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Predictive position coding

Attentional account of motion-induced position shifts

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Abstract

Localizing objects in space is one of the central functions of the visual system. When an observer or a target is moving, the motion of the eye or the object can be taken into account to compute the current object locations. It has been shown many times that visual motion can strongly influence the perceived position of an object. For example, a stationary patch containing moving texture (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990), a flash presented on (Cavanagh & Anstis, 2013) or next to (Whitney & Cavanagh, 2000) a moving texture, and even the onset and offset positions of the moving targets (Fröhlich, 1923; Freyd & Finke, 1984) are perceived as shifted in the direction of motion. In this thesis we explore the relationship between these motion-induced position shifts and visual attention in the following forms: 1) transient spatial attention, 2) global and local attention 2) sustained spatial attention, and 3) object-based attention.

In the first series of experiments we looked at whether and how attention modulates the localization of motion onset. When an object suddenly appears in motion, its initial position is perceived as being shifted in the direction of its motion (Fröhlich effect). In Experiment 1 we measured Fröhlich effect under different cueing conditions (valid, invalid or neutral) and established that invalid cues produced larger perceptual shifts, although the Fröhlich effect was still present for valid and neutral cues. In Experiment 2 we found that the Fröhlich effect increased when the valid cue arrived more than 100 ms after the start of motion, suggesting again that a delay in attention's arrival shifted the location of the perceived motion onset. In Experiment 3 we compare the motion-induced shifts when the subjects attended to a set of moving stimuli as a group and when they attended to an orientation singleton. We showed that the Fröhlich effect was only present when the target was individuated and disappeared when the stimulus was perceived globally. Thus, the Fröhlich effect appeared to be both produced and modulated by focal attention.

Having established that temporal delays of attention increase motion-induced position shifts, the next study explored if spatial distribution of attention has a similar effect. In this study we used the flash-grab effect — an illusory position shift seen when a target is briefly flashed on top of a moving background that abruptly changes direction (Cavanagh & Anstis, 2013). We created a new variation of the flash-grab

stimulus that allowed us to produce even larger position shifts (15 times bigger than the size of the target) and to increase the spatial uncertainty of the target. Trials were presented in blocks and before each spatial block a cue indicated a range of possible target locations (0°, 45°, 90°, 180° or 360°). We found that the flash-grab effect was reduced if the spatial distribution of targets within a block was limited to a range of 90° or less. Cuing a narrow range would allow attention to reach the target sooner whereas cuing a larger range would delay the arrival of focal attention to the moving target. The result here is therefore in agreement with the results of the previous project, in that delayed attention increases the position shift.

The final study asked whether motion shifts the perceived position of an object as a whole or alternatively if separate features of a single object are shifted independently. To test this we used the flash-grab paradigm and briefly presented a shape on top of a moving background at the moment it changed direction. In this study we were interested not only in the position of this shape, but also in its appearance. We tested five different objects, both outlines and filled shapes, at different levels of background contrast, and asked subjects to adjust these shapes to match a symmetrical reference. For instance, for the "T", subjects shifted the vertical stem until it appeared aligned to the center of the horizontal bar. For the "circle", participants adjusted its left and right curvature until it appeared circular. The results showed that the features of the target that were orthogonal to the background motion were shifted most, whereas the features parallel to the motion were less shifted, distorting the appearance of the briefly presented shape. This suggests that motion interacts with the position of the object's features (and focal attention selects them) before they are bound together into an object.

In conclusion, we applied a variety of attentional manipulations to motion-induced position shifts, and examined the link between the strength of the illusion and the characteristics of attention used in a particular task. First, we found that motion-induced position shifts require focused attention and the possibility to track an individual motion trajectory. Second, we showed that allowing attention to be allocated more efficiently in space reduces the illusion. Finally, we found that motion-induced shifts operate on the feature-based and not object-based level.

Résumé

La localisation des objets dans l'espace est une des fonctions centrales du système visuel. Lorsqu'un observateur ou une cible est en mouvement, le mouvement de l'œil ou de l'objet peut être pris en compte pour calculer la position de l'objet à n'importe quel moment. Il a été démontré à plusieurs reprises que le mouvement visuel peut fortement influencer la position perçue d'un objet. Par exemple, un patch stationnaire contenant une texture en mouvement (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990), un flash présenté sur (Cavanagh & Anstis, 2013) ou à côté (Whitney & Cavanagh, 2000) d'une texture en mouvement, et même les positions de départ et d'arrivé des cibles en mouvement (Fröhlich, 1923) sont perçus comme étant déplacés dans la direction du mouvement. Dans cette thèse, nous explorons la relation entre ces déplacements de position provoqués par le mouvement et l'attention visuelle sous les formes suivantes: 1) l'attention spatiale transitoire, 2) l'attention globale et locale, 3) l'attention spatiale soutenue, et 4) l'attention basée sur les objets.

Dans la première série d'expériences, nous avons examiné si et comment l'attention module le déplacement de la localisation au début du mouvement (effet Fröhlich). Dans les Expériences 1 et 2, nous avons mesuré l'effet Fröhlich sous des différentes conditions de cueing et nous avons établi que les indices invalides ou tardifs produisent de plus grands déplacements perceptifs. Dans l'Expérience 3, nous comparons les déplacements provoqués par le mouvement lorsque les sujets portaient leur attention sur un ensemble de stimuli en mouvement qui formaient un groupe comparé à quand il n'y avait qu'un seul stimulus avec l'orientation recherché. Nous avons montré que l'effet Fröhlich était présent lorsque la cible était individué et disparaissait lorsque le stimulus était perçu au niveau global. Ainsi, l'effet de Fröhlich semble être à la fois produit et modulé par l'attention focale.

