6.7 Hz for 833 ms.

The experimental stimulus consisted of a white radial bar (0.17° x 1.74° visual angle) on a black background, moving one quarter of a circle around the central fixation cross. The inner end of the bar was at 6.4° eccentricity from fixation. In two conditions the bar either started moving at the 12 o'clock position and moved clockwise, thereby fading constantly until it disappeared at the 3 o'clock position (clockwise fading, cw-fad), or it started moving counter-clockwise at 3 o'clock gradually appearing from background luminance until it reached full contrast at 12 o'clock, where it suddenly disappeared (counter-clockwise appearing, ccw-app; see Figure C.1). These two conditions had low-contrast offsets or onsets in the region near the horizontal meridian, respectively. Two more conditions, referred to as high-contrast onset/offset conditions, had exactly the opposite pattern. The bar was switched on abruptly at 3 o'clock and faded out towards 12 o'clock (counter-clockwise fading, ccw-fad) or appeared gradually at 12 o'clock and moved towards 3 o'clock, where it was switched off abruptly (clockwise appearing, cw-app). The rotation velocity of the bar in all conditions was 108 °s<sup>-1</sup>; the motion sequence lasted 833 ms.



**Figure C.1** Illustration of the moving stimuli: In the clockwise fading condition (cw-fad) a radial bar appeared abruptly at the 12 o'clock position and moved in a clockwise direction around the fixation point, while gradually fading. At the 3 o'clock position, on the horizontal meridian, it vanished. Oppositely, the counter-clockwise appearing stimulus (ccw-app) started moving from the 3 o'clock position and gradually increased in contrast until the 12 o'clock position, where it disappeared abruptly. These two conditions are referred to as low-contrast onset/offset conditions; they had weak transients near the region of interest just below the horizontal meridian. The other two conditions (cw-app and ccw-fad; not shown) had strong transients at the horizontal meridian.

### C.2.3 Design

We used a rapid event-related functional MRI design with a total of eight conditions: the four motion conditions (cw-fad, ccw-app; cw-app, ccw-fad), the three checkerboard conditions (cb-up, cb-mid, cb-low), and a fixation condition, where only the central fixation cross was visible. A trial of each condition started with the presentation of the visual stimulus for 833 ms and lasted a total of 3000 ms. The central fixation cross was always visible. Participants were instructed to keep fixation on the central fixation cross at all times and view the stimuli passively.

The trials (130 trials of each condition, 1040 trials in total) were presented in a pseudo-random sequence that was counterbalanced for a trial history of two trials (Buracas & Boynton, 2002). This sequence was split into six runs of 175 trials. Each run, except for the first one, began with the last two trials of the previous run to keep the balanced trial history. Further, each run started with 8 s and ended with 10 s of the fixation condition. In total, each run consisted of 540 recorded volumes, lasting 9 minutes.

#### **C.2.4 MRI acquisition**

Magnetic resonance imaging data were obtained with a 3T Siemens Trio MR Imaging device (Siemens Medical Solutions, Erlangen, Germany) at the Brain Imaging Center Frankfurt. Each scanning session consisted of six functional runs and one anatomical scan, usually after the third functional run. High-resolution anatomical scans of the whole brain were recorded using a T1-weighted magnetization prepared rapid gradient echo sequence (TR = 2250 ms, TE = 4 ms, flip angle = 8°, 256 sagittal slices) with 2 x 1 x 1 mm voxel resolution. For functional data acquisition we used an echo planar imaging sequence (TR = 1000 ms, TE = 30 ms, flip angle = 60°, 16 slices, voxel size = 3.3 x 3.3 x 4.0 mm) with slices oriented approximately parallel to the Calcarine sulcus.

#### **C.2.5 Functional MRI data analysis**

All data analysis was done with the BrainVoyager QX software package (Brain Innovation, Maastricht, The Netherlands) and MatLab (The Mathworks Inc., Natick MA, USA). The functional data was preprocessed with 3D-motion correction, intra-

session alignment, slice scan time correction, linear trend removal, and a temporal high-pass filter at 0.01 Hz. Functional data were then coaligned with the anatomical scan from the same session and transformed into Talairach space (Talairach & Tournoux, 1988).

The rapid event-related design used closely spaced trials with one trial every 3 s. This led to considerable overlap of the hemodynamic response to each trial. A general linear model (GLM) was fitted to the functional time course of each voxel to estimate the underlying hemodynamic responses to each stimulation condition by deconvolution (Serences, 2004). For each condition there were 20 GLM predictors for the 20 volumes recorded after each trial stimulus onset, covering the typical range of a BOLD response.

We identified regions of interest (ROIs) in early visual cortex of each participant with the following method. We aimed to contrast the BOLD responses to the different motion conditions in retinotopic regions just under the horizontal meridian. However, the activations in response to the three localiser checkerboards were spatially overlapping. Therefore we contrasted each voxel's activation in response to the upper and lower checkerboard (in a 5-7 s peristimulus time window, when the BOLD responses peaked) against the fixation condition. We displayed the relative contribution (RC) of the upper and the lower checkerboard condition to the activation on a statistical map. A RC value of 1 means that the activation of the voxel is completely explained by the GLM predictors from the lower checkerboard condition, and a RC value of -1 means that the upper checkerboard explains the activation completely. We defined ROIs by selecting voxels with positive RC values that were more activated by the lower checkerboard. Thresholds were individually adjusted to achieve roughly equal sizes of ROIs. In this way we identified ROIs in early visual cortex for the lower checkerboard

in V1, on the V2d-V3 border, and in area V3A of the left hemisphere (see Table C.1). In two participants the ROI in V2d/V3 was not clearly identifiable. The location of ROIs in retinotopic areas was verified in two subjects using retinotopic mapping data (Sereno et al., 1995) from another scanning session and projecting them on an inflated representation of the cortical sheet (see Figure C.2). ROIs in other cortical maps, especially in MT/V5, could not be selected with this method, as receptive field sizes and thus the overlap of activation to the different checkerboard conditions were too big.

For these ROIs we then computed convolution-based GLMs by averaging voxels within each ROI and concatenating time courses from all participants. To account for differences between conditions in latency to peak and dispersion of the BOLD response we fitted gamma functions to the beta values of the GLM of the form

$$f(t) = k \left( \frac{t}{t_p} \right)^\alpha e^{-\frac{t-\alpha}{\beta}} + c,$$

$$\alpha = \frac{t_p^2}{w^2} * 8 \log(2),$$

$$\beta = \frac{w^2}{t_p * 8 \log(2)},$$

where  $k$  is a scaling factor,  $t_p$  is the time to peak,  $w$  is the width at half maximum and  $c$  is a constant offset. We quantified the BOLD response by the product  $pw$  [where  $p = f(t_p)$  is the peak amplitude], which represents the triangular area between the peak point and the two half-peak points under the curve of the gamma functions. Additionally, to compute statistical contrasts between the separate motion conditions and t-test statistics we selected all those predictors from the GLM that were significantly different from zero ( $p < 0.01$ , uncorrected).

**Table C.1** Individual threshold values, Talairach coordinates, and sizes of regions of interest for all participants.

Area	Left V1				
Participant	Threshold RC	Talairach x	y	z	Number of voxels
1	0.1	-9	-78	6.7	150
2	0.1	-10	-82	-6.1	272
3	0.08	-12	-78	5.4	352
4	0.1	0.14	-85	-10	188
5	0.1	-13	-78	-11	141
6	0.08	-14	-72	-9.8	159
7	0.1	-13	-85	4.2	162
8	0.13	-13	-82	-2.7	131
9	0.08	-8.5	-79	-1.2	145
10	0.1	-10	-79	-0.11	227
Group average		-10	-80	-2.5	193

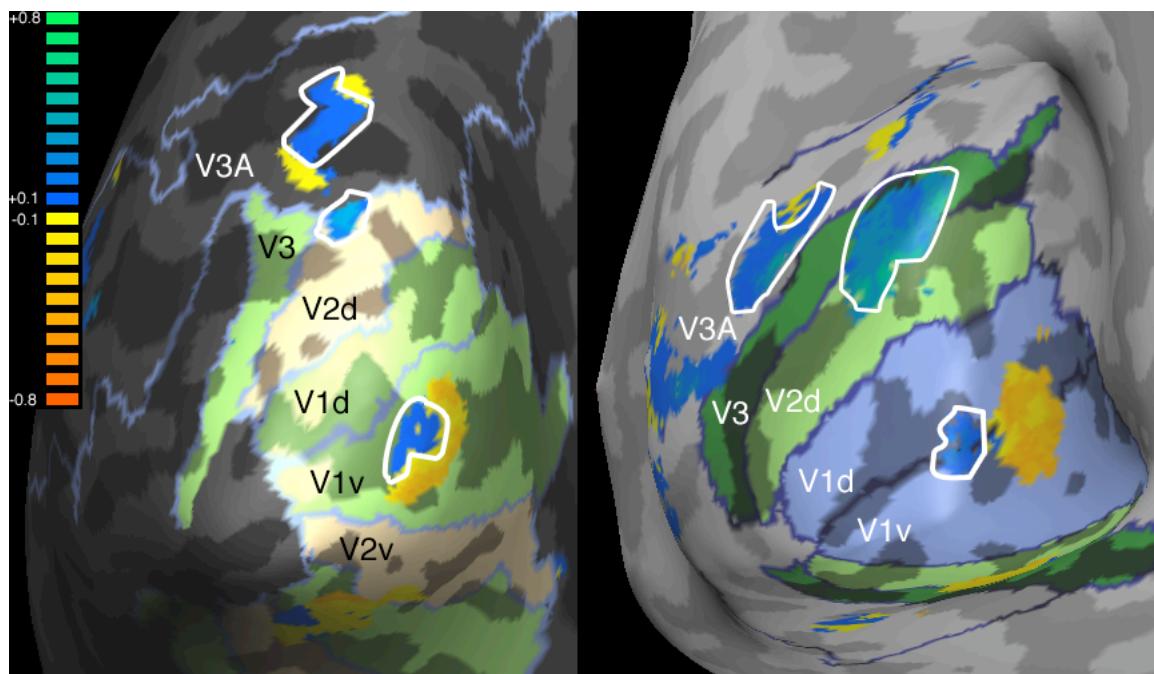
Area	Left V2d/V3				
Participant	Threshold RC	Talairach x	y	z	Number of voxels
1	0.1	-4.1	-85	7.1	340
2	0.1	-11	-89	10	396
3	0.07	-6.4	-93	2.9	212
4	0.11	-20	-86	3.8	392
5	0.1	-21	-87	14	286
6					
7	0.1	-20	-89	18	240
8	0.12	-9.4	-88	14	328
9					
10	0.08	-9.3	-90	21	232
Group average		-13	-88	11	311

Area	Left V3A				
Participant	Threshold RC	Talairach x	y	z	Number of voxels
1	0.1	-6.3	-94	16	385
2	0.08	-26	-85	8.3	243
3	0.07	-20	-88	11	207
4	0.067	-37	-82	1.7	372
5	0.1	-30	-87	17	257
6	0.08	-23	-89	16	364
7	0.1	-25	-83	15	207
8	0.1	-24	-88	19	320
9	0.1	-19	-92	10	270
10	0.1	-17	-84	23	188
Group average		-23	-87	14	281

### C.3 Results

Figure C.2 shows the selected ROIs for two participants, projected onto an inflated representation of visual cortex. Blue-green areas represent positive RC values, where the lower checkerboard contributed more to the voxels' activation than the upper checkerboard, and therefore indicate retinotopic positions just below the horizontal meridian. Yellow-red areas are negative RC values just above the horizontal meridian. In this way we defined ROIs for all participants in areas V1, V2d/V3 and V3A just below the horizontal meridian.

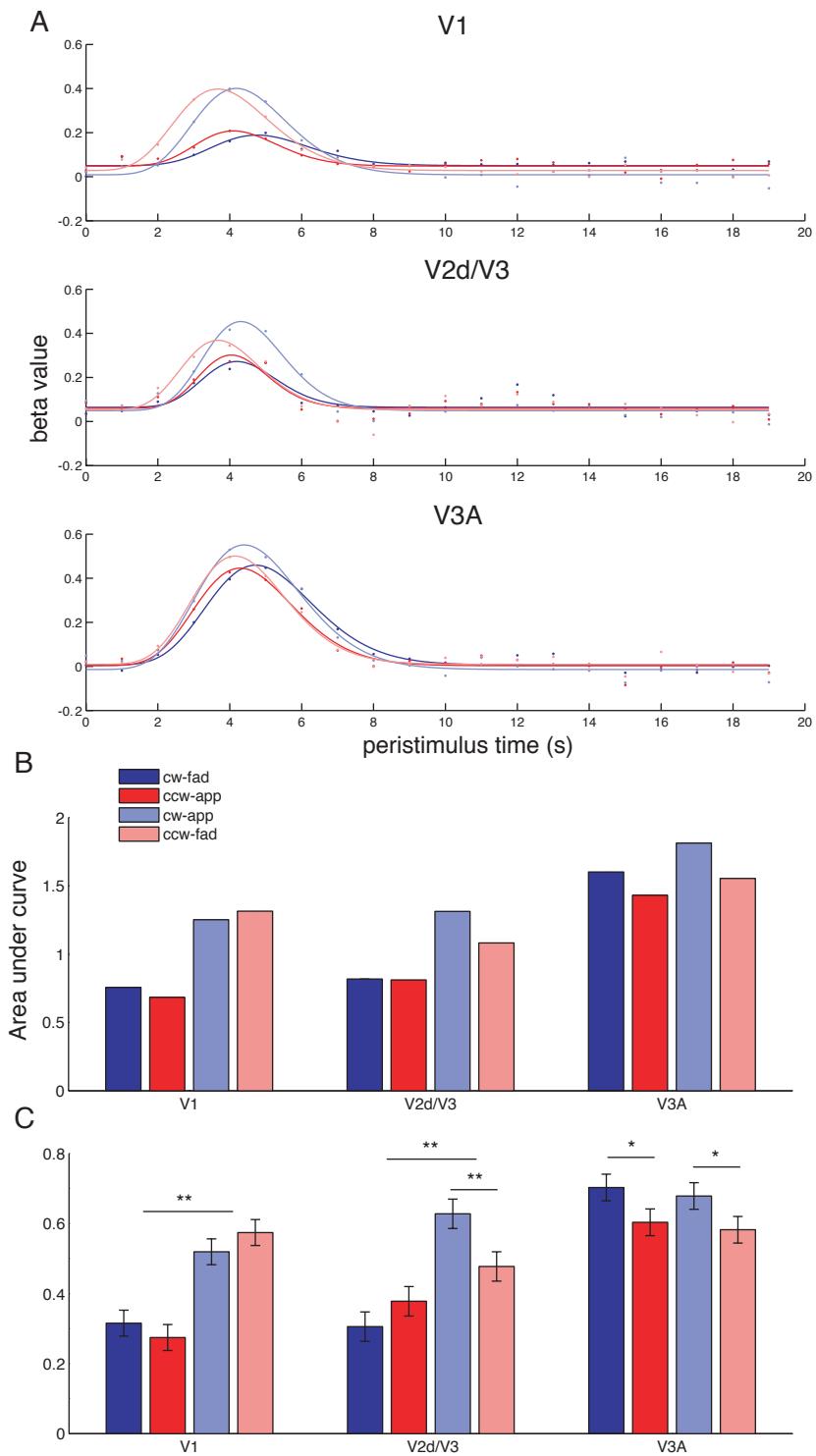


**Figure C.2** The regions of interest (ROIs) in the left hemisphere of two participants. The view is on the occipital pole of ‘inflated’ cortices with demarcated borders of visual areas V1, V2, V3, and V3A. ROIs in V1, at the V2d-V3 boundary and in V3A were identified. Blue-green areas show positive, yellow-red negative RC values.