Ayant établi que les délais temporels de l'attention augmentent les déplacements de position provoqués par le mouvement, la prochaine étude explorait si la distribution spatiale de l'attention a un effet similaire. Dans cette étude, nous avons utilisé le flash-grab - un changement de position illusoire aperçu quand une cible est

brièvement flashé sur un fond en mouvement qui change soudainement de direction (Cavanagh & Anstis, 2013). Les essais étaient présentés en blocs et avant chaque bloc un indice indiquait une plage d'emplacements de cible possibles. Nous avons constaté que le flash-grab était réduit quand la distribution spatiale des cibles était limitée à une plage de 90° ou moins.

La dernière étude demandait si le mouvement déplace la position perçue d'un objet dans son ensemble ou si les caractéristiques distinctes d'un même objet sont déplacées indépendamment. Pour tester cela nous avons utilisé le paradigme flash-grab et brièvement présenté une forme au-dessus d'un fond en mouvement au moment où il a changé de direction. Les résultats montrent que les caractéristiques de la cible qui étaient orthogonale au mouvement du fond étaient déplacées, alors que les caractéristiques parallèles au mouvement étaient intactes. Ceci suggère que le mouvement interagit avec la position des caractéristiques de l'objet (et l'attention focale les sélectionne) avant qu'elles ne soient liés ensemble dans un objet.

En conclusion, nous avons appliqué une variété de manipulations attentionnelles à des changements de position provoqués par le mouvement, et nous avons examiné le lien entre la force de l'illusion et les caractéristiques de l'attention utilisées dans une tâche particulière. Nous avons constaté que 1) les changements de position provoqué par le mouvement nécessitent une attention ciblée et la possibilité de suivre une trajectoire de mouvement individuelle; 2) quand l'attention est réparti plus efficacement dans l'espace l'illusion est réduite; et 3) les décalages provoqués par le mouvement fonctionnent au niveau des caractéristiques et non au niveau des objets.

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Table of contents

Part I. Introduction

Encoding of positional information is vital for successful interaction with the environment. We need to know where something is before we can move our eyes to examine it more closely, reach out our hand to grab it, or decide to run away from it. Even more basic visual functions such as binding visual features into objects (Treisman & Gelade, 1980) depend on the accurate representation of spatial proximity.

From the moment that light enters the eye, the spatial organization of the image is carefully maintained in the visual brain. The idea that the cortex represents an orderly map of the visual features was supported by the neurophysiological findings already in the 19th century (Henschen, 1893), and was preceded by the detailed studies of the optics of the eye by 16th century physiologists (Popple, Levi, 2005). The theories of local sign and labeled lines were put forward to account for the encoding of position (Hering, 1899; Lotze, 1886, von Helmholtz, 1962). Despite the differences in the exact proposed mechanisms, these theories shared the basic idea that each receptor of the retina is connected to the retinotopically organised brain by a dedicated nerve fiber, meaning that this unique neural pathway is by itself an indicator of the precise location of the light on the retina. Modern neuroimaging studies confirm that a series of topographic maps in the brain organise visual information through all its transformations. Sixteen or more retinotopic maps have been described in the human cortex (Wandell, Dumoulin, & Brewer, 2007), with many more located subcortically (Schneider, Richter, & Kastner, 2004; Kastner et al., 2004). However, there are many circumstances in which factors other than retinal information influence the perceived location, challenging the labeled line approach. Eye movements (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Ross, Morrone, & Burr, 1997, Ross, Morrone, Goldberg, & Burr, 2001), frames of reference (Roelofs, 1935; Bridgeman, Peery, & Anand, 1997), attention (Suzuki & Cavanagh, 1997; Kerzel, 2004; Kosovicheva, Fortenbaugh, & Robertson, 2010), memory (Sheth & Shimojo, 2001) and adaptation (Whitaker, McGraw, & Levi, 1997) are among the factors contributing to the dissociation between the physical and the perceived position of an object. The focus of the present work is a group of pronounced perceptual mislocalizations resulting

from visual motion (Fröhlich, 1923; Whitney, 2002; Cavanagh & Anstis, 2013). Before describing these perceptual effects in more detail, I would like to briefly review the neural substrate of motion perception.

1.1 Processing of motion in the visual system

The visual system infers motion from the changing pattern of light on the retina. Visual motion signals are encoded and processed in a network of subcortical and cortical structures. Most of our knowledge about the motion processing systems comes from the single cell studies in nonhuman primates and cats.

1.1.1 The retino-geniculo-striate pathway

`Retina`

The analysis of visual motion starts in the retina. The retina comprises three functional layers: rods and cones, bipolar cells, and ganglion cells. Ganglion cells, located in the innermost part of the retina, receive their input from photoreceptors via bipolar cells, convert the visual information into the nerve spikes and transfer it to the thalamus. There are two major and well-studied types of ganglion cells, although many more are described in the literature (Sanes & Masland, 2015). Midget retinal ganglion cells (70–80% of the ganglion cells) have small bodies and small receptive fields. Their responses are relatively slow and they are sensitive to higher contrast. Parasol retinal ganglion cells (10% of the ganglion cells) are much bigger in size and have larger receptive fields comprising many photoreceptors. They have faster conduction velocity and sensitivity to low-contrast stimuli.