Figure C.3A shows the averaged BOLD timecourses in the ROIs in response to the four motion conditions. The counter-clockwise motion conditions (red curves) led to earlier BOLD peaks than the clockwise motion conditions (blue curves). This earlier

peak is predicted from our stimulus design, because in the counter-clockwise conditions the motion started near the ROI at the beginning of each trial, whereas in the clockwise conditions the stimulus moved towards the ROI and terminated there 833 ms after trial onset.

Figure C.3B shows the BOLD indices calculated from the triangular area under the curve. This data gives a measure for BOLD amplitude and dispersion without being influenced by the latency to peak. In area V1 activity was highest in response to the ccw-fad and cw-app conditions (light colours), as these stimuli had high-contrast offsets or onsets near the ROI. In the other two conditions (dark colours) the stimulus was barely visible in the region near the ROI, and BOLD responses accordingly were weaker. Differences between the clockwise (cw) and counter-clockwise (ccw) conditions in V1 are small, however, there seemed to be a tendency in the low-contrast conditions for greater activations in response to the cw-fad stimulus moving towards the ROI. Figure C.3C shows another way of quantifying the BOLD responses, averaging all significant GLM predictors from each condition. These averages were used to calculate t-test statistics. The BOLD response in the high-contrast onset/offset conditions was higher than in the low-contrast onset/offset conditions ( $t = 9.22, p < 0.001$ ). The contrasts between cw-fad and ccw-app, as well as cw-app and ccw-fad did not reach statistical significance (cw-fad > ccw-app:  $t = 1.06, p = 0.288$ ; cw-app > ccw-fad:  $t = -1.43, p = 0.154$ ).



**Figure C.3 (A)** Averaged timecourses of BOLD activity in response to the four motion conditions and fitted gamma-functions (V1 and V3A:  $n = 10$ , V2d/V3:  $n = 8$ ). **(B)** BOLD indices, calculated as the triangular area between peak and half-peak points of the fitted gamma functions. **(C)** Averages of all significant ( $p < 0.01$ ) GLM parameter values for all motion conditions with standard errors of the mean (\*  $p < 0.02$ ; \*\*  $p < .001$ ).

For V2d/V3 it has to be noted that anatomically this region of interest does not include representations of the upper visual field, as the retinotopic maps of dorsal V2 and V3 are mirror-reversed along the horizontal meridian. Nevertheless we measured reliable BOLD activation in response to our motion stimuli (see Figure C.3A). Again, clockwise motion conditions peaked earlier than counter-clockwise motion conditions. The conditions with high-contrast onsets/offsets led to stronger activation ( $t = 7.30, p < 0.001$ ). The different motion directions did not show different activations in the low-contrast onset/offset conditions ( $t = -1.20, p = 0.230$ ), but higher activation was measured for clockwise motion towards the ROI in the high-contrast condition ( $t = 3.43, p < 0.001$ ).

In area V3A BOLD responses to both high- and low-contrast conditions are roughly equal ( $t = -0.83, p = 0.405$ ). Here, stimulus contrast seems to be less important than motion direction for the magnitude of the BOLD response. In both the strong and the weak onset/offset conditions clockwise motion towards the ROI elicited higher BOLD responses than motion away from the ROI (cw-fad > ccw-app:  $t = 2.50, p = 0.012$ ; cw-app > cew-fad:  $t = 2.41, p = 0.016$ ). As the ROI is localised below the horizontal meridian in retinotopic space, stronger activation for motion towards versus away from the region of interest means that the neural representation of the moving stimulus in area V3A is shifted forward in the direction of motion beyond the final position of the trajectory for both gradual and abrupt motion offsets.

#### C.4 Discussion

In summary, activity in area V3A showed a prediction for positions of moving stimuli. Activity in a ROI abutting the end point of the trajectory of a moving object

was higher, when the object moved towards the ROI than when it moved away from the ROI. The ROI was chosen to lie just below the horizontal meridian, where the object was never presented. The measured activity is likely to result from a spread of neural and/or hemodynamic activity in the cortex. Apart from the direction of motion, physical stimulation was identical between the compared conditions, and we measured a reliably higher spread of activity in the direction of motion than in the opposite direction. This finding is consistent with a neural anticipation of the moving stimulus ahead of actually stimulated retinotopic positions (Berry et al., 1999; Jancke et al., 2004a). In area V3A this shift was found for both high contrast objects that started moving at low luminance and increased before being switched off near the ROI, and for low contrast objects that started moving at high contrast and decreased gradually until disappearing from view near the ROI. Activity in these two conditions was statistically equal, consistent with reports of high sensitivity to low-contrast stimuli in V3A (Tootell et al., 1997).

In area V1 the biggest difference in activity was between high-contrast and low-contrast stimuli. Differences between motion directions were small and did not reach statistical significance. However, it seems that a predictive pattern similar to that found in V3A is more prevalent in the low-contrast conditions, i.e. for those conditions that also show a psychophysical forward shift of the moving object (Maus & Nijhawan, 2006), but not in the high-contrast conditions. Measuring more participants to increase statistical power might reveal the validity of this observation.

The pattern of activity along the border area of dorsal V2 and V3 is harder to interpret. Again there was predictive activity in response to motion towards the ROI, but only for the high-contrast condition. It is noteworthy that the ROI in V2d/V3 is truly

representing areas at and below the horizontal meridian, as the upper visual hemisphere is not represented in the dorsal part of area V2 and V3. If neural activity here is caused by lateral spread it is not from cortically adjacent areas, but retinotopically adjacent areas, i.e., ventral V2 and/or VP. In other words, activity cannot be due to faulty sampling of a region of interest that indeed represents visual locations from above the horizontal meridian or due to excessive spread of the hemodynamic signal.

We were unable to find fading-specific neural extrapolation. In other words, none of the areas investigated clearly resembled the behavioural findings (Maus & Nijhawan, 2006), showing extrapolated position representations for fading objects only, but accurate localisation for abrupt offsets. Activity in V1 might show such a pattern, but from the current data we cannot draw such conclusions. We did however find stronger BOLD activity in V1 in response to transient changes, i.e. abrupt stimulus onsets and offsets, with no apparent differences between motion directions for high contrast transients. Area V3A showed predictive activity overshooting the trajectory end point, regardless of whether motion was terminated in a strong or a weak transient. It is therefore feasible to conclude that area V3A predicts positions of moving objects. A similar predictive pattern of activity has been found in single cell recordings from macaque area V4 (Sundberg et al., 2006). V4 cells showed a shift of their retinotopic activity in the direction of motion in a related colour-flash mislocalisation illusion (Cai & Schlag, 2001). Interestingly this shift of activity also occurred, when the colour flash was in the last position of the motion trajectory and no forward shift was perceived.

The current findings imply that the cortex represents separate positions for a moving object. Representations in motion sensitive areas (e.g. V3A) utilise the

information of the past motion trajectory to create an anticipation of object position, regardless even of other object features like contrast. This extrapolated representation is possibly fed back to the fine-grained retinotopic map in V1, where it biases object position towards future positions (Erlhagen, 2003; Sterzer et al., 2006). However, V1 activity is more strongly influenced by retinal inputs, which can override the motion predictions in the event of sudden stimulus events like an abrupt offset. The transient signal elicited by an abrupt offset on the retina might inhibit the perception of extrapolated positions. The final perceived position is based on an interplay of the extrapolated representation in motion-sensitive areas and bottom-up information expressed in area V1 about the nature of the disappearance. In the presence of a strong transient signal there, the extrapolated position is corrected. In the absence of strong transients however, the extrapolated position is perceived.

Area V3A is highly motion-selective. Interestingly, in the present study V3A does not respond differentially to high and low stimulus contrasts. The sole determinant of V3A activity in the paradigm investigated seems to be direction of motion, regardless of contrast, consistent with earlier reports (Tootell et al., 1997). Recently, area V3A and nearby areas along the transverse and lateral occipital sulci have been implicated in the perception of apparent motion of complex three-dimensional shapes (Weigelt, Kourtzi, Kohler, Singer, & Muckli, 2007) and ambiguous structure from motion (Brouwer & van Ee, 2007). Another study has shown that anticipatory activity in area V3A can predict perceptual accuracy of observers performing in a spatial attention cuing paradigm (Sylvester, Shulman, Jack, & Corbetta, 2007).

It has to be noted that our focus on area V3A was mainly due to technical reasons. Another strong candidate to look for extrapolated position representations for moving objects is the human motion complex MT/V5. In the present study area V5 was activated by all motion conditions and the checkerboard localisers (data not shown). It was however not possible to define ROIs in the same ways as in V1, V2d/V3 and V3A, because the overlap of activity in response to the different localisers was too big. Receptive fields of neurons in MT/V5 are larger than in V1 and V3A, and retinotopic organisation is known to be less prevalent. It is, however, likely that MT/V5 plays a similar role in motion extrapolation as V3A proposed here. TMS studies of MT/V5 revealed the functional necessity of the area in the perception of motion (Pascual-Leone & Walsh, 2001; Sack et al., 2006; Silvanto et al., 2005b). Senior et al. (2002) showed that V5 also seems to be important in related forward displacement phenomena in visual short-term memory. In their study TMS over area MT/V5 interfered with a forward shift of remembered positions of objects in a dynamic visual scene. The functional necessity of area MT/V5 in the forward shift of moving objects as seen in the flash-lag effect has so far not been investigated. TMS experiments on the flash-lag effect would be a worthwhile enterprise.

Recently Maus and Nijhawan (2008, Article III) showed that objects moving into the blind spot are perceived to disappear inside the blind area, in unstimulated areas of the visual field. Using fMRI it has been shown that activity in response to static stimuli does not passively spread into the cortical representation of the blind spot (Awater, Kerlin, Evans, & Tong, 2005). This case presents maybe a better opportunity to show predictive activity in primary visual cortex, using the blind spot representation

as a region of interest that can clearly be identified (Awater et al., 2005; Tong & Engel, 2001), avoiding problems of overlapping active regions.

To conclude, the present study presents evidence for a forward shift of the neural representation of a moving object in motion-sensitive area V3A. This predictive activity may contribute to perceptual forward displacements such as the flash-lag effect (Nijhawan, 1994) and the forward shift of the final positions of fading objects (Maus & Nijhawan, 2006). Strong representations of transient signals in area V1 can interfere with these higher-level representations and thus facilitate the accurate localisation of final positions of abruptly disappearing objects.

## D Article III

### Motion Extrapolation into the Blind Spot<sup>5</sup>

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#### Abstract

In the flash-lag effect a moving object is seen ahead of an aligned flash. There has been an ongoing discussion about this and related findings. One proposal argues that objects are shifted forward by an extrapolation mechanism; another states that positions are determined in retrospect, after the object has passed the flash-position. Here we present strong evidence for spatial extrapolation. Observers judged the final perceived position of a moving bar disappearing in the retinal blind spot. Unlike abrupt motion offsets, the bar's final position was perceived as shifted forward, disappearing in blind areas of the retina. This perceived position must be based on a predictive mechanism. When a moving stimulus abruptly disappears from the retina, it elicits transient signals that mask extrapolated positions and facilitate accurate localisation of final positions. No such transients are elicited when the moving stimulus disappears in the blind spot, so the extrapolated position is perceived.

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<sup>5</sup> An edited version of this article has been submitted for publication to *Psychological Science*.

## D.1 Introduction

Objects moving across the visual field constantly change their position over time. Neural responses to moving stimuli are delayed, and persist for a significant duration after stimulation ceases. The delay in the neural response should cause a moving object to be seen in a position lagging its physical position, and response persistence should cause the moving object to appear smeared. However, moving objects appear less smeared than expected (Burr, 1980), and the instantaneous perceived position of a moving object is shifted forward in the direction of motion, as illustrated in a class of visual phenomena, most prominently in the flash-lag effect (Nijhawan, 1994). If a brief flash is presented in alignment with a moving object, the moving object is seen to be ahead of the flash. Several theories have been brought forward to explain this forward shift (reviewed in Krekelberg & Lappe, 2001; Nijhawan, 2002). Temporal integration theories state that the visual system samples positions of a moving object over an extended period of time and produces an average position, possibly weighted towards more recently sampled positions (Brenner et al., 2006; Krekelberg & Lappe, 2000; Roulston et al., 2006). The postdiction account additionally assumes that a flash resets this integration process and mainly uses positions from after the flash to produce the averaged outcome (Eagleman & Sejnowski, 2000). More recently the same authors argued for a different account, proposing that motion signals from after the flash bias the localisation of objects towards the direction of motion (Eagleman & Sejnowski, 2007). Alternatively, motion extrapolation posits that the visual system uses motion information from the previous trajectory to predict the moving object's position in the near future in order to compensate for neural processing delays in the visual pathway (Nijhawan, 1994, 1997, in press).

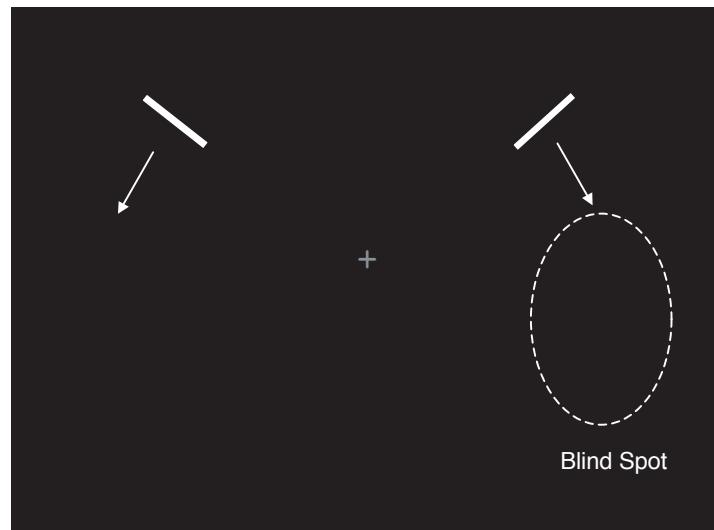
One particular observation concerning the flash-lag effect has in the past been used to argue against the visual prediction model: When the moving object disappears (Eagleman & Sejnowski, 2000) or reverses direction (Whitney & Murakami, 1998) at the time of the flash, it does not perceptually overshoot the point of disappearance or reversal. This absence of a predictive overshoot has been a major difficulty for the motion extrapolation account. However, abrupt offsets and direction changes of moving objects elicit retinal transient signals, which carry precise positional information. It has been argued that these signals can mask the visibility of an extrapolated object representation and thus facilitate accurate localisation of the object's final position despite predictive mechanisms (Maus & Nijhawan, 2006; Maus & Nijhawan, in press; Nijhawan, 2002). When a moving object disappears from view without eliciting a retinal transient signal, it should be seen to disappear in an extrapolated position. For example, when a moving object is gradually decreasing in luminance contrast and thus disappearing from view without a strong transient signal, it is seen disappearing in positions beyond its detection threshold (Maus & Nijhawan, 2006). The final perceived position is at a location, where the stimulating luminance contrast alone is not sufficient to produce a percept. This forward shift of the perceived position could be explained by lowered thresholds along the anticipated trajectory (Jancke et al., 2004b), or by a predictive localisation mechanism.

Here we present converging evidence that moving objects disappearing from view are indeed extrapolated beyond their final position when the disappearance is not accompanied by a transient signal. Furthermore, we rule out suggestions that the perceived position of moving objects is solely based on a temporal integration

mechanism, or that motion signals retrospectively cause the forward shift in object position.

In the present study observers judged the last visible position of a bar moving into the blind spot in relation to the last visible position of a second moving bar that was abruptly switched off. We simultaneously presented two bars in monocular viewing: One bar, ipsilateral to the viewing eye, moved on a circular trajectory and disappeared in the blind spot. A comparison bar on the contralateral side of the viewing eye was presented in the mirror image positions of the first bar and was switched off near the mirror image of the blind spot border (see Figure D.1). Observers performed a temporal order judgement task, indicating which bar they perceived as disappearing first. As the two bars occupied exactly mirrored positions, the point of subjective simultaneity for the disappearances also gave the last seen position of the bar on the blind spot side. In an additional condition one bar started moving inside the blind spot and the other bar abruptly in full view of photoreceptors. The task for observers here was to indicate which bar they saw starting to move first, and equivalently we measured the first seen position of the bar appearing from within the blind spot.

In contrast to an object disappearing in full view of photoreceptors, an object moving into the blind spot does not elicit a transient retinal Off-signal carrying precise position information. Therefore, we predict that if the perceived position of the object is extrapolated, it should be seen disappearing in a position shifted forward past the blind spot boundary into the ‘blind’ area. Temporal integration and postdiction would predict the object to perceptually disappear at (or slightly before) the blind spot boundary, because positions cannot be sampled from un-stimulated retinal areas.



**Figure D.1** Illustration of the stimulus used in the experiment. In the case shown viewing is with the right eye, therefore there is a blind spot  $\sim 15^\circ$  to the right of the fixation cross. Two bars start moving from  $45^\circ$  on both sides, exact mirror images of each other. The right bar disappears in the blind spot, whereas the left bar disappears abruptly from screen in a position determined by the experimental software. Observers make a temporal order judgement, indicating which bar they perceived to disappear first.

## D.2 Methods

### D.2.1 Participants

Five observers, including author GM volunteered to participate in the experiment. The remaining four observers were naive to the hypotheses. All observers had normal or corrected to normal vision.

### D.2.2 Apparatus and Stimuli

Stimuli were presented on a 21" CRT monitor (Formac Elektronik GmbH) at 100 Hz vertical refresh rate using MATLAB and the Psychophysics toolbox extensions (Brainard, 1997; Pelli, 1997). Observers kept a constant distance of 56 cm from the

screen with their heads partially immobilised by means of a chin rest. Viewing was monocular. An eye patch prevented stimulation of the opposite eye.

The stimulus consisted of two moving white bars ( $2.0^\circ \times 0.1^\circ$  visual angle) on a black background (Figure D.1). In all conditions the two bars were mirror images of each other, mirrored along the vertical meridian. The bars moved on circular trajectories around the fixation point with the bars' centres at  $15^\circ$  eccentricity. The angular velocity of each bar was  $61.3^\circ \text{ s}^{-1}$  (tangential velocity  $16^\circ \text{ s}^{-1}$ ). In the two stimulus offset conditions both bars started moving at an angle of  $45^\circ$  either from the upper or the lower visual field. The bar ipsilateral to the viewing eye moved into the blind spot, while the contralateral bar was switched off abruptly. In the two stimulus onset conditions one bar appeared from within the blind spot, whereas the contralateral bar started moving abruptly, and the bars were switched off when they reached the  $45^\circ$  position.

The task for observers in all conditions was to indicate with a key press, which bar they saw disappearing or appearing first. The positions of stimulus offsets and onsets of the contralateral bar were manipulated systematically in a method of constant stimuli. In the stimulus offset conditions the contralateral bar was switched off in one of seven possible positions between 40 ms before to 200 ms after the ipsilateral bar crossed the blind spot boundary in steps of 40 ms (i.e., between  $-2.4^\circ$  and  $12.2^\circ$  from the position of the mirrored blind spot boundary in steps of  $\sim 2.4^\circ$ ). For the stimulus onset conditions the contralateral bar was switched on in positions ranging from 120 ms before to 120 ms after the ipsilateral bar crossed the blind spot boundary (i.e.,  $\pm \sim 7.3^\circ$ ). In pilot experiments these positions of constant stimuli were determined to be ideal for the fitting of psychometric functions. As the two bars always occupied exactly mirrored

positions, the temporal order tasks in the stimulus offset and onset conditions effectively also measured the last visible position of the bar disappearing in the blind spot and the first visible position of the moving bar appearing from within the blind spot, respectively.

### **D.2.3 Measurement of blind spots**

Prior to the experiment the experimenter estimated the extent of observers' blind spots for each eye by slowly moving a small crosshair mouse pointer from different directions into the blind area. The observer indicated when they saw the pointer disappear. The experimental software recorded these positions and calculated the area of the blind spot (see Table D.1). Note that moving the mouse pointer into the blind spot resulted in slightly smaller estimates for the blind area (Incze, 1928). Next, the accuracy of the measurement was verified by presenting a single static frame from the motion sequence, where the bar was just inside the measured blind area. Observers confirmed that the bar was not visible. But if the bar was still visible it was moved further into the blind spot by one or more frames until it was definitely invisible. This bar position, which lies entirely within the blind spot, was defined as the blind spot boundary (0 position in Figure D.2) for the experiment.

### **D.2.4 Procedure and Analysis**

The experiment consisted of one block of trials of the stimulus offset and onset conditions for each eye. Stimulus presentation in the upper and lower visual field was randomised within each block. All blocks consisted of 140 trials (2 visual fields [upper/lower] x 7 constant stimulus position x 10 trial repetitions), so in total there were 280 trials for each viewing eye. The order of blocks was counterbalanced across the

naïve observers. Independent psychometric functions were fitted to each observer's responses at four separate blind spot boundaries (upper and lower boundary for the blind spot of the left and right eye). For two blind spot boundaries (out of a total of 20 examined) fitting psychometric functions was not possible due to inaccurate measurements of the blind spot area. These two measurements were excluded from further analysis. Points of subjective simultaneity and hence also perceived positions for stimulus offsets and onsets were calculated from the 50% threshold points of psychometric functions.

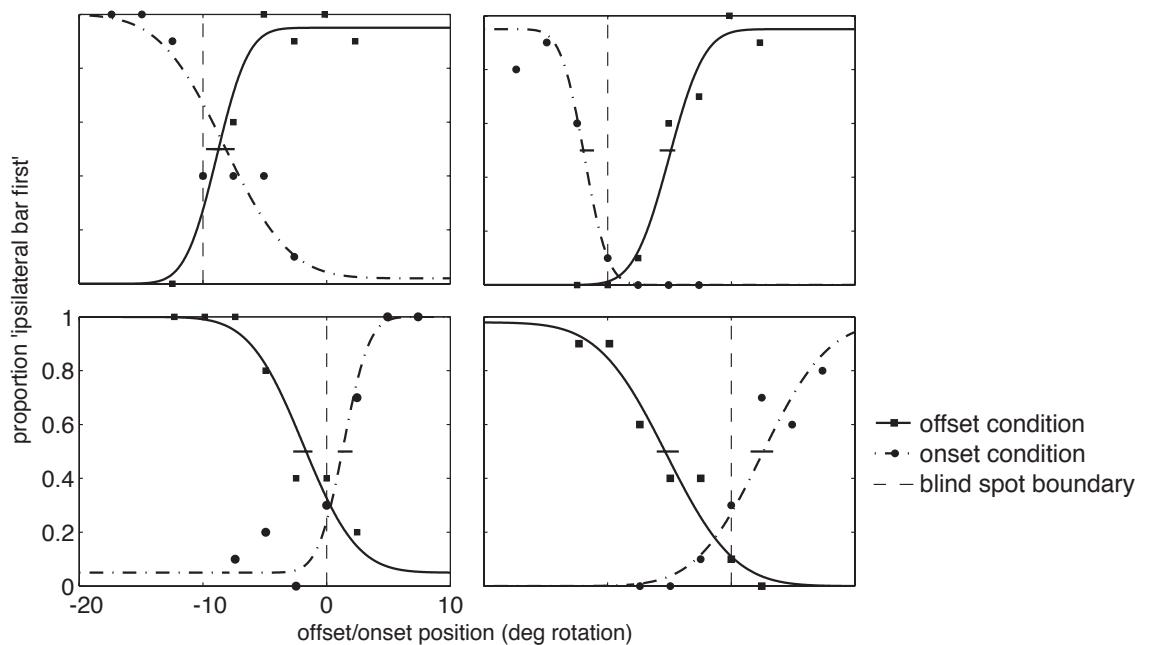
**Table D.1** Results of blind spot measurements for the five observers. Listed for each blind spot are the coordinates of the centroid of the polygonal area of the blind spot in degrees visual angle from the central fixation cross, the horizontal and vertical diameter, and the total area of the blind spot in degrees squared.

Observer	Eye	Centroid X	Centroid Y	horizontal Ø	vertical Ø	Area
NZ	left	14.44	-1.36	4.35	6.31	19.55
	right	15.17	-0.23	4.62	7.65	23.17
GM	left	14.92	-1.36	4.96	6.04	21.09
	right	15.09	-0.70	4.77	5.43	17.74
ZW	left	14.64	0.45	4.42	5.16	16.06
	right	14.40	-0.62	4.27	5.00	13.05
CJ	left	15.55	-2.65	4.73	7.65	25.69
	right	15.70	-0.62	4.85	5.73	20.84
RH	left	14.76	-2.20	4.35	7.50	25.93
	right	14.67	-0.22	4.81	6.00	20.86
Mean		14.93	-0.95	4.61	6.25	20.40
SEM		0.14	0.30	0.08	0.32	1.28

### D.3 Results and Discussion

Psychometric functions for one naïve observer are shown in Figure D.2, and average perceived first and final positions for all observers are shown in Figure D.3. All observers perceived the bar moving into the blind spot as shifted well into the blind area. The average forward displacement was 3.1° rotational angle (*SEM* 0.5°, one sample t-test  $t(17) = 6.17$ ,  $p < 0.001$ ,  $r = 0.83$ ) on the circular trajectory of the bar,

equivalent to  $\sim 51$  ms (*SEM* 8.3 ms) or  $0.81^\circ$  visual angle (*SEM*  $0.13^\circ$ ). The bar moving out of the blind spot was reliably detected at the same time as when the bar on the contralateral side started moving, with on average no displacement,  $0.0^\circ$  (*SEM*  $0.6^\circ$ , one sample t-test  $t(17) = 0.04, p = 0.965, r = 0.01$ ). The last perceived position of the disappearing bar and the first seen position of the appearing bar were significantly different from each other (paired samples t-test  $t(17) = 3.94, p = 0.001, r = 0.69$ ).



**Figure D.2** Psychometric functions for one typical naive observer (NZ).

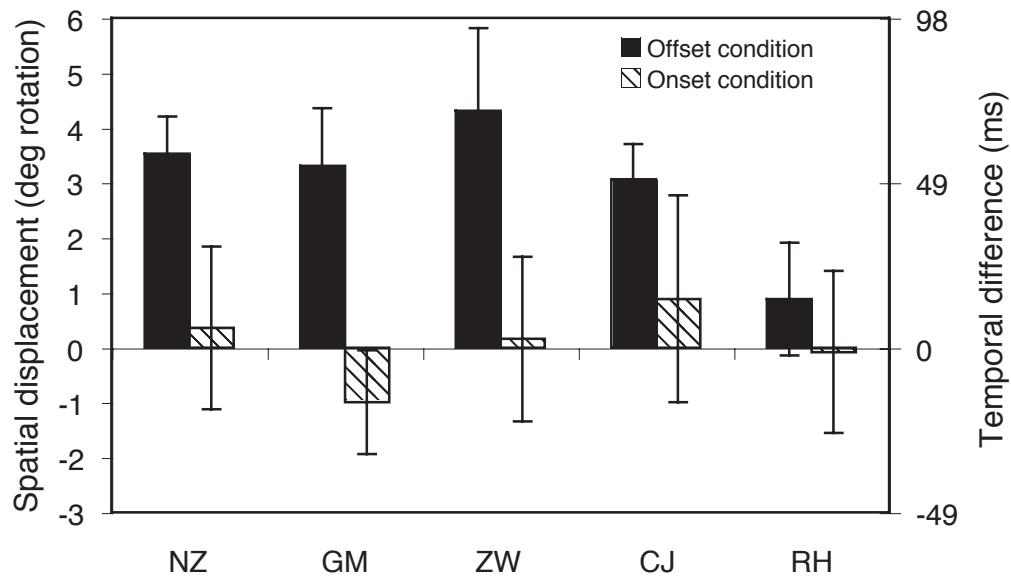
The four panels represent the four blind spot boundaries, at which the experimental task was performed: at the upper and lower border of both left and right blind spots. The x-axis denotes the position of the abrupt offset or onset of the contralateral bar in degrees rotation (0 is at the blind spot boundary, positive numbers are positions rotated downwards). The y-axis denotes proportion of responses indicating that the offset/onset was perceived on the side of the blind spot first. Horizontal lines represent confidence intervals for points of subjective simultaneity of the fit.

The null result in the stimulus onset condition does not imply that observers perceived the bar starting right at the blind spot boundary, or at the true position of the

stimulus onset. The bars are likely to be perceived as shifted forward from their true positions due to the Fröhlich effect (Fröhlich, 1929; Kirschfeld & Kammer, 1999). Interestingly, the null result indicates that a bar appearing from within the blind spot is perceived no differently from a bar abruptly appearing in full view of the photoreceptors. However, the bar disappearing from view in the blind spot is perceived differently than a bar with an abrupt offset. The final position is perceived as shifted forward and it perceptually disappears well inside the blind area.

In contrast to previous experiments investigating the perceived final position of a fading visual object (Maus & Nijhawan, 2006), in the present experiments there was no sub-threshold stimulation that led to a percept, so lowered thresholds for bottom-up input due to preceding stimulation cannot explain the perceived forward shift of the moving object. Furthermore, our findings cannot be explained by a temporal integration mechanism, as there is no bottom-up input from within the blind area to integrate. Neither can the perceived position be shifted forward by later motion signals, acquired from after the object passed the blind spot boundary (Eagleman & Sejnowski, 2007), as no motion signals emanate from within the blind spot.

Could a filling-in process at the blind spot be involved in the visibility of the bar in unstimulated ‘blind’ areas? Perceptual filling-in occurs only if two opposite blind spot edges are stimulated (Ramachandran, 1992; Walls, 1954). Using functional brain imaging methods, it has recently been shown that early visual areas maintain a veridical retinotopic map in the vicinity of the blind spot, arguing against a passive spread of activity as the mechanism for filling-in (Awater et al., 2005). This opposes an explanation of our finding in terms of integration of filled-in positions.



**Figure D.3** Mean displacements of offset/onset positions from the blind spot boundary within each of the five observers. Positive numbers denote forward displacements in the direction of motion. Values are given in both degrees of rotation and milliseconds ( $\pm$  SEM).