Barlow & Levick (1965) describe a subset of direction-selective ganglion cells in the rabbit retina. Direction-selectivity means that if a stimulus presented to the receptive field of a cell moves in its preferred direction, the spiking rate of the cell increases above spontaneous activity. Usually, if the stimulus moves in the opposite direction, the firing rate decreases below spontaneous activity. In the primate retina, however, these cells are rarely encountered (Schiller & Malpeli 1977; DeMonasterio, 1978).

LGN

Lateral geniculate nucleus (LGN) is located in the dorsal part of the thalamus and acts as a relay between the retina and the cortex. Midget and parasol ganglion cells project to the different layers of the LGN, preserving pathway specificity. Parasol cells send their axons to the innermost layers (1-2) of the LGN, known as magnocellular layers. Midget cells are connected to the layers 3-6 of the LGN, or parvocellular layers. Magnocellular cells have large receptive fields and show fast transient responses with high temporal resolution. In contrast, parvocellular cells have small receptive fields, low temporal resolution, and show slow sustained responses. Relying on these characteristics, parvo system is optimal for conveying information about static form, while magno system carries information about motion (DeYoe & Van Essen, 1988; Livingstone & Hubel, 1988). Both magnocellular and parvocellular units respond to moving stimuli, some of them showing direction selectivity. In the parvo system, the cells are more broadly tuned to velocity (Lee, Creutzfeldt, & Elepfandt, 1979).

There is also a third route connecting the retina to the V1 – the koniocellular pathway. This pathway originates in a small heterogeneous group of ganglion cells (Schiller & Malpeli, 1977; Perry & Cowey, 1984; Perry, Oehler, & Cowey, 1984). In LGN, koniocellular layers are located ventrally to the magno and parvocellular layers. This pathway has been mostly implicated in color processing (Martin et al., 2007; Reid et al., 1997), however, it is often associated with motion processing due to the presence of the direction-selective cells (Casagrande, 1994) and its projections to motion-processing cortical areas (Seidemann et al., 1999; Wandell et al. 1999).

Primary visual cortex

V1, also known as Brodmann's area 17 or striate cortex, is the first cortical destination of the visual signal. Magno, parvo and konio cells send their input to the different layers of V1, but the signal are merged in the subsequent areas. At least 30% of the V1 cells, especially the complex cells, are direction selective (Hubel & Wiesel 1959, 1968; Figure 1.1). Further studies showed that many of these cells have broad speed tuning (Wurtz, 1969). These motion-selective cells are often considered to be the basic units of motion processing (Livingstone & Hubel, 1988), and they are more likely to project to motion-specialised area MT/V5 than to other extrastriate areas

(Movshon & Newsome, 1996). Essentially, V1 neurons filter the image in space and time, computing the motion of small oriented elements (Adelson & Bergen, 1985).

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Figure 1.1. V1 direction selectivity.

Data from Hubel and Wiesel's early experiments on V1. The dashed rectangles on the left indicate a V1 neuron's receptive field. The superimposed lines are the stimuli that were used, and their direction of motion. The arrows above each recording indicate the direction of motion. This V1 neuron responds best to the up-right motion but not at all to down-left motion.

1.1.2 Extrageniculate pathway

The geniculostriate pathway connecting the retina to the cortex via LGN is followed by 80%-90% of retinal ganglion cells. In addition, there is a direct route from the retina to superior colliculus (SC), which then sends information to the pulvinar nucleus of the thalamus (Harting, Huerta, Frankfurter, Strominger, & Royce, 1980; Berman & Wurtz, 2010) and terminates in the visual cortex bypassing V1. This extrageniculate system is dominated by the magnocellular output, and thus is important for the analysis of motion and location. Functionally, it contributes to the shifts of visual attention, facilitates saccades and head movements (Krauzlis et al., 2004; Kato, Takaura, Ikeda, Yoshida, & Isa, 2011).

`Superior colliculus`

SC is a part of the "roof" of the midbrain. The colliculi have a laminated structure, where superficial layers receive visual inputs (both from the retina and from the cortex), and deeper layers contain auditory and somatosensory information (Wallace, Meredith, & Stain, 1998). About 10% of ganglion cells project in the SC (Hubel et al., 1975). Collicular cells receiving retinal input have very small response latencies, broad speed tuning, and respond more strongly to stimuli oriented orthogonally to their motion direction. The sensory input of SC appears to be particularly important for the guiding of orienting movements (Horwitz, Batista, & Newsome, 2004).

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Pulvinar
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Pulvinar is a part of the thalamus well connected to visual and associative structures of the brain. This region is often associated with visuospatial attention and visually guided actions (Robinson & Petersen, 1992; Guillery, 1995; Chalupa, Coyle, & Lindsley, 1976). Cells in lateral posterior pulvinar have been found to encode velocity and direction of motion, as well as the relative motion between the stimulus and its background (Casanova & Savard, 1996). Moreover, pulvinar is able to integrate local motion signals into a coherent moving percept (Merabet, Desautels, Minville, & Casanova, 1998).

1.1.3 Extrastriate visual cortex

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Areas V2, V3, V4
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A small percentage (around 15%) of V2 cells are direction selective (Zeki, 1978). These cells are located within the orientation-selective zones or thick/pale stripes of V2 (Lu, Chen, Tonigawa, & Roe, 2010), and, as most of the direction-selective cells in the other areas, respond strongest to the stimuli oriented orthogonally to their preferred direction. Area V3 has about 40% of direction-selective cells (Gegenfurtner, Kiper, & Levitt, 1997). Some of these cells respond to the motion of a pattern rather than to the motion of its individual components. This form of higher-motion processing seems to originate in V3, as it appears there for the first time in cortical processing pathways. Overall, area V3 is important for dynamic form analysis (Zeki, 1993). Area V4 is mostly implicated in object perception and colour analysis. However, a number of studies show considerable direction selectivity in V4 (reviewed in Roe et al., 2012), ranging from 5% to 30% of cells depending on the recording method. According to an influential hypothesis (Braddick, 1993; Zhou et al., 2000) this motion signal is used for figure-ground segregation of the moving object. While motion integration is required to combine local motion signals into a coherent percept, motion differentiation, possibly taking place in V4, helps to identify the borders of the moving object and segregate tt from its background.

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Middle temporal area
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Area MT (or V5) is considered to be the hub of motion processing. Almost all MT neurons (90%) are direction-selective, and many of them are also sensitive to the speed of visual stimulation (Zeki, 1974; Orban, 2008). Although MT receives most of its input through areas V1-V3, there are at least two pathways bypassing this main route through direct LGN to MT or V1 to MT projections (Sincich, Park, Wohlgemuth, & Horton, 2004; Nassi, Lyon & Callaway, 2006). Importantly, MT combines and interprets motion signals coming from the earlier visual areas. It is not a trivial task, since early motion signals are inconclusive about the direction of motion. This 'aperture problem' is resolved by MT neurons, resulting in a coherent response to global motion (Pack & Born, 2001).

A number of studies have shown a direct link between MT neural activity and psychophysical performance in a motion discrimination task (Britten, Shadlen, Newsome, & Movshon 1992; Salzman, Murasugi, Britten, & Newsome, 1992; Newsome, Shadlen, Zohary, Britten, & Movshon, 1995). Motion discrimination and speed discrimination, but not color perception or visual acuity, are largely impaired after a lesion in MT (Newsome & Pare, 1988; Cowey & Marcar, 1992; Schiller, 1993). In humans, damage to the posterior parietal and occipital regions of the brain can lead to the inability to perceive motion (cases reviewed in Zeki, 1993). The most studied case was first presented by Zihl, Von Cramon, & Mai (1983). The patient, L.M. could not perceive the direction and speed of motion, although her color and depth perception as well as letter and object recognition were intact. Moreover, she could judge the tactile or auditory motion -- the deficit was only visual.

Medial temporal superior area and superior temporal sulcus

The role of areas beyond MT is less understood (Rokszin et al., 2010). Cells in the areas MST (medial superior temporal area) and STS (superior temporal sulcus) receive strong input from MT and are likely to analyze information about self-motion and optic flow (Britten & Van Wezel, 2002; Warren, 2008). Dorsal part of MST hosts cells responding to complex moving patterns, such as rotation in a particular direction, contraction or expansion (Tanaka & Saito, 1989; Duffy & Wurtz, 1991). These cells respond better to large fields of moving dots. In contrast, neurons in lateral MST respond more strongly to small moving patterns, suggesting that this area performs

figure-ground segmentation (Tanaka et al., 1993). In addition, STS is implicated in integrating multisensory information (Beauchamp et al., 2008) and perception of biological motion (Beauchamp et al., 2003; Pelphrey & Morris, 2006).

The cortical areas processing visual information are thought to form two relatively independent streams: ventral ("what", perceptual pathway) and dorsal ("where"/ "how" / action pathway). The ventral pathway comprises certain structures within areas V1 and V2 as well as area V4 and inferior temporal cortex. It receives both magnocellular and parvocellular input and responds selectively to the information relevant for object identification, such as shape and color. The dorsal pathway starts from the other parts of V1 and V2 and includes areas V3, V3a, MT, MST as well as inferior parietal cortex. This pathway receives predominantly magnocellular input and is associated with movement for action and processing of spatial aspects of objects, such as direction and speed of motion (Ungerleider & Haxby, 1994; Milner & Goodale, 2008). However, as outlined above, even areas belonging to the ventral pathway (such as V4) include direction-selective cells, which suggests they do play a role in motion perception (Ferrera, Rudolph, & Maunsell, 1994; Gilaie-Dotan et al., 2013). This indicates that the specialization of the processing streams and of the separate areas is rather relative and not fully understood yet.

It is also worth noting here that in addition to the feedforward processing, the visual system is rich in horizontal and feedback projections. This abundance of connections leads to the possibility that some anatomically more high-level areas receive information faster than areas located earlier in the processing hierarchy (Lamme & Roelfsema, 2000). For instance, and importantly for the present work, area MT has very short response latency. Lamme and Roelfsema (2000) report that cells in macaque area MT respond on average in 76 ms, with the earliest activation detected 39 ms after stimulus onset. This is not dramatically later than the response of area V1 (mean latency 72 ms, earliest response at 35 ms). In context of motion-position interactions this could allow motion information to enter the primary visual cortex via MT (i.e. from higher areas) around the same time as the information about the other features of the object coming from the anatomically earlier stages of processing.