The present findings show that the perceived position of moving objects is shifted forward based on information from the past trajectory. The visual system computes a prediction of where an object will be to overcome neural processing delays inherent in the visual pathway (Nijhawan, 1994; *in press*). In the case of contradicting bottom-up input, for example an abrupt stimulus offset registered by the retina, this prediction is corrected or masked from visibility, and the new information can be integrated into the percept (Maus & Nijhawan, *in press*; Nijhawan, 2002). When such a signal is absent, as in the case of motion terminating in the blind spot or gradually decreasing below stimulation threshold (Maus & Nijhawan, 2006), the extrapolated position is perceived as the final position of the motion trajectory. The same should be true for other acquired or natural scotoma, like the blue scotoma in the fovea (Magnussen, Spillmann, Sturzel, & Werner, 2004; Wilmer & Wright, 1945). When

objects move behind an occluder, there is similarly no synchronised transient signal from all parts of the object, as the object disappears gradually with the leading portions first and trailing portions later. However, in this case no ‘overshoot’ of the moving object is usually perceived, i.e. the moving object is not seen in front of the occluder. There is however evidence for a continuous neural representation of moving objects behind occluders (Assad & Maunsell, 1995; Baker, Keysers, Jellema, Wicker, & Perrett, 2001). This representation is not visible, but can be used in cognitive tasks like timing the reappearance of the object on the other side of the occluder.

To date few studies involving motion across the blind spot have been published. When a moving object deviates from a straight trajectory, the deviation can be grossly overestimated. This error is even larger when the direction change occurs in the blind spot (Tripathy & Barrett, 2006). In these experiments the object motion was sufficiently fast to be perceived as continuous through the blind spot. Consistent with the results of the present study motion was perceived to continue straight through the blind spot and only afterwards changing direction from its original trajectory. Another study showed that a singleton feature in a sequence of bars in apparent motion (e.g. a long bar amongst short bars) can be mislocalised in the direction of motion (Cai & Schlag, 2001). This forward mislocalisation also works into the blind spot. When a single long bar amongst a sequence of short bars was presented just before the blind area, it was perceived to lie within the blind spot (Cai & Cavanagh, 2002). In this study the motion continued after the blind spot, and the authors argued for path interpolation as a mechanism for creating the illusory percept. We claim both these findings (Cai & Cavanagh, 2002; Tripathy & Barrett, 2006) and the present experiment can be explained

by a spatial extrapolation mechanism, relying on the past trajectory of a moving object to predict the current object position.

## E Article IV

# Going, Going, Gone: Localising Abrupt Offsets of Moving Objects<sup>6</sup>

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## **Abstract**

When a moving object abruptly disappears, this profoundly influences its localisation by the visual system. In Experiment 1 two aligned objects moved across the screen and one of them abruptly disappeared. Observers reported seeing the objects misaligned at the time of the offset, with the continuing object leading. Experiment 2 showed that the perceived forward displacement of the moving object depended on speed and that offsets were localised accurately. Two competing representations of position for moving objects are proposed; one based on a spatially extrapolated internal model, the other based on transient signals elicited by sudden changes in the object trajectory that can correct the forward-shifted position. Experiment 3 measured forward displacements for moving objects that disappeared only for a short time or abruptly reduced contrast by various amounts. Manipulating the relative strength of the two position representations in this way resulted in intermediate positions being perceived, with weaker motion signals or stronger transients leading to less forward displacement. This two-process mechanism is advantageous because it uses available information about object position to maximally reduce spatio-temporal localisation errors.

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<sup>6</sup> This article has been accepted for publication in the *Journal of Experimental Psychology: Human Perception and Performance* (Maus & Nijhawan, in press).

## E.1 Introduction

In the flash-lag effect a moving object appears to be ahead of a spatially aligned flashed object. This finding has sparked a debate about how the nervous system processes moving objects and determines their perceived position. This is an important problem as neural delays in the retina and the visual pathway are liable to lead to spatial localisation errors. One hypothesis, termed motion extrapolation, states that moving objects are spatially shifted forward to counteract the influence of neural delays in the visual pathways on the perceived position of moving objects (Nijhawan, 1994). If one assumes that perceptual awareness of the position of an object requires cortical activity, then a delay in the pathway from the photoreceptors to the primary visual cortex of about 80 ms (Schmolesky et al., 1998) would imply, that moving objects are always perceived to lag their ‘true’ position by the distance they moved in that time. However, by analysing the speed and direction of a moving object the visual system could extrapolate its position forward by an appropriate amount and so compensate for these processing delays. In the flash-lag effect this forward shift is apparent, because the flash does not undergo an equivalent spatial shift, thereby resulting in a perceived gap between the moving object and the flash, although they are physically aligned.

Several alternative accounts have been brought forward to explain the findings of the flash-lag effect, amongst them differential attentional deployment (Baldo & Klein, 1995), differential latencies (Purushothaman et al., 1998; Whitney & Cavanagh, 2000a; Whitney & Murakami, 1998), and temporal integration (Brenner & Smeets, 2000; Brenner et al., 2006; Eagleman & Sejnowski, 2000; Krekelberg & Lappe, 2000; Roulston et al., 2006). There has been considerable debate about which framework is able to explain the experimental data best (for reviews see Krekelberg & Lappe, 2001;

Nijhawan, 2002). One key argument against motion extrapolation has been made from stimulus displays in which the object's motion after the flash is terminated (Eagleman & Sejnowski, 2000) or changes its direction (Whitney & Murakami, 1998). If the moving object is stopped or disappears at the time of the flash, the forward displacement of the moving object is abolished and the flashed and the moving objects are perceived to be aligned. When motion is reversed at the time of the flash, the moving object appears shifted in the direction of motion after the flash.

It has previously been argued (Maus & Nijhawan, 2006; Nijhawan, 2002) that these findings do not necessarily contradict the extrapolation account for moving objects. Clearly if a moving object undergoes an abrupt change in its trajectory (such as an abrupt offset or a reversal of direction) the extrapolated output would not represent the object's true spatial position. Thus, a second mechanism would be required to correct the extrapolated output if things in the world changed suddenly. Precisely such a mechanism has been known for a long time. In backward masking the presentation of a visual mask can suppress the perception of a previously presented target (Alpern, 1953; Breitmeyer, 1984).

In this paper we directly test the two-mechanism model. Let us assume that the position of a continuously moving object is maintained by an internal model in the visual system, which is spatially shifted forward (e.g. Erlhagen, 2003). When the moving object suddenly disappears, a transient neural Off-signal is elicited from the retina. This transient is accurately localised with fixed retinotopic coordinates—like a ‘stamp’ on the retina. It is known that stimulus offset can act as a mask in backward masking paradigms (Breitmeyer & Kersey, 1981) and exhibit strong lateral inhibitory

effects (Macknik et al., 2000). At the level of the internal model, the best hypothesis of the system is that the moving object is still in its spatially forward-shifted position on the motion trajectory. The transient, however, provides new evidence that the moving object disappeared in its offset position. This offset position information will be integrated with the extrapolated position representation to yield a percept. The visual system is faced with contradictory information and – as the object cannot be perceived as disappearing in one position and continuously moving in another – needs to resolve this conflict, in order to come up with an unambiguous percept of the visual scene.

Neural competition has been suggested as a mechanism that deals with conflict resolution in the context of visual attention, visual masking, and rapid serial visual presentation (Desimone, 1998; Keysers & Perrett, 2002). Applied to the present case of an abrupt offset, the two distinct and incommensurate representations of the internal model and the retinal transient will compete. The accurately localised Off-transient wins the competition because of its strength and recency, leading to a perceptual suppression of the extrapolated position.

A hallmark of competition models is that when the weightings of the competing representations are changed, the perceptual outcome is changed. As noted above, moving objects that disappear abruptly do not usually appear to overshoot their final positions. Although representational momentum (Freyd & Finke, 1984; Hubbard & Bharucha, 1988) states that moving objects are remembered as having disappeared beyond their final position, these findings can be explained by cognitive processes or eye movements and visual persistence (Kerzel, 2000; Kerzel et al., 2001). In the flash-terminated flash-lag display, no overshoot of the moving object is perceived. However, some stimulus conditions, for example when stimuli are presented peripherally or are

blurred, do lead to perceptual overshoots for abruptly stopping objects (Fu et al., 2001; Kanai et al., 2004). The crucial feature that enables the correct localisation of the disappearance position of a moving object may be a strong, accurately localised retinal Off-transient, that wins the neural competition and therefore masks any extrapolated position representation, that would otherwise be perceived (Maus & Nijhawan, 2006). On this view neural competition acts as a correction mechanism to reduce spatio-temporal localisation errors for moving objects disappearing from view. The present study directly investigates the above hypothesis.

### **E.1.1 A novel visual localisation illusion: Offset-lag**

The above hypothesis predicts a new visual illusion of ‘offset-lag’: If a part of a moving object disappears abruptly while the rest of the object continues to move, the object should ‘break apart’ at the time of the offset, with the continuing part being perceived further ahead in the direction of motion, in a position distinct from the disappearing part. This is indeed what we observed. In initial displays we presented a vertical bar, moving horizontally across the screen while observers maintained steady fixation. When the bar had moved half way across the screen, either its upper or lower half abruptly disappeared (a demonstration of the stimulus can be found at <http://www.sussex.ac.uk/Users/gwm21/demos/offsetlag.mov>). Observers reported seeing the bar break apart into two separate half bars located in different positions prior to the disappearance of one of them. The continuing half-bar was always described as leading the offset half-bar. Some observers described the disappearing half-bar as ‘jumping back’ before disappearing. Additionally the stimulus used here gave rise to the well-known line-motion illusion (Hikosaka et al., 1993; Jancke et al., 2004a; Wertheimer, 1912). The offset half-bar seemed to disappear gradually from one end to

the other. Some observers also reported the existence of an invisible object that occluded half of the bar. A similar illusion has previously been described by Palmer and Kellman (2001, 2002, 2003). However, in these previous displays an actual occluder was always clearly visible to the observers. For a detailed discussion of the similarities and differences between these displays and those used in our experiments see *General Discussion* in section E.7.1.

Here, using psychophysical experiments, we investigate the hypothesis described above, that the perceived position of a moving object's final position is the outcome of a neural competition process between an internal model and transient retinal signals. The stimuli we used were similar to those described above involving comparisons of the perceived positions of continuously moving and abruptly disappearing objects. In Experiments 1 and 2 we quantify the magnitude of the new illusion and show that the effect scales as a function of the speed of the moving object.

If the perceived position of a moving object is the outcome of a competition between two representations, it should be possible to influence this outcome by manipulating the relative strength of those representations. In a recent study Off-transients were weakened by gradually decreasing a moving object's luminance until it became invisible (Maus & Nijhawan, 2006; Article I). An object disappearing without a strong transient was indeed perceived to vanish in an extrapolated position. In Experiment 3 we took the opposite approach and introduced new transients into an otherwise undisturbed motion trajectory. We interrupted the motion of the object for brief varying durations or introduced transients of varying strength into a continuous motion trajectory to investigate how this influenced perceived positions.

## E.2 Experiment 1 – Matching task

In the first experiment we aimed to quantify the offset-lag effect and see if it depends on the speed of the moving object. To suppress the perception of the line-motion illusion that some of our observers reported in initial observations (see above), we introduced a spatial gap between the two half-bars. To measure the size of the misalignment between the offset bar and the continuing bar we used a simple matching task: Observers viewed a motion sequence of two bars moving across the screen, one of which disappeared abruptly. Afterwards they were asked to indicate their perception of the relative positions of the two bars at the time of disappearance by adjusting the positions of two stationary bars.

### E.2.1 Methods

#### *E.2.1.1 Participants*

Four observers, including author GM (three female; three naïve to the purpose and hypothesis of the study), took part in the experiment. All had normal or corrected to normal visual acuity.

#### *E.2.1.2 Apparatus and stimuli*

Stimuli were presented on a 21" CRT monitor (Formac Elektronik GmbH) at 100 Hz vertical refresh rate using MATLAB and the Psychophysics toolbox extensions (Brainard, 1997; Pelli, 1997). Observers kept a constant distance of 80 cm from the screen with their heads partially immobilised by means of a chin rest.

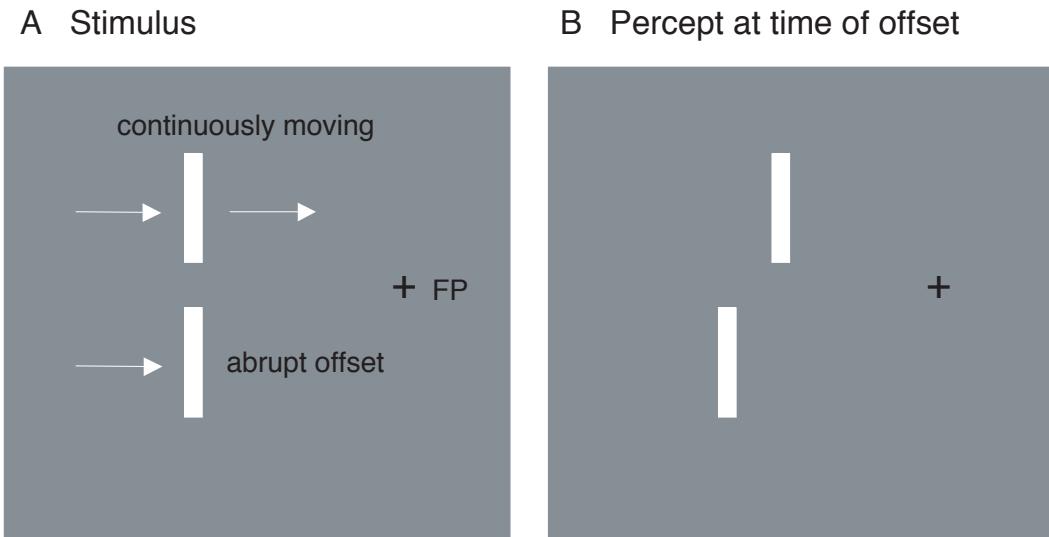
The stimuli consisted of two white vertical bars ( $0.14^\circ \times 2.7^\circ$ ,  $71.3 \text{ cdm}^{-2}$ ) on a mid-grey background ( $10.6 \text{ cdm}^{-2}$ ). The bars (aligned above each other and separated by

a spatial gap of  $1.0^\circ$ ) moved horizontally across the screen from left to right at one of three possible speeds ( $8.1 \text{ }^\circ\text{s}^{-1}$ ,  $15.9 \text{ }^\circ\text{s}^{-1}$ ,  $23.1 \text{ }^\circ\text{s}^{-1}$ ). After having traversed about half of the screen (randomly jittered by  $\pm 0.27^\circ$ ) one of the two bars (the offset-bar) disappeared abruptly, while the other bar continued moving to the right edge of the screen (see Figure E.1A). Depending on the speed, the entire motion sequence lasted 3410 ms, 1700 ms or 1130 ms. Throughout the experiment observers fixated a black fixation cross ( $0.27^\circ \times 0.27^\circ$ ) in the right half of the screen,  $6.9^\circ$  to the right of the midpoint.

Observers were asked to ‘recreate’ their percept of the positions of the two bars at the time of the abrupt offset. To do so a comparison stimulus consisting of two stationary bars was shown after each motion sequence (see Figure E.1B). One bar was presented in the position where the offset-bar disappeared in the motion sequence. The other bar, representing the continuing bar of the motion sequence, appeared in a random position between  $0.68^\circ$  to the left and the right of the offset position. The latter bar could be moved horizontally with the arrow keys on the keyboard. Observers were instructed to move this bar so that it matched the perceived relative positions of the bars at the time of disappearance.