1.2 Low-level and high-level (attention-based) motion

Motion processing as described above requires the stimulation of directionally selective neurons or other local motion detectors. However, this is not the only situation when motion is perceived. For instance, if a stimulus presented at one location alternates with another stimulus presented at a different location within an appropriate temporal and spatial interval, we perceive a single stimulus moving back and forth rather than two separate flickering objects (Wertheimer, 1912; Anstis, 1970, 1980; Kolers, 1972). This phenomenon is termed apparent motion, emphasising that the percept of motion here doesn't come from the summation of "real", velocity-based local motion signals. Instead, the object is identified and matched at a different locations across the time interval[1] (Anstis, 1980; Braddick, 1980). Cavanagh (1992) masked a drifting luminance grating with a superimposed color grating moving in the opposite direction. The bars of the luminance grating could not be perceived because of the masking, however, its motion signal was registered and it determined the perceived rotation of the entire stimulus. On the other hand, when the observers paid attention to the color grating, the perceived direction of motion followed the drift of the color bars. This stimulus convincingly demonstrated that low-level motion can be separated from attentive tracking.

Thus, motion can be classified as low-level if it is based on local motion detectors (Anstis, 1980; Braddick, 1980; Cavanagh & Mather, 1989; Julesz, 1971), or high-level if it is based on the tracking of the object's changing position (Cavanagh, 1992; Lu & Sperling, 1995; Seiffert & Cavanagh, 1998). Importantly, the low-level system does not need to know what is moving; it works directly with the motion signal. The high-level system, however, uses form and position as inputs, thus it is thought to emerge later in the processing. It has been argued that attention is the key for this tracking process (Wertheimer, 1912; Verstraten, Cavanagh & Labianca 2000). This is supported by neuropsychological data: patients with right parietal damage experience, among a variety of attentional difficulties, a large loss in the perception of

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[1] Apparent motion stimuli taking small steps relative to their size can still drive low-level detectors, however, at least a subset of apparent motion stimuli are supported by a higher-level mechanism (Verstraten, Cavanagh, & Labianca, 2000).

apparent motion (Battelli et al., 2001). Similarly, neurophysiological investigations show the involvement of higher parietal cortex in the representation of subjective motion percepts (Williams, Elfar, Eskandar, Toth & Assad, 2003).

High-level motion or attentive tracking is an independent system and not just an accumulator of low-level motion signals. In a way, attentive tracking is similar to smooth pursuit. When we lock our gaze on the target and follow it with our eyes the target has very little motion on the retina, however, we see it move. This perception of motion is provided by the signal responsible for the eye movement (the efference copy). Attentive tracking can be thought of as a "covert efference copy", providing the perception of motion when the eyes are not moving but attention is (Cavanagh, 1992; Cavanagh, Battelli, & Holcombe, 2014). A contrast sensitivity probe placed along the tracking path reveals smooth shift of sensitivity peak that accompanies attention-based motion, supporting smooth displacements of attention (Shioiri, Yamamoto, Kageyama, & Yaguchi, 2002). In fact, targets can be tracked even if they do not drive low-level motion signal.

Most moving stimuli engage both low-level and high-level motion systems. However, certain stimuli produce predominantly motion of one type. For instance, if the stimulus moves too fast and too unpredictably to be tracked, high-level motion processes are impaired (Verstraten et al., 2000; Murakami, 2001; Fukiage, Whitney, & Murakami, 2011). On the other hand, to test high-level motion perception while controlling for low-level motion, ambiguous stimuli are typically used, with the perceived direction of motion depending on the focus of attention (Shim & Cavanagh, 2005; Tse, Whitney, Anstis, & Cavanagh, 2011).

To conclude, motion processing is a complex process that involves a number of cortical and subcortical structures. Some of them are more specialised for motion, like MT, and some represent motion information despite being mostly involved in the processing of other features (like V4). Motion can also be perceived without the direct stimulation of local motion detectors with the help of an independent system: high-level motion or attentive tracking.

1.3 Motion-induced position shifts: theories and illusions

In this subsection I would like to introduce the family of motion-induced position illusions, discuss their main characteristics and potential explanations.

1.3.1 Fröhlich effect

In 1894, the Norwegian astronomer O. Pihl noticed that the initial percept of a moving target appearing in a window is not adjacent to the edge of the window, but instead is considerably displaced in the direction of motion. Later this effect was systematically studied by F. W. Fröhlich (1923). The illusion was originally used as a measure of "sensation time" – the delay between the physical presentation of the stimulus and the moment of its perception. Fröhlich reported multiple experiments, some of which presage more recent discoveries (reviewed in Kerzel, 2010).

Fröhlich effect has been described as a consequence of metacontrast masking (Pieron, 1935), cumulative lateral inhibition (Geer & Schmidt, 2006), attention shifts (Müsseler & Aschersleben, 1998), or a combination of metacontrast and attention (Kirschfield & Kammer, 1999). The pure metacontrast explanation suggests that each position of the moving stimulus entering the visual field is suppressed by the subsequent position of the same stimulus as it moves. The problem of this hypothesis is that it does not explain how the stimulus recovers from masking and becomes visible. Indeed, if masking were the only cause, the stimulus would only become visible at its offset, when it is no longer followed by the next position. To overcome this problem, Kirschfield & Kammer (1999) suggested that the motion onset triggered a shift of spatial attention, and the stimulus was only masked before this shift was completed. A similar explanation, not involving masking, was proposed by Müsseler and Aschersleben (1998). In their version of the attention-shifting explanation, the shift of focal attention is required for the stimulus to reach conscious awareness. Therefore, while the attention shift is under way, the stimulus isn't perceived. Both these accounts have a common problem: the Fröhlich effect is reduced but not eliminated even if attention is fully allocated to the onset position (Whitney & Cavanagh, 2000; Kerzel & Müsseler, 2002), and it is not clear what explains the remaining illusion. This problem will be discussed in more detail in section 2.1.

A less studied but related effect is onset repulsion. It was first described by Thornton (2002), and reported in a number of studies since then (Actis-Grosso & Stucchi, 2003; Kerzel, 2002; Kerzel & Gegenfurtner, 2004). Onset repulsion is the exact reversal of the Fröhlich effect: the onset position of the moving object is mislocalized opposite the direction of motion. This illusory shift is also smaller in size. Onset repulsion often replaces the Fröhlich effect when the uncertainty about the position of the upcoming target is high (Müsseler & Kerzel, 2004). This, and the fact that unlike the Fröhlich effect, onset repulsion is stable across target velocities, led to the conclusion that onset repulsion is a cognitive bias rather than a perceptual illusion. According to Kerzel (2010), in highly uncertain conditions observers retrospectively extrapolate the path of the suddenly appearing object, which leads to position errors in the opposite direction.

1.3.2 Displacement by internal motion

The Fröhlich effect is a transient illusion and can only be observed momentarily. However, some motion induced position shifts are stable displacements. Ramachandran and Anstis (1990) reported that random dots moving within a stationary window shift the edges of the window in the direction of motion. This effect is the strongest if textures within and outside the window are equiluminant, and if the window is observed as a "figure" rather than the "ground". Similarly, De Valois and De Valois (1991) reported that a grating drifting behind a stationary window appears shifted in the direction of the drift (Figure 1.2). Both illusions depend on the temporal and spatial frequencies of the stimuli, but are very pronounced in all the cases. They are detectable even at short motion durations (as short as 53 ms) and increase as a function of motion duration until a steady state is reached (Arnold, Thompson, & Johnston, 2007; Chung, Patel, Bedell, & Yilmaz, 2007).

There are other, probably related, cases where internal motion induces a position shift. For instance, radial internal motion influences the size of the object – internally contracting stimuli appear smaller than internally expanding ones (Whitaker, McGraw, & Pearson, 1999). In the stereoscopic world, motion towards the observer brings objects perceptually closer, and motion away from the observer makes them appear further away (Edwards & Badcock, 2003; Tsui, Khuu, & Hayes, 2007).

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Figure 1.2 Illusory displacement by internal motion. Left column shows physical positions of three Gabor patches, they are vertically aligned. Arrows represent the direction of the internal drift. Right column shows the perceived positions. The envelopes are shifted and are no longer perceived as aligned. Adapted from De Valois & De Valois (1991)

Two main hypotheses were put forward as possible explanations. First, the displacement could be caused by the anticipatory shift of the receptive fields of V1 neurons (Fu, Shen, Gao, & Dan, 2004). However, this is at odds with the finding that the illusion can be produced by global motion, which implies a later stage of processing (Mather & Pavan, 2009). Another hypothesis suggests that motion changes relative contrast such that the leading edge of the stimulus appears to be of higher contrast compared to the trailing edge. This change of contrast affects the visibility of the trailing part, creating an apparent position shift (Arnold et al., 2007; Tsui, Khuu, & Hayes, 2007). However, the contrast modulation might be too small to account for the full magnitude of the perceptual shift (Hisakata & Murakami, 2009).

1.3.3 Representational momentum

This example of the illusory position shift concerns the offset position of a moving stimulus. In the original paradigm of Freyd and Finke (1982) the observers viewed three discrete instances of a rotating rectangle, implying rotation in a consistent direction. After a brief retention interval, the fourth image appeared, which served as a probe. The observers had to judge whether the probe was the same orientation as the third inducer rectangle, and they were found to be biased in the direction of rotation (Figure 1.3). In other words, they remembered the offset position beyond the physical vanishing point. The same tendency was observed with the smooth motion (Hubbard & Bharucha, 1988). The representational momentum was found to be modulated by a number of factors including but not limited to velocity and direction of motion (Freyd & Finke, 1985; Hubbard & Bharucha, 1988), expectation about the future motion (Verfaillie & d'Ydewalle 1991; Johnston & Jones

2006) implied weight of the target (Hubbard, 1997), presence of landmarks (Hubbard & Ruppel, 1999), and the distribution of attention (Hayes & Freyd, 2002; Joordens et al., 2004; Munger & Owens, 2004). As the name of the illusion suggests, the mislocalization was attributed to the internalization of the physical principle of momentum (Finke, Freyd & Shyi, 1986). More recent theories include spatiotemporal coherence (Freyd, 1993) and anticipatory eye movements (Kerzel, 2005), however, all the existing explanations only partly account for the effect. It is important to note the representational momentum reflects the shift of the remembered position, and thus might not be fully a perceptual illusion.