#### *E.2.1.3 Procedure*

Trials were structured as follows: The two bars appeared moving and either the upper or the lower bar disappeared near the midline. The other bar continued moving until it reached the right edge of the screen. Immediately afterwards the comparison stimulus appeared. Observers adjusted the bars to match their percept of positions in the motion sequence and pressed another key when they were finished. Following this the next trial started.



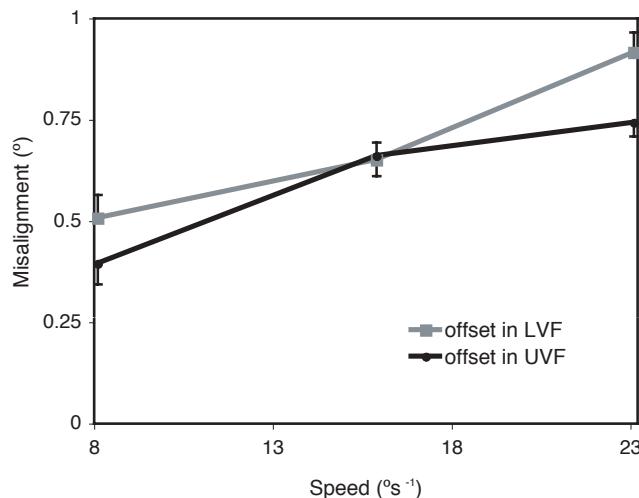
**Figure E.1** (A) The stimulus used in Experiment 1. Observers were instructed to fixate the fixation point (FP) at all times. Two perfectly aligned vertical bars ( $0.14^\circ \times 2.7^\circ$ ), separated by  $1.0^\circ$ , moved across the screen, until one of them abruptly disappeared. The other bar continued to move. (B) Observers perceived the continuing bar to be further ahead in the direction of motion when the other bar abruptly disappeared. In Experiment 1 two static bars representing the previously shown moving bars were presented after each trial. One appeared in the offset position, while observers could horizontally adjust the other to match their percept at the time of the offset.

In an initial training period observers familiarised themselves with the stimuli and the task. In the experiment there were three speeds of movement and two possibilities for which bar disappeared, either the bar in the upper or in the lower visual hemifield. Observers performed 20 trials in each condition for a total of 120 trials (3 speeds  $\times$  2 offset hemifields  $\times$  20 trials). Trials of all conditions were randomly intermixed. During the experiment there were two short breaks.

### E.2.2 Results

All observers adjusted the position of the continuously moving bar to be ahead of the disappearance position of the offset-bar. The mean perceived misalignments of the bars are shown in Figure E.2. A two-way independent measures ANOVA on

observers' mean adjustments revealed significant effects for both speed and visual hemifield of the offset (speed:  $F(2,474) = 31.68, p < 0.001$ , partial  $\eta^2 = 0.118$ ; offset hemifield:  $F(1,474) = 5.58, p = 0.019$ , partial  $\eta^2 = 0.012$ ), however, the differences for bars disappearing in the upper or the lower visual field are rather small. Collapsed over the two hemifields, the mean misalignment was  $0.45^\circ$  ( $SEM = 0.04^\circ$ ) for the slow speed of  $8.1 \text{ } ^\circ\text{s}^{-1}$ ,  $0.65^\circ$  ( $0.03^\circ$ ) for the medium speed of  $15.9 \text{ } ^\circ\text{s}^{-1}$ , and  $0.82^\circ$  ( $0.03^\circ$ ) for the fast speed of  $23.1 \text{ } ^\circ\text{s}^{-1}$ . These misalignments amount to a temporal forward shift of 55.6 ms (4.9 ms), 40.9 ms (1.9 ms), and 35.5 ms (1.3 ms), respectively.



**Figure E.2** Mean misalignments between the offset-bar and the continuing bar in Experiment 1, plotted as a function of speed, separately for offsets in the upper and lower visual field (UVF, LVF). Error bars show standard error of the mean between observers.

### E.2.3 Discussion

The sudden offset of a moving object can influence its perceived position in a more complex way than one would assume. Differing from previous experiments measuring perceived offset positions (Kerzel, 2000; Kerzel et al., 2001), we did not use static probes for comparison of positions, but a continuously moving object. For the

first time we directly compared the perceived positions of moving objects with abruptly disappearing objects. The results show that the mechanisms underlying the perception of the offset position of moving objects differ crucially from those underlying the perception of the instantaneous position of moving objects. Assuming that the offset position is perceived veridically (see Experiment 2B), our results show a forward displacement of the perceived position of the moving object. The forward displacement scales with the speed of motion.

Although not explicitly tested it is reasonable to assume that observers perceived the two bars as aligned in the first half of each trial, when both bars were presented moving. Given this, it is remarkable that observers adjusted the two bars as being not aligned at the time of disappearance of one of the bars, because this was contradictory to their prior experience with the relative positions of the two bars. They were always physically and perceptually aligned until the offset-bar disappeared. However, anecdotally some observers reported the matching task to be “illogical”, because the bars were clearly aligned before one of them disappeared. Asking if there was any misalignment could therefore be misleading for observers. Having a priori knowledge about the relative positions of the bars might also bias observers to cognitively correct for any perceived misalignments of the bars, which may actually explain the non-linearity of the temporal forward shift.

To eliminate these limitations we conducted Experiment 2, in which the two bars moved in opposite directions. Thus, observers did not have any a priori information about the relative positions of the two bars. We changed the design to a more controlled two-alternative forced-choice method that depended less on perceptual memory.

### **E.3 Experiment 2A – Forced choice task**

The purpose of this experiment was to verify the illusory misalignment of disappearing and continuing moving bars of Experiment 1 with a more controlled psychophysical method. In this experiment two bars moved in opposite directions, so observers did not have any a priori knowledge about the relative positions of the two bars. By varying the relative positions of the bars at the time one of them disappeared we were able to ask observers a two-alternative forced-choice question. This stimulus display lacked the counter-intuitive, illusionary character of the stimulus in Experiment 1, but using motion in opposite directions generalises the effect to a wider range of stimuli.

#### **E.3.1 Methods**

##### *E.3.1.1 Participants*

Six observers (three female) volunteered to take part in this experiment, including author GM. Five of the observers were naïve as to the purpose of the experiment. All had normal or corrected to normal visual acuity.

##### *E.3.1.2 Apparatus and stimuli*

The same setup as in Experiment 1 was used. Observers fixated a black fixation cross in the center of the screen. Two vertical bars (same dimensions as in Experiment 1) moved horizontally across the screen in opposite directions, starting at opposite edges of the screen and passing each other near the midline. One of the two bars abruptly disappeared at the midline (randomly jittered by  $\pm 0.27^\circ$ ).

The alignment of the continuing bar with the offset position of the other bar was systematically manipulated. By starting the movement of one bar slightly earlier than the other bar, the continuing bar could either already have passed the offset position, be perfectly aligned with it, or still be slightly short of it. Observers had to indicate in a two-alternative forced-choice task if the continuing bar was visible to the left or to the right of the offset position at the time of the offset.

On every trial both bars moved at the same speed ( $8.1 \text{ }^{\circ}\text{s}^{-1}$ ,  $15.9 \text{ }^{\circ}\text{s}^{-1}$ , or  $23.1 \text{ }^{\circ}\text{s}^{-1}$ ). As either the upper or the lower bar continued to move, there were four possible conditions: The continuing bar performed either (a) *leftward* motion in the *upper* visual field (LU), (b) *rightward* motion in the *upper* visual field (RU), (c) *leftward* motion in the *lower* visual field (LL), or (d) *rightward* motion in the *lower* visual field (RL).

#### **E.3.1.3 Procedure**

On every trial observers watched the motion sequence and responded with a key press. Trials of the four motion conditions (LU, RU, LL, RL) were blocked. Before each block observers were informed about which bar would disappear and which would continue to move. The three bar speeds were randomly intermixed within the blocks, and block order was balanced between observers. After an initial training block observers performed one block of 120 trials for each of the four conditions. There were 40 trials for each speed in all conditions for a total of 480 trials (3 speeds x 4 conditions x 40 trials).

For efficient measurement of psychometric functions we used an adaptive method: For each trial the horizontal distance between the position of the continuing bar and the offset position of the offset-bar was determined online by the experimental

software. Trial misalignments were centred around the observer's current point of subjective alignment (PSA), as calculated from the QUEST threshold estimation algorithm (Watson & Pelli, 1983). QUEST estimates the current most likely PSA from the performance on all previous trials. In each block there were three independent QUEST estimators, one for each speed of motion. A random jitter taken from a Gaussian distribution with a standard deviation of  $\sigma = 20 \text{ ms} * v$ , where  $v$  is the speed of the bars in this trial, was added to the current estimated PSA and rounded to the nearest multiple of  $0.8 * \sigma$ , so that a coarser distribution of misalignments was used in trials with faster speeds. This method ensured that most trials were placed at the most useful values close to the observer's PSA, but there were also a few trials with greater distance between the two bars' positions that were easier for observers to judge. Independently of this method, after the experiment psychometric functions were fitted with the probit procedure to estimate PSAs and compute bootstrap confidence intervals for each condition and speed (Finney, 1971; Wichmann & Hill, 2001a, 2001b).

### **E.3.2 Results**

The group mean PSAs were analysed in a  $2 \times 2 \times 3$  repeated measures ANOVA (hemifield of continuing bar  $\times$  motion direction of continuing bar  $\times$  speed). There was a significant main effect for speed,  $F(2,4) = 14.05, p = 0.016$ , partial  $\eta^2 = 0.875$ , but not for visual hemifield or motion direction and no significant interactions.

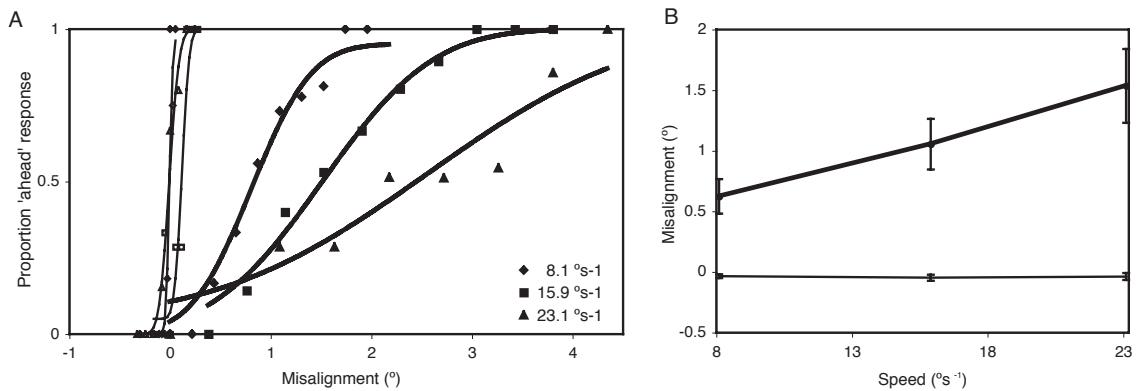
Because the ANOVA did not show any systematic differences between visual hemifields and motion directions, all conditions were collapsed and new psychometric functions (based on 160 trials) were fitted for each speed. Psychometric functions for one naïve observer are shown in Figure E.3A. For all observers the continuing bar was

required to be short of the offset position to be perceived as aligned at the time of the offset. For the individual data none of the confidence intervals for thresholds included 0 (with the exception of one observer, whose overall mislocalisation effects were small). This observer showed a very shallow psychometric function for the fastest speed, including 0 in the confidence interval). Figure E.3B shows the group mean PSAs for each speed. The mean perceived overshoots of the continuing bar from the disappearance point were  $0.62^\circ$  ( $SEM\ 0.14^\circ$ ) for the slowest speed of  $8.1\text{ }^\circ\text{s}^{-1}$ ,  $1.05^\circ$  ( $0.21^\circ$ ) for the medium speed of  $15.9\text{ }^\circ\text{s}^{-1}$ , and  $1.54^\circ$  ( $0.30^\circ$ ) for the fastest speed of  $23.1\text{ }^\circ\text{s}^{-1}$ . These misalignments amount to a temporal forward shift of 76.5 ms (1.7 ms), 66.0 ms (1.3 ms), and 66.7 ms (1.3 ms), respectively, which reveals a roughly linear relationship between speed and amount of forward displacement.

### **E.3.3 Discussion**

All observers perceived the continuously moving bar as further ahead in the direction of motion than the bar that disappeared abruptly. The size of the misalignment of the two bars depended linearly on the speed of motion. The moving bar was shifted forward by a constant amount of time, roughly between 60 and 80 ms. The slopes for psychometric functions decreased for increasing speeds, indicating that observers were more confident in judging positions of bars moving at slower speeds.

Contrary to Experiment 1, in this experiment observers did not report any impression of invisible occluders. The use of movement in opposite directions excluded the possibility that the offset-lag effect depends on observers inferring the existence of invisible occluders. The size of the effect is in the same range of what is usually observed in the flash-lag effect (Eagleman & Sejnowski, 2000; Nijhawan, 1994).



**Figure E.3 (A)** Raw data and fitted psychometric functions from Experiment 2A (filled symbols, thick lines) and Experiment 2B (open symbols, thin lines) for one naïve observer. In Experiment 2A two bars moved in opposite directions and one of them disappeared abruptly. Observers judged the relative positions at the time of the offset. Points of subjective alignment (PSAs) are the points of the fitted functions crossing 0.5 proportion of ‘ahead’ responses. All PSAs are significantly different from 0 and increase linearly with speed. The slopes of psychometric functions decrease with speed, indicating more uncertainty in observers’ responses. PSAs in Experiment 2B, where both bars disappeared, are all close to 0 with no apparent speed dependency; slopes were much steeper than in Experiment 2A. **(B)** Mean PSAs for six observers in Experiment 2A (thick line) and four observers in Experiment 2B (thin line). Error bars show standard errors of the mean between observers.

Assuming that the offset position was perceived veridically, the measured forward shift is consistent with our hypothesis, that the perceived instantaneous position of the continuously moving bar is based on an internal model representing the predicted position of moving objects. The disappearing bar’s offset position, however, is perceived correctly due to a correction mechanism based on transient signals that inhibits the perception of the predicted position.

An alternative view to that presented above is that the disappearance position is perceived as shifted in the direction opposite to the motion direction. There are reports

of abruptly disappearing moving objects appearing to vanish slightly short of their actual offset position (Müsseler et al., 2002; Roulston et al., 2006). If this were the case in the present experiments, then in Experiment 2A the instantaneous position of the moving object is not extrapolated forward and, instead, the disappearance position is perceptually mislocalised in the direction opposite to motion direction. This possibility was explored in Experiment 2B, which directly measured the perceived final position of the abruptly disappearing moving bars.

## **E.4 Experiment 2B – Control experiment with two offsets**

This experiment served as a control for Experiment 2A to investigate the accuracy with which the offset positions of the disappearing bars were perceived. Two bars moved across the screen in opposite directions and both of them disappeared abruptly. In a two-alternative forced-choice task observers judged their relative offset positions.

### **E.4.1 Methods**

#### *E.4.1.1 Participants*

Four observers (two female) including author GM, who previously participated in Experiment 2A, took part in this control experiment in a separate session.

#### *E.4.1.2 Apparatus and stimuli*

Stimuli were identical to Experiment 2A. The only difference was that both bars disappeared simultaneously close to the midline. The experimental manipulation was the time of the offset, which could be slightly before or after the two bars crossed each other.

#### **E.4.1.3 Procedure**

Observers were instructed to base their judgement on either the upper or the lower bar and indicate whether it disappeared to the left or to the right of the other bar. Again there were four possible conditions: the ‘judgement bar’ could be moving leftward or rightward, and could be presented in the upper or the lower visual hemifield (LU, RU, LL, RL; see Methods of Experiment 2A). This way of posing the question reduced the possibility of a judgement bias. If observers were asked whether the two bars did or did not cross before disappearing, a perceived perfect alignment could be assigned to either of the two categories. In our way of posing the question a bias to subsume perceived perfect alignments to either the ‘left’ or ‘right’ response category would become apparent in the analysis of responses in the separate conditions.

For the placement of trial values the same adaptive method as described in Experiment 2A was used. After an initial training block observers performed one block of 39 trials in each condition (13 trials for each speed) for a total of 156 trials (3 speeds x 4 conditions x 13 trials). The order of blocks was balanced between observers.

#### **E.4.2 Results**

Observers gave very consistent responses, and although there were only 13 trials for one speed in each condition, psychometric functions were exceptionally steep. The PSAs were analysed in a  $2 \times 2 \times 3$  repeated measures ANOVA (hemifield of judgement bar x motion direction of judgement bar x speed) that revealed no significant main effects or interactions.

The data from all four conditions were then collapsed to fit new psychometric functions for each speed (based on 52 trials). The thin lines in Figure E.3 A and B show one naïve observer's psychometric functions and the group's mean PSAs. The two bars had to cross each other to be perceived as aligned at the time of disappearance (with the exception of one observer, who showed a small effect in the opposite direction). Thus observers actually perceived the bars to disappear *before* they reached their physical offset position. None of the individual psychometric functions' confidence intervals included 0. However, the effect was at least an order of magnitude smaller than the misalignment measured in Experiment 2A. The mean absolute misalignments (distances from the actual disappearance point of the bars) were  $-0.07^\circ$  ( $0.01^\circ$ ),  $-0.09^\circ$  ( $0.02^\circ$ ), and  $-0.07^\circ$  ( $0.03^\circ$ ) for the slow, medium and fast speeds, respectively. These values result in temporal shifts of  $-8.6$  ms ( $1.2$  ms),  $-5.7$  ms ( $1.3$  ms), and  $-3.0$  ms ( $1.3$  ms), less than the time for a full refresh cycle of the monitor ( $10$  ms).

#### **E.4.3 Discussion**

Experiment 2B showed that the abrupt offset of a moving object is perceived relatively accurately. Indeed, in line with earlier studies (Müsseler et al., 2002; Roulston et al., 2006), we found a small but significant perceptual undershoot of the offset position of the moving bar. A speed dependency of this effect, however, as reported by Roulston et al. (2006), could not be confirmed in this experiment. Furthermore, this small mislocalisation of abruptly disappearing objects cannot explain the effect we found in the previous experiment. The undershoots measured here were at least an order of magnitude smaller than the overshoot of continuously moving objects reported in Experiment 2A. This leads us to conclude that the misalignment measured in

Experiment 2A is indeed a forward displacement of the instantaneous position of the continuously moving object.

## **E.5 Experiment 3A – Interruption of motion for different durations**

In the previous two experiments we presented empirical evidence that demonstrates the substantial role that retinal Off-transients play in the visual system's ability to localise moving objects. Together with an earlier study that showed how objects disappearing without such transients are mislocalised (Maus & Nijhawan, 2006), this lends support to our central hypothesis, that the perceived position of a moving object is the outcome of a neural competition between two distinct position representations. One representation is maintained by an internal model that is spatially shifted forward to compensate for neural processing delays, while the other is mediated by the bottom-up retinal transients and is localised accurately.

This hypothesis also predicts that it should be possible to influence the perceptual outcome of this competition process by manipulating the relative strength of these two representations. In the studies presented above one bar was moving continuously, so the perceived position was fully determined by the internal model. In contrast, the offset bar disappeared with a strong retinal transient. Additional evidence supporting the internal motion model for the offset bar was not available after the offset, so the transient won the neural competition and observers perceived the bar vanishing in its 'real' offset position.

In a further experiment we used stimuli ranging between those two extremes. We introduced a brief blank of varying durations into an otherwise undisturbed motion trajectory. The moving object was simply turned off for a variable period ranging from 20 to 120 ms and turned back on in the position it would have occupied had it continued to move at constant speed (see Figure E.4 A and B). Equivalently one might say the object passed behind an invisible occluder, although one crucial difference is, that an occluded object will move out of view gradually, with its leading edge disappearing first and the trailing edge later. In our stimulus the entire object dis- and re-appeared all at once. The abrupt offset resulted in a transient Off-signal; the fact that the object reappeared shortly afterwards, however, resulted in additional evidence for the internal motion model and therefore changed the relative strengths of the two position representations.

To measure the effect of blanks in the motion trajectory on the perceived position we used a flash-lag nulling method (e.g. Baldo & Klein, 1995). Observers were presented with two brief flashes above and below the trajectory of a moving bar. The task was to adjust the position of these flashes, such that they would appear to be aligned with the bar. At the same time as the flashes the bar could be blanked for a short period of up to 120 ms. For a trajectory without a blank we expected to find a typical flash-lag effect, i.e., observers would adjust the flashes to be physically ahead of the moving bar's position. We predict that for long blanks the transient would win the competition, as it did in Experiments 1 and 2, and as reported in the flash-terminated flash-lag condition, where usually no flash-lag effect is found. For shorter blanks between the two extremes, however, we expected the moving object to be perceived in intermediate positions. Although there is an Off-transient, it would not be able to exert

its full effect on the perceived position due to the short interval before new evidence for the internal motion model is accumulated.

### **E.5.1 Methods**

#### *E.5.1.1 Participants*

Six observers (three female) including author GM took part in this study. All had normal or corrected to normal visual acuity.

#### *E.5.1.2 Apparatus and stimuli*

Observers fixated a black fixation cross in the right half of the screen, 6.8° from the midline. A white vertical bar (0.14° x 2.7°) moved horizontally from the left of the screen to the right at a constant speed of 15.9 °s<sup>-1</sup>. When the bar reached the midline (randomly jittered by ± 0.14°), two bars (0.14° x 1.4°) were flashed for one refresh frame (10 ms), 1.0° above and below the moving bar's trajectory. In the next refresh frame, the moving bar either continued moving (0-blank condition) or was turned off for 20, 40, 60, 80, 100, or 120 ms. The bar then re-appeared in a position consistent with its constant speed (Figure E.4 A and B).

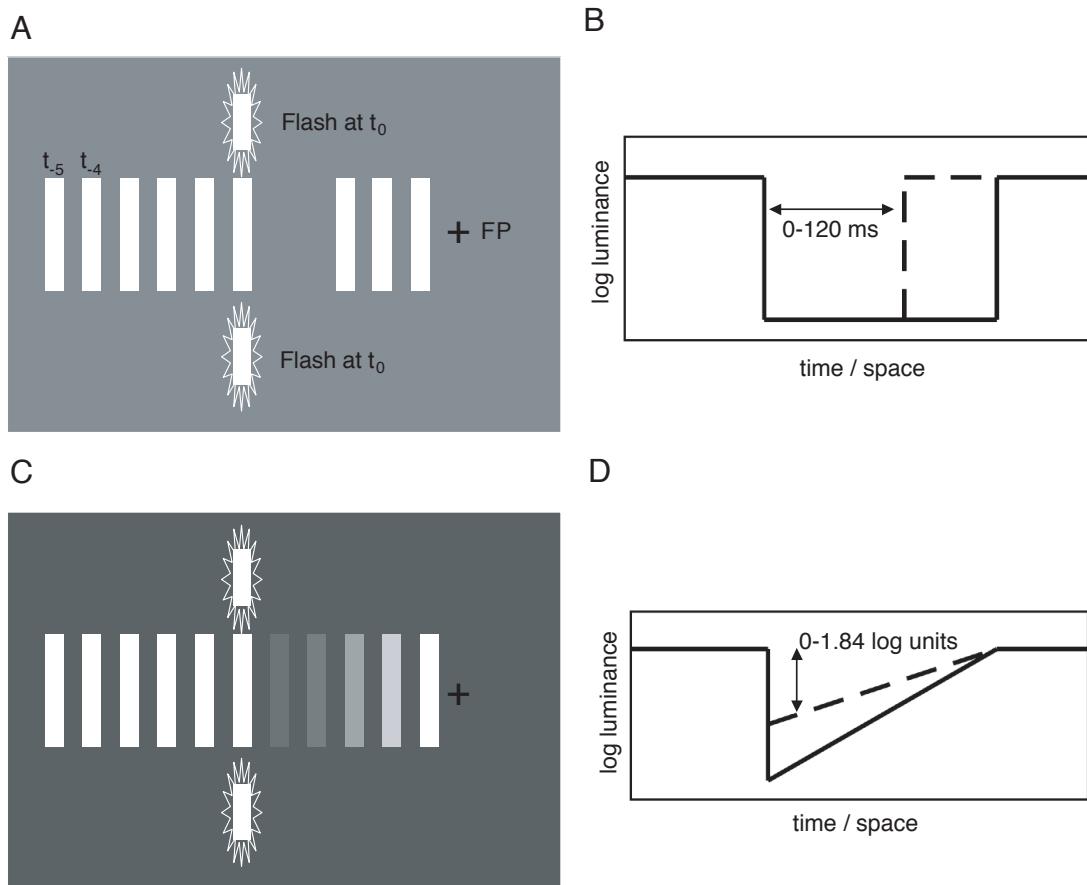
The two flashed bars were initially placed in a random position between 1.7° and 2.3° to the left or the right of the moving bar's position. The observers' task was to align the flashes with the moving bar. To do so, after the motion sequence the two flashed bars were presented again, this time continuously visible, and observers could move them horizontally in either direction by using the arrow keys. To see the motion sequence with their adjusted flash positions again, observers pressed the space bar. They could repeat this cycle of stimulus presentation and adjustment as often as

necessary, until they felt the flashes were aligned with the moving bar. When observers pressed the return key, the experimental software registered their adjusted flash position, and the next trial started.

#### ***E.5.1.3 Procedure***

Trials of all six blank durations and the 0-blank condition were randomly interleaved. In each condition the initial flash-position was equally often to the right and to the left of the moving bar, so that the directions of observers' adjustments were counterbalanced.

Observers first performed 24 trials of training to familiarise themselves with the task. In the actual experiment there were twelve trials for each of the six blank durations and for the 0-blank condition for a total of 84 trials. Note that each trial consisted of repetitive viewings of the same motion sequence, so the actual number of stimulus presentations was higher. Trials, in which observers viewed the motion sequence only once, were excluded from further analysis, as it could not be assumed that observers performed the task properly on these trials. Furthermore trials in which observers' adjustments deviated more than two standard deviations from their mean adjustment in this condition were also excluded. A total of 2.6% of trials were excluded in accordance with these criteria.



**Figure E.4 (A)** Snapshots of discrete time points of the stimulus used in Experiment 3A. The white bar moved smoothly from left to right, indicated by the shift in position from time  $t_{-5}$  to  $t_{-4}$  and so on. At  $t_0$  two bars were flashed above and below the moving bar's trajectory. In the illustration the flashes are physically aligned with the moving bar. In the experiment observers had to adjust the position of these flashes to appear perceptually aligned with the moving bar. Following the flash the moving bar was turned off for a variable duration, after which it came back on and continued moving. **(B)** The luminance profile of the moving bar. Following the flash the luminance of the bar was abruptly decreased to the level of the background and then turned back up to the original intensity up to 120 ms later. **(C-D)** Snapshots and luminance profile of the stimulus in Experiment 3B. Here the luminance was decreased abruptly to various intensity levels at the time of the flash. During the subsequent 200 ms it was logarithmically increased to its original intensity.

### E.5.2 Results

Figure E.5A shows the means of observers' adjustments in all conditions. In the 0-blank condition observers showed a baseline flash-lag effect of 45.1 ms ( $SEM = 4.8$  ms). A one-way repeated measures ANOVA on observer's mean adjustments revealed a significant effect of blank duration on the size of the flash-lag effect,  $F(6,30) = 11.75, p < 0.001$ , partial  $\eta^2 = 0.701$ . Linear regressions for each individual observer showed negative slopes ( $M = -0.26, SEM = 0.04$ , one-sample t-test  $t(5) = -6.34, p = 0.001$ ), indicating that for all observers the introduction of blanks led to a reduction in the size of the forward displacement. However, even for the longest blank of 120 ms there was still a small but significant flash-lag effect ( $M = 13.80$  ms,  $SEM = 3.03$ , one-sample t-test  $t(5) = 4.56, p = 0.006$ ).

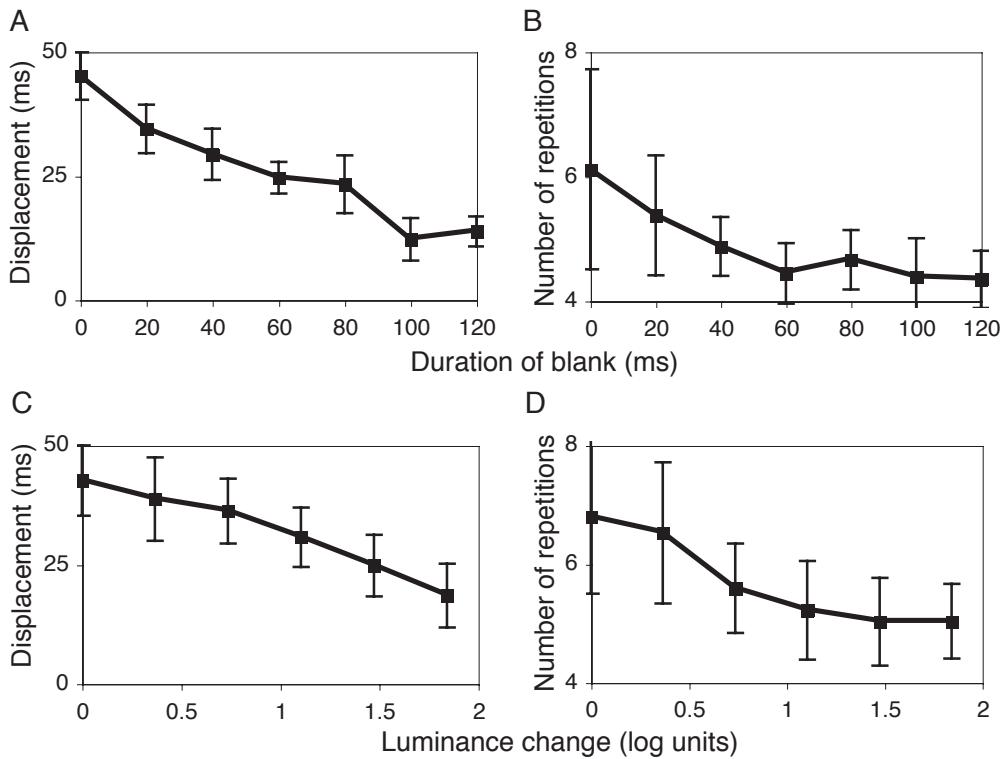
During the debriefing, none of the five naive observers were able to identify the way in which stimuli were manipulated across different trials. However, all observers reported that in some trials the task seemed far easier than in others. This was also reflected in the number of repetitions observers used in each condition (Figure E.5B), 6.1 ( $SEM = 1.6$ ) repetitions in the 0-blank condition, compared to 4.3 (0.5) repetitions in the 120 ms-blank condition. It seems the longer the blank lasted, the easier the task got and the more confident observers were with their adjustments. However, a one-way repeated measures ANOVA could not confirm this trend,  $F(6,30) = 1.74, p = 0.147$ , partial  $\eta^2 = 0.258$ .