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Figure 1.3 The original paradigm used in Freyd & Finke (1982). Observers are likely to choose probe B when asked about the offset position of the stimulus.

1.3.4 Flash-lag

The flash-lag illusion is perhaps the most known and the most extensively studied example of motion-position interaction. It can be produced using a variety of stimuli with a common theme: a briefly presented stationary object (flash) appears to lag behind a continuously moving stimulus (Figure 1.4). The illusion was first described by Metzger (1932) and was rediscovered by MacKay (1958), who demonstrated, among many other versions of the effect, that under a strobe light, the glowing tip of the moving cigarette appears to float ahead of its base. Many years later, Nijhawan (1994) reinterpreted the illusion, starting a new wave of flash-lag research. Over the years a number of theories have tried to explain the mechanism behind the illusion. However, most of them fail to fully account for the rich phenomenology of the flash-lag illusion. Below I will briefly describe the main explanations and their shortcomings.

`Motion extrapolation`

Nijhawan (1994) proposed that the flash-lag reflects predictions made by the visual system in order to overcome processing delays. Indeed, it takes up to 100 ms to process a visual stimulus, and in case of a moving object such a delay would lead to a considerable lag in the perceived position. Thus, it is necessary to extrapolate the

motion trajectory and predict the future position of the object using its prior trajectory. Since the position of the moving object is extrapolated, and the position of the stationary flash is not, they are perceived in misalignment. However, the data showed that if the motion is abruptly stopped right after the presentation of the flash (flash-terminated cycle, Eagleman & Sejnowski, 2000; Khurana & Nijhawan, 1995), the flash-lag is not observed. This doesn't fit the motion extrapolation hypothesis, since the target trajectory did not extrapolate beyond the vanishing point. By contrast, in the flash-initiated cycle (when motion onset coincides with the presentation of the flash) the illusion is observed (Eagleman & Sejnowski, 2000; Nijhawan et al, 2004), although motion extrapolation is not expected. Finally, if the moving target reverses direction at the time of the flash, it appears shifted in the post-flash direction, and not in the pre-flash direction as motion extrapolation theory would predict. Burr and Thompson (2011) suggest that if flash-lag was linked to neural delays, its magnitude would likely scale with latency. However, with low-luminance stimuli that have increased processing latencies (Purushothaman, Patel, Bedell, & Ogmen, 1998), the effect diminishes, which contradicts the prediction (Krekelberg & Lappe, 1999).

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Figure 1.4 Different flash-lag inducing displays. The left column shows the physical position of objects, and the right column - their perceived positions. In all cases, the flashed object appears to lag behind the continuously moving one. A. The target is the rotating bar, and the dashed lines flash when they are aligned with the bar. B. The target is an annulus moving along a circular path. The disk is flashed inside the annulus. C. The target is a bar moving along a linear trajectory. A similar bar is flashed next to the target when the two are aligned. D. Two vertically aligned bars move together, the third bar is flashed between them. Figure from Hubbard (2014).

More recently, the motion extrapolation theory was updated to accommodate the effects produced in the flash-initiated and flash-terminated cycles. For instance, Nijhawan (2008) proposed that the strong offset transient in the flash-terminated cycle masks the predictive extrapolation of the moving target. This hypothesis was supported by a number of studies showing that the reduced salience of the motion offset leads to forward shifts of motion endpoints (Maus & Nijhawan, 2006). Thus,

motion extrapolation theory is still considered, however, it needs a number of additional conditions and processes to account for the flash-lag data.

Differential latencies

An alternative theory proposed that flash-lag occurs because the moving object is processed faster than the flashed object. According to this theory, the position of the moving object is not actively predicted, but its representation is more up-to-date at any given moment due to faster neuronal latency (Whitney & Cavanagh, 2000; Whitney & Murakami, 1998; Purushothaman, Patel, Bedell, & Öğmen, 1998). The differential latency explanation accommodates some of the findings that were troublesome for the motion extrapolation account. It is consistent with the lack of overshoot when the moving stimulus abruptly reverses direction (Whitney & Murakami, 1998) and with the scaling of the flash-lag with the relative luminance of the moving object (Purushothaman et al., 1998). However, studies of temporal order judgement on flashed and moving stimuli revealed that flashes may in fact have a processing advantage (Nijhawan, Watanabe, Khurana, & Shimojo, 2004) or at least are processed equally fast (Eagleman & Sejnowski, 2000). Physiological data exist supporting both hypotheses. Neurons in macaque MT respond faster to transient stimuli (Raiguel, Lagae, Gulyàs, & Orban, 1989), whereas population activity in the cat primary cortex showed 30% reduction in processing time for the moving objects. Additionally, it is known that perceptual grouping (Watanabe, 2004) or semantic context (Nagai & Yagi, 2001) influence the flash-lag effect, which is hard to reconcile with simple latency. In sum, differential latency account has advantages over the simple motion extrapolation hypothesis; however, this difference in latencies might be more flexible than it was initially suggested.

Attention shifting

The attentional account of flash-lag effect (Baldo & Klein, 1995) is not dissimilar from the attention shifting explanation of the Fröhlich effect (Müsseler & Aschersleben, 1998). It is based on the assumption that attention is focused on the moving target, and upon the presentation of the flash an attention shift is initiated. While the shift is under way, the target continues to move. By the time attention lands on the flashed stimulus and it reaches awareness, the target has already travelled some

distance, which causes the perceived misalignment. Baldo and Klein (1995) supported this theory with a number of experiments that varied the distance between the moving object and flash. They found that when the initial focus of attention is farther away from the flash, larger flash-lag is perceived, presumably because attention shift took more time. In accord with this explanation, when the position of the flash is cued so that attention is directed to it before the flash is presented, the illusion is reduced (Baldo, Kihara, Namba, & Klein, 2002; Namba & Baldo, 2004; Chappell, Hine, Acworth, & Hardwick, 2006; Sarich, Chappell, & Burgess, 2007, although see also Khurana, Watanabe, & Nijhawan, 2000). However, without additional assumptions attention shifting explanation fails to account for the flash-lag in flash-initiated displays, where a shift from the motion to the flash is not required.

Temporal integration and postdiction

Temporal integration (also known as position integration) theory suggests that the current position of an object is estimated based on the positions it occupied over some period of time. For the flashed object the only position that counts is its actual position, whereas for the moving object the estimate also includes the positions it occupied after the flash, shifting the average ahead of the location of the flashed object (Krekelberg & Lappe, 1999, 2000; Krekelberg, 2001). Postdiction is a special case of temporal integration theory, which emphasises that the flash "resets" position integration, so that only the post-flash events account for the perceived target position. Once post-flash position averaging is complete, the information is used to "post-dict" the target position at the moment of the flash. This term reflects the fact that this proposed process is the opposite of motion prediction, since none of the pre-stimulus information is used, and the result of the motion processing is attributed backwards in time. More recently, Eagelman & Sejnowski (2007) updated the theory to the include not only flash-lag but also other motion-induced position shifts, and gave it the new name -- motion-averaging model. However, these theories too make predictions that are not observed in the data. For instance, Whitney and Cavanagh (2000) suggested that if the flash resets motion integration, a continuously moving objects accompanied by a repeatedly presented flash would never be perceived. Furthermore, as Nijhawan (2008) noted, given the identical processing delay of the moving object and the flash, for both objects to reach awareness simultaneously and appear misaligned, the moving object would need to perceptually speed up around the time of the flash, and

this is not observed in the data. Finally, temporal integration approach doesn't account for the forward displacements produced in the absence of the flashed stimulus (Fu, Shen, & Dan, 2001; Maus & Nijhawan, 2006; Shi & Nijhawan, 2012).

An interesting flash-lag related illusion occurs when instead of moving in physical space the target moves through the feature dimensions such as color, luminance or spatial frequency. For instance, when one disc is continuously changing color and another color-matched disc is briefly flashed nearby, the observers judge the color of the flashed disc to lag behind the color of the continuously changing item (Sheth, Nijhawah, Shimojo, 2000). A similar effect is observed with the streams of changing letters (Bachmann, Luiga, Poder, & Kalev, 2003).

To sum up, currently there is no universal agreement on the mechanism of the flash-lag effect. As Burr and Thompson (2011) conclude, the flash-lag effect possibly opened more questions than it has solved. However, this debate helped to shape major approaches to motion-induced mislocalizations and produced an abundance of empirical facts that a good theory of motion-induced shifts should be able to explain. A major drawback of this illusion is that the position judgment is necessarily relative between the stationary and the moving part of the stimulus, making the effects harder to interpret. More recently discovered motion-induced position shifts offer a more straightforward way to measure illusory displacements.

1.3.5 Flash-drag

In the illusions described above, motion shifted the perceived locations of objects directly concerned with this motion: containing it (displacement of kinetic edges) or producing it (Fröhlich effect, representational momentum). Whitney and Cavanagh (2000) showed for the first time that motion can shift the location of a distant object (Figure 1.5B). In their original paradigm a pair of lines was flashed on both sides of a rotating grating. These lines appeared misaligned in the direction consistent with the direction of rotation. This effect was observed even when the lines were quite far away from the moving stimulus (up to 35 degrees of visual angle). Note that the direction of flash-drag is opposite than that of flash-lag. In fact, the two shifts may even influence the position judgement simultaneously, with flash-drag diluting flash-lag (Whitney & Cavanagh, 2000; Eagleman & Sejnowski, 2007). Interestingly,

the largest flash-lag is observed not when the flash is spatiotemporally closest to motion, but when it is has a slight temporal lead (Durant & Johnston, 2004; Watanabe, Sato, & Shimojo, 2003; Watanabe, 2005). Whitney and Cavanagh (2000) suggested that flash-drag is a result of motion distorting visual space, and that the position of any object in the visual field takes into account dominant motion signal over a large area of space. Cai and Schlag (2002) suggested an alternative explanation whereby a flash is interpreted as an extension of the moving object itself. Overall, the discovery of the flash-drag effect shifted the theoretical focus behind the studies of motion-induced position shifts from "What is the difference between the coding of a stationary and a moving object" to "How does motion influence the localization of both stationary and moving objects".

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Figure 1.5. Stimuli configurations producing flash-lag, flash