### E.5.3 Discussion

This experiment showed that the introduction of an abrupt offset into an otherwise undisturbed motion trajectory reduces the forward displacement of a moving

object as measured with the flash-lag effect. Blanking the moving object for 100 ms or longer achieved a maximal reduction of the flash-lag effect. Turning the moving object off for a long period is basically equivalent to the often-cited flash-terminated flash-lag condition. However, in this experiment we did not find a total elimination of the flash-lag effect; a small but significant forward displacement for blanks of 120 ms was still measured. This effect is likely due to the fact that observers did not foveate the position of the flash, a finding which is consistent with Kanai et al. (2004), who reported a flash-lag in the flash-terminated condition for peripherally presented stimuli. In previous pilot studies, where stimuli were presented foveally and the separation between the moving object and the flashes was smaller, observers actually achieved close to perfect localisation performance, that is, a total elimination of the flash-lag effect (data not presented).

Longer blanks lead to a larger reduction of the flash-lag effect. Although the transient is equally strong in all conditions, the degree to which it influences the perceived position is determined by its relative strength compared to the internal motion model. When after a short blank new evidence for the motion model is acquired (i.e. the moving object is registered in the predicted position) the perceived position remains closer to the forward displaced position, as in the baseline flash-lag with no transient. Varying the time until such evidence is accumulated again influences the relative strength of the motion model. In Experiment 3B we directly manipulated the strength of the transient, rather than the strength of the motion representation (see below).



**Figure E.5** (A) Mean flash-lag effects in milliseconds as a function of blank duration in Experiment 3A. The left-most data point (blank duration 0 ms) shows the baseline flash-lag effect that reduced as motion was interrupted for increasing durations. All error bars are standard errors of the mean. (B) The mean number of repetitions observers used in the flash-lag nulling task plotted against blank duration. (C) Mean flash-lag effects as a function of the amplitude of luminance change at the time of the flash in Experiment 3B. (D) Mean number of repetitions plotted against luminance change.

Interestingly the abrupt offset not only seems to make perceptual localisation more accurate, but also easier. The longer the blank, the less stimulus repetitions observers needed to be confident with their adjustment (see Figure E.5B). This is consistent with the idea that the Off-transient is an accurately localised retinal signal that gains influence over the perceived position as the strength of the internal motion model decreases. Kanai and colleagues (2004) attributed mislocalisations in the flash-lag effect to higher perceptual uncertainty (see also Brenner et al., 2006). Our finding here is consistent with this idea. The number of repetitions observers use in the nulling

task is a simple measure of perceptual uncertainty and correlates nicely with the size of the spatial mislocalisation.

It is worth noting that the abrupt re-appearance of the moving bar after the blank in this experiment does not seem to influence the perceived position at the time of the flash. It is known that the flash-initiated flash-lag condition, in which the moving object abruptly starts at the same time as the flash is shown, leads to an unabated flash-lag effect (Khurana & Nijhawan, 1995). In other words, an abrupt onset does not lead to a reduction in error or a more accurate localisation, as we propose the offset does here. In fact, if the onset had played any role in our task, it would be expected that a later onset (i.e. a longer blank) would lead to a larger forward displacement, which is contrary to our results. Our findings also pose a challenge to common temporal integration models for the flash-lag effect (see section E.7.2).

## **E.6 Experiment 3B – Transients of different magnitude**

Instead of varying the temporal interval for which the internal motion model was not supported by visual input, in this experiment we directly manipulated the strength of the abrupt offset. We varied the amplitude of a decrease in luminance contrast of the moving bar in the frame following the flash. Either the luminance contrast of the bar was reduced to zero in the frame following the flash (as in the previous experiment) or it was reduced to intermediate levels between full- and zero-contrast. In the 200 ms following the abrupt change, the luminance was quickly ramped back to its full contrast (see Figure E.4 C and D) to avoid possible influences of luminance contrast on the perceived speed of motion (Hess, 1904).

### **E.6.1 Methods**

#### *E.6.1.1 Participants*

Six observers including author GM (three females) participated in this study.

Four observers earlier took part in Experiment 3A; two new observers were naïve to the experiment.

#### *E.6.1.2 Stimuli and procedure*

The stimuli were now shown on a dark grey background ( $1.5 \text{ cdm}^{-2}$ ). Again, the white bar ( $71.3 \text{ cdm}^{-2}$ ) moved across the screen, and white flashes appeared for one refresh frame when the bar crossed the midline (see description of Experiment 3A). In the next refresh frame the luminance of the moving bar was abruptly reduced to the background level (luminance change of  $1.84 \log$  units) or various fractions of the luminance value for the white bar (which corresponded to luminance changes of  $1.48, 1.11, 0.74$ , or  $0.37 \log$  units). In the 200 ms following the abrupt change the moving bar's luminance was logarithmically increased until it matched the pre-flash contrast (Figure E.4 C and D). To measure the baseline flash-lag effect there was also a no-change condition, in which the luminance of the white bar remained unchanged throughout the motion sequence.

The task was identical to the task in Experiment 3A. Observers adjusted the flashes to appear aligned with the moving bar (flash-lag nulling method). Again, each trial consisted of repeated presentations of the same stimulus, until observers were satisfied with their alignment of the flashes and the moving bar. Twelve trials of all six conditions were randomly interleaved for a total of 72 trials. A total of 3.5% of trials were excluded due to the same criteria as mentioned in Experiment 3A.

### E.6.2 Results

Figure E.5C shows the mean adjustments observers made in all conditions. Observers showed a baseline flash-lag effect (in the no-change condition) of 42.6 ms ( $SEM = 7.4$  ms). A one-way repeated measures ANOVA on observers' mean adjustments revealed a significant effect of the magnitude of luminance change on perceived forward displacements,  $F(5,25) = 17.64, p < 0.001$ , partial  $\eta^2 = 0.779$ . Linear regressions for each individual observer showed negative slopes ( $M = -12.9, SEM = 2.0$ , one-sample t-test  $t(5) = -6.41, p = 0.001$ ), indicating that for all observers stronger transients led to smaller forward displacements. The largest change, when the luminance was abruptly decreased to the background level, led to a reduced flash-lag effect of just 18.5 ms (6.7 ms), which is significantly different from 0, one-sample t-test:  $t(5) = 2.77, p = 0.039$ , but much less than the baseline flash-lag.

Again, all naive observers were unable to identify the specific manipulation of the stimuli, and reported that on some trials the task was much easier to perform than on others. Figure E.5D shows the number of stimulus repetitions observers used for their adjustment in each trial. A one-way repeated measures ANOVA showed a significant effect of transient magnitude on the number of repetitions,  $F(5,25) = 3.73, p = 0.012$ , partial  $\eta^2 = 0.427$ . In the no-change condition they used 6.8 (1.3) repetitions, compared to 5.0 (0.6) in the condition with the largest change, indicating that a larger luminance change made the adjustments easier.

### E.6.3 Discussion

Introducing an abrupt offset into a motion trajectory reduced the size of the flash-lag effect. Stronger transients, i.e. bigger changes in luminance, led to more

accurate localisation of the moving bar and higher confidence of the observers in their adjustment performance, as indicated by the number of stimulus repetitions.

Contrary to the previous experiment, where we interrupted the continuous motion of the object for varying amounts of time, here the object motion never got completely disrupted. Just one frame after the abrupt decrease in the bar's luminance it appeared brighter again and continued to ramp back to its full pre-flash intensity in just 200 ms. Therefore the strength of the internal motion model remained almost undiminished. And indeed, even the strongest transient – when the luminance of the bar was reduced to the background level – still led to a considerable flash-lag effect. Due to the parafoveal viewing and the fact that motion was never stopped, we did not expect a total elimination of the flash-lag effect. Our manipulation produced a similar pattern of reduction of forward displacements as in Experiment 3A. Even weak transients led to a dramatic reduction in the size of the flash-lag effect.

We hypothesised that two processes, an extrapolated internal motion model and transient retinal signals compete to determine the perceived position of an abruptly disappearing moving object, and that it is possible to influence the outcome of this competition by manipulating the relative strengths of these two processes. The findings of Experiments 3A and B provide empirical support for this idea.

## **E.7 General Discussion**

### **E.7.1 Summary of present findings and proposed model**

The findings presented in this article demonstrate crucial differences between how the visual system processes positions of abruptly disappearing and continuously

moving objects. Experiment 1 showed that a continuously moving object is seen shifted forward in the direction of motion when compared with the position of an abruptly disappearing moving object, in a way similar to other well-known visual illusions such as the flash-lag effect (Nijhawan, 1994) and the Fröhlich effect (Fröhlich, 1923). Experiments 2 A and B examined this finding more systematically and found this forward displacement to be robust to different directions of motion, linearly dependent on speed, and a consequence of a true forward displacement of the continuously moving object, rather than a backward displacement of the offset object.

Preliminary findings on a similar illusion have been previously reported by Palmer and Kellman (2001, 2002). In their ‘aperture capture illusion’ an occluded moving bar seen through misaligned apertures is perceptually distorted. In another version of their display (Palmer & Kellman, 2003) only one part of a bar became occluded, while the other part remained visible. This resulted in a percept equivalent to the one described in our Experiment 1. They explained the misalignment by perceptual persistence of the occluded part of the bar together with an under-estimation of velocity for occluded objects. However, the stimulus used in the present experiments differs in important aspects. First there is no occluder. The offset bar disappears abruptly, that is, it is fully presented in its last position and completely absent in the next frame. When objects become occluded, as in Palmer and Kellman’s displays, their parts disappear sequentially over time, with the leading edge disappearing first and the trailing edge last. Even if observers inferred the existence of an invisible occluder in the display in Experiment 1, an explanation in terms of an underestimation of velocity of occluded parts of the bar can be ruled out. In Experiment 2A, where the two half bars moved in opposite directions, observers never had the impression of one moving bar that gets

partially occluded, but rather of two independently moving objects. Our proposed model might actually explain the findings of Palmer and Kellman (2001, 2002, 2003) at a much lower level of the visual system, without assuming any special role for object occlusion.

We proposed a two-process model to explain the current findings and previous results in the literature on the flash-lag effect and other similar illusions (Maus & Nijhawan, 2006). One process is active whenever an object is moving on a consistent, predictable trajectory. The visual system analyses the speed and trajectory of the moving object and uses this information to predict positions of the object in the near future. This prediction is advantageous in the control of behaviour, because any information about a moving object's position available to the nervous system is subject to processing and conduction delays within the retina and the visual pathway extending to the cortex. The system therefore is able to prevent a spatial lag of the perceived position of moving objects behind their physical position (Erlhagen, 2003; Nijhawan, 1994). However, if the system relied exclusively on a predictive model, abruptly disappearing objects would suffer another localisation error: They would overshoot their offset position. Thus, the second process serves as a correction mechanism, similar to the mechanisms underlying backward masking and metacontrast (Breitmeyer, 1984), relying on the accurate spatial information provided by the retinal transient of the abrupt offset of the moving object. This mechanism changes the perceived position and incorporates newly acquired information about the object's disappearance into the percept. The two-process mechanism we propose is advantageous because it minimises spatio-temporal localisation errors for both continuous easily predictable events, and sudden unpredictable events.

When two processes produce contradicting outcomes, the conflict needs to be resolved to form a coherent percept of the visual scene. In the case of abruptly disappearing objects, as presented here, two separate position representations compete for perceptual awareness: one based on extrapolated information and the other on the retinal Off-transient. In most cases investigated previously, for example in the flash-terminated flash-lag display, and in the present Experiments 1 and 2, the Off-transient wins this competition for perception. However, in Experiment 3 we actively manipulated the relative strengths of the two competing representations and as a result measured intermediate positions being perceived. In Experiment 3A we introduced an abrupt offset of the moving object and varied the time until it became visible again, in other words the time duration for which the support for the extrapolated model was suspended. In Experiment 3B the strength of the retinal transient was manipulated. Both manipulations led to reductions in the measured size of the flash-lag effect, with stronger transients or longer disruption of motion leading to a smaller forward displacement. Both Experiments 2 and 3 also showed that position judgements based on visual Off-transients are less ‘noisy’—that is, they lead to steeper psychometric functions and more confident judgements from observers.

### **E.7.2 Implications for theories of the flash-lag effect and the localisation of moving objects**

Several theories attempting to explain the flash-lag findings have been proposed; some of them aim to be general accounts of how moving objects are localised by the visual system (for reviews see Krekelberg & Lappe, 2001; Nijhawan, 2002). Several researchers have stated that the forward displacement of the moving object in the flash-

lag effect can be explained by differential latencies for moving and flashed objects (Purushothaman et al., 1998; Whitney & Cavanagh, 2000a; Whitney & Murakami, 1998). Others suggest that the positions of a moving object are sampled over an extended time window and then integrated to yield the perceived position, thereby explaining the mismatch in position between moving and flashed objects (Brenner et al., 2006; Eagleman & Sejnowski, 2000; Krekelberg & Lappe, 2000; Roulston et al., 2006). Finally, some researchers claim that in the flash-lag effect—and in general—the perceived position of moving objects is spatially extrapolated resulting in a forward shift, possibly to overcome neural processing delays in the visual pathway (Berry et al., 1999; Kanai et al., 2004; Nijhawan, 1994; Sheth et al., 2000). The present study has important implications for aforementioned theories.

#### **E.7.2.1 *Differential latencies***

The differential latency account assumes that moving objects are processed faster than flashes. In a flash-lag paradigm by the time the flash is being processed, the moving object has moved on, therefore leading to the spatial misalignment. On this view the flash-lag effect is a purely temporal effect, that is, any spatial misalignment results from a temporal processing advantage for the moving object. When the moving object abruptly disappears, it never overshoots, but is perceived in its veridical position, like the flash.<sup>7</sup> In Experiment 1 we employed two aligned objects, moving side by side at the same speed. They should be processed with the same latency. Nevertheless, when one of them abruptly disappeared, it seemed to lag behind the continuously moving

<sup>7</sup> The differential latency account predicts that in a flash-terminated flash-lag display, the moving object should be seen to disappear before the flash is perceived. However, temporal order judgement tasks have not revealed a generally shorter latency for moving objects (Nijhawan et al., 2004).

object. The differential latency account, at least in its simplest version, does not readily explain this finding.

A special role for an abrupt offset of a moving object, such as proposed in this paper, is usually not assumed in the differential latency account. However, the transients of the flash and the transient of an abrupt offset are physiologically similar. If the moving object were perceived to disappear only when the slower transient signal is registered at some cortical level, this would offer an explanation for the present findings in the framework of differential latencies. It remains unclear, however, what is perceived in the time between the motion signal being registered at a particular retinotopic position and the transient signal later being registered at the same position.

In Experiment 3A we measured a baseline flash-lag effect of 45 ms, that is, on the differential latency account the difference in the latencies of the flash and the moving object in this particular stimulus display should be approximately 45 ms. Presumably this would also be the additional delay the offset transient undergoes. When the motion was disrupted briefly for just 20 ms, the flash-lag effect was reduced, although by the time the flash was registered the motion should again be processed normally as in the baseline flash-lag effect. In a similar fashion to the present proposal, the differential latency account would have to resort to interactions between separate representations for the moving object and the transient to explain these findings. In this case differential latency as an explanation for the flash-lag phenomenon loses its appeal of simplicity. However, for the case of continuously moving objects the proposals of faster processing or spatial extrapolation remain indistinguishable, and might well share common underlying neural mechanisms (see below).

### **E.7.2.2 Temporal integration**

Temporal integration theories state that all positions an object occupies over a certain time window (typically about 100 ms) are integrated and averaged to yield the perceived position of the object. To account for the flash-lag effect it has to be additionally assumed that this time window extends into the future, or rather that the outcome of such an averaging process is then ‘postdicted’, that is, the percept is assigned back in time to an earlier moment (Eagleman & Sejnowski, 2000).

Temporal integration is incompatible with the findings of Experiment 3A. Consider Figure E.4A: To explain the baseline flash-lag effect the time window from which positions are sampled to determine the perceived position at  $t_0$  (the time of the flash) has to include mainly positions after the flash (in the figure to the right of the flash). As the duration of the blank is increased, fewer positions in the immediate vicinity of the flash contribute to the average, shifting the output of the integration mechanism to the right. This would predict an increase in the size of the flash-lag effect, which is contrary to what we found. Only for long blanks, when the duration of the blank is longer than the duration of the integration window, does the temporal integration account predict accurate localisation. The same reasoning holds true for an integration window that is centred around the time of the flash, but weighted towards more recently sampled positions (Roulston et al., 2006).

Temporal integration of some manner is certainly also necessary in our proposed two-process model. Motion is defined as change of position over time, thus in order to initialise the extrapolation process positions need to be sampled over some time interval. This interval however, can be remarkably short (Nijhawan, in press). Once the

system has identified a coherently moving object it relies on the predicted internal model to provide an estimated position at a certain point in time. Abrupt events, such as sudden offsets, can however override this position estimate.

#### **E.7.2.3 *Motion extrapolation***

One feature that distinguishes the extrapolation account of the flash-lag phenomenon from the two previously discussed accounts is that it involves a spatial shift of the moving object's position, rather than an underlying temporal effect. This spatial shift is dependent on the previous motion of the object, which conveys the information necessary to compute the current position of the object, despite the fact that the information is out of date due to delays in earlier visual pathways. Motion extrapolation is, however, prone to errors when sudden events, like the offset of the moving object, contradict the predicted information. These predicted errors are not apparent in most cases (Eagleman & Sejnowski, 2000; Kerzel, 2000). In this article we show how the visual system uses a correction mechanism to minimise such errors.

#### **E.7.3 Prediction versus postdiction**

Postdiction originally maintained that the flash resets motion integration (temporal averaging), so that the perceived position of the moving object is determined by the average of positions after the flash. This average position then gets 'postdicted', i.e. reassigned, to the time of the flash (Eagleman & Sejnowski, 2000). Apart from experimental findings on the standard flash-lag paradigm this account assumes that moving objects are perceived to trail their physical position. Thus, this account also predicts a speeding up of the moving object at the time of the flash to get ahead of this position, which has never been observed (Nijhawan, 2002). In a more recent account Eagleman and Sejnowski (2007) claim that motion signals from after the flash bias the

position of the moving object towards the direction of motion, a proposal more similar to the original motion extrapolation account (Nijhawan, 1994). The crucial difference in these two positions now is, whether the spatial shift depends on past motion signals, so it is in fact a prediction, or whether it depends on future motion signals, in other words it is a postdictive determination of the perceived position.

It should be noted here that there are no a priori reasons why one or the other possibility should be preferred, or why they should be mutually exclusive. Some of the experimental data on the flash-terminated flash-lag seems to favour a purely postdictive account. While it might be tempting to apply Occam's Razor and accept a postdictive account as the simpler model, even the newer account (Eagleman & Sejnowski, 2007) has one major disadvantage: It states that our perceptual awareness of the world *always* lags temporally behind the physical events giving rise to these perceptions.<sup>8</sup> In a purely postdictive account the position of a moving object can be perceived spatially correct, but temporally incorrect—at a time when the physical object is actually occupying a different position. This is problematic when we consider that the ultimate goal of perceiving the environment is to enable an organism to interact with its surroundings. For dynamic interactions with moving objects a temporal localisation error is equally disadvantageous as a spatial localisation error. An organism will certainly benefit from being able to anticipate changes of position of behaviourally relevant stimuli at the earliest possible processing stage. Further, retrospective computations of position are

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<sup>8</sup> This is nicely demonstrated in Figure 2 of Rao, Eagleman, and Sejnowski (2001), in which subjective time is viewed as an entirely different entity to physical time and therefore plotted on a different axis.

costly. Visual information of an extended time period would need to be held in some kind of sensory store and subsequently integrated, whereas an on-the-fly extrapolation of incoming data can in principle be implemented by a process as simple as a linear filter (Grush, 2005).

The two-process account outlined here, involving both prediction and retroactive correction, is advantageous because it minimises computational cost as well as spatial and temporal localisation errors in the best way possible depending on the information available at any given time. If an object is moving continuously and predictably, an organism will benefit from using some kind of prediction. If however sudden, unpredictable events make this prediction inaccurate, retroactive mechanisms correct what is now faulty perceptual content (Grush, 2005; Maus & Nijhawan, 2006).

#### **E.7.4 Possible neural mechanisms**

The model we propose consists of two separate processes: (a) an extrapolation process shifting the position of a coherently moving object forward in the direction of motion and (b) a retroactive correction mechanism that is based on transient retinal signals. There is substantial evidence in the literature that both these processes exist and are at work in several phenomena of visual processing.

##### ***E.7.4.1 Extrapolation mechanism for the forward shift of moving objects***

Several studies have shown that lateral interactions between neurons in retinotopic maps can cause an asymmetric spread of neural activity in response to moving visual stimuli, as early as in retinal ganglion cells (Berry et al., 1999), but also in retinotopic cortical maps (Jancke et al., 2004a; Sundberg et al., 2006; Whitney et al., 2003). In effect, these interactions cause the peak of neural activity to be at the leading

edge or even ahead of the stimulus in retinotopic neural space. Additionally, it is well known that in the wake of a moving stimulus neurons are inhibited, a process, which arguably contributes to the deblurring of a moving stimulus (Burr, 1980). These local excitatory and inhibitory interactions have been proposed as the underlying mechanisms of the flash-lag effect, either by facilitating shorter processing latencies in the path of moving objects (Whitney & Murakami, 1998) or by biasing localisation forward in the direction of motion (Kanai et al., 2004; Kirschfeld & Kammer, 1999). Computational simulations have shown that travelling waves of activity in a map of neurons can be self-sustained to some extent (Erlhagen, 2003), i.e. they can keep moving even in the absence of continued bottom-up input. Such a self-sustained wave of activity could be the underlying mechanism of an internal model for object motion. Feedback connections from an area maintaining such a model can then shift the neural peak activity in another retinotopic map even further in the direction of motion.

The role of cortical feedback in perception has recently received much attention (Lamme & Roelfsema, 2000). For example, several studies using transcranial magnetic stimulation have shown that feedback from motion-sensitive areas to earlier retinotopic maps seems to be pivotal for the perception of motion (Pascual-Leone & Walsh, 2001; Sack et al., 2006; Silvanto et al., 2005b). Even thalamic neural activity in response to moving stimuli, supposedly forming the ‘bottom-up’ input to the visual cortex, is highly shaped by cortical feedback (Sillito et al., 2006; Sillito & Jones, 2002). It is reasonable to assume that these feedback connections are also active when stimuli involving moving objects (such as those used in the present experiments) are presented. The role of feedback in causing the flash-lag effect and related forward displacement illusions remains to be examined in more detail.

#### **E.7.4.2 Retroactive correction based on transients**

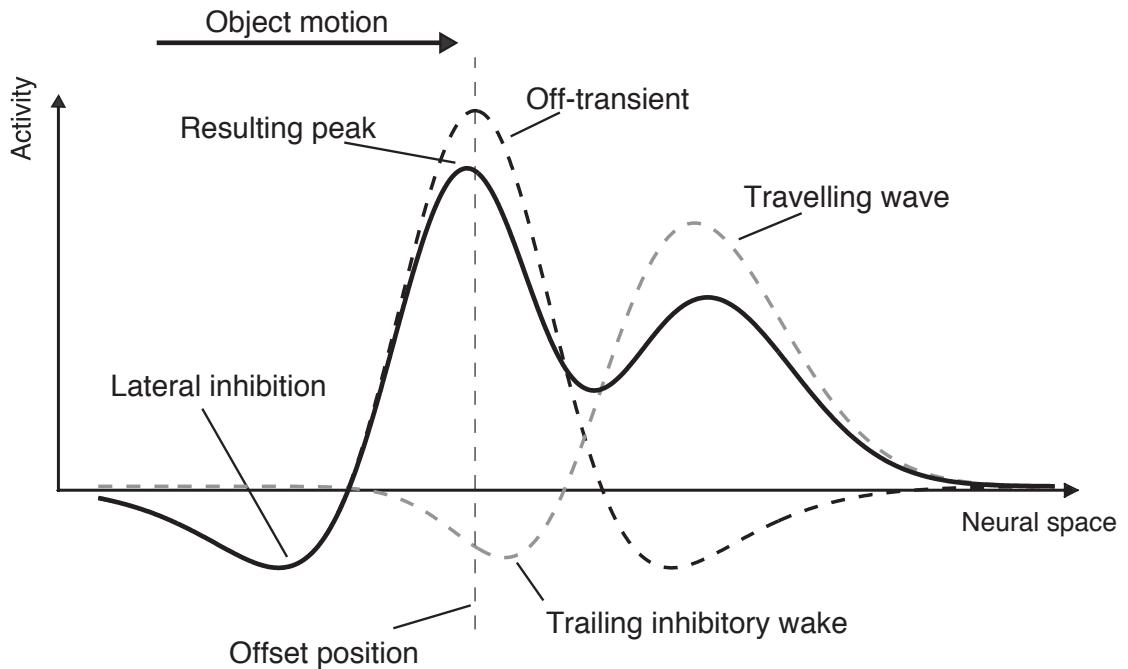
The second ingredient in the present model is a mechanism that corrects the forward shift, when a bottom-up transient signal from the retina indicates that the moving object is no longer moving, but has actually disappeared in a certain position. This process works retroactively, that is, it changes the percept of an earlier time point, although the physical process underlying this percept occurs later, namely when the transient signal is registered.

Similar retroactive changes of percepts are apparent in a number of visual phenomena (Dennett & Kinsbourne, 1995; Grush, 2005), most prominent of which is backward masking (Alpern, 1953; Breitmeyer, 1984), in which a visual target is rendered invisible by a subsequently presented mask. In masking the transients of both the onset and offset of the mask elicit lateral inhibition that render the target less visible or invisible (Macknik et al., 2000). Lateral inhibition, elicited by the offset of the moving object, might suppress the extrapolated neural representation. Figure E.6 schematically shows the neural activity in a retinotopic map in response to the abrupt offset of a moving object. The grey dashed curve represents the travelling wave of activity in response to a moving object (cp. Kanai et al., 2004; Kirschfeld & Kammer, 1999). Its peak is shifted forward by the mechanisms suggested above. Trailing behind the peak is a wake of inhibitory activity. The black dashed curve represents the transient Off-signal from the sudden offset of the moving object, accompanied by lateral inhibition (Macknik et al., 2000). The peak of the transient is accurately localised and less spread out than the travelling wave. Assuming a linear interaction of these two signals, the resulting summed activity pattern is displayed by the solid black line. The lateral inhibition of the transient leads to an attenuation of the travelling wave's peak.

The global maximum peak of the resulting pattern is accurately localised near the true offset position of the stimulus. The trailing inhibitory wake might in fact lead to a small undershoot of the stopping object, as we experimentally found in Experiment 2B. However, physiological evidence (Borg-Graham, Monier, & Fregnac, 1998; Shu, Hasenstaub, & McCormick, 2003) and computational considerations (Gutkin, Laing, Colby, Chow, & Ermentrout, 2001) give reasons to believe that the transient's inhibitory effects are non-linear, resulting in a shunting of the self-sustained activity of the travelling wave. In this case, the resulting activity pattern would feature a more complete suppression of the travelling wave and directly reflect the perceptual outcome of an accurately perceived offset position. Manipulating the relative strengths of the two signals (the dashed curves in Figure E.6) might lead to the perception of intermediate positions, as found in Experiment 3.

### **E.7.5 Limitations and future directions**

The theory presented in this paper has one important limitation: The experiments focused on abrupt offsets. Abruptly stopping objects that remain visible or abrupt changes of direction have similar effects on the localisation of moving objects (Eagleman & Sejnowski, 2000; Whitney & Murakami, 1998). However, it is known that changes in the direction or speed of a moving stimulus elicit strong electrophysiological responses in the visual system stemming from motion-sensitive areas (Ahlfors et al., 1999; Clarke, 1972; Pazo-Alvarez et al., 2004). Moreover, it has recently been shown that the abrupt reversal of direction of a moving object can elicit a strong synchronised peak of activity in retinal ganglion cells (Schwartz et al., 2007). These 'change transients' can probably elicit similar mechanisms as an Off-transient does. This proposal remains to be tested in further detail.



**Figure E.6** Schematic illustration of the pattern of neural activity in a cortical retinotopic map in response to the abrupt offset of a moving object. The graph depicts a snapshot of neural activity at the time when the Off-transient has been fully registered by neurons at this site. The abscissa denotes space in the retinotopic map, the ordinate neural activity. Object motion is indicated by the large arrow; the abrupt offset occurs at the dashed vertical line. The grey dashed line depicts the travelling wave of activity, the basis for the internal motion model, and is shifted forward from the object's position in the direction of motion to compensate for temporal delays in neural pathways. Neurons in the wake of this wave are being inhibited to reduce motion smear. The black dashed line depicts the neural response to the transient Off-signal. It is centred around the true offset position and features symmetric lateral inhibition. The black solid line is the resulting neural activity produced by adding the two activity patterns. The peak of the travelling wave is attenuated, rendering the resulting maximum close to the true offset position. Due to the inhibitory wake the peak could actually be shifted slightly in the opposite direction of motion.

A strong argument for a predictive mechanism for localisation of moving objects can be made from findings, where moving objects are seen in un-stimulated retinotopic space after disappearing without providing a transient for correction of position (Maus

& Nijhawan, 2006, Article I). We recently investigated the final perceived position of a moving object disappearing in the blind spot, and found that the object is visible well into the ‘blind’ area (Article III). This finding can only be explained by a spatial shift of perceived position based on past motion signals, as there is no bottom-up position (or motion) information from within the retinal blind spot.

Our proposal that Off-transients play an active role in the localisation of final positions of moving objects entails a special involvement of the M-pathway. This could be further investigated using isoluminant stimuli. Additionally, the advent of more advanced techniques, e.g. neuro-navigated transcranial magnetic stimulation (Sack et al., 2006), will make direct study of the involvement of cortical feedback from motion-sensitive areas to earlier retinotopic maps possible.

### **E.7.6 Conclusions**

Abrupt offsets of moving objects have profound effects on their localisation by the visual system. In a display where two identical aligned objects move and one of them disappears abruptly, the offset is perceived in its veridical position, whereas the object in continuous motion is perceived displaced forward. We propose that the forward shift can be explained by an internal model entailing predicted positions of coherently moving objects, and a correction mechanism for the forward shift based on the retinal transient when the object disappears. When the relative strengths of these two mechanisms are manipulated, intermediate positions are perceived. Such a two-process model of object motion perception is advantageous for an organism, because it maximally reduces spatio-temporal localisation errors of the visual system.

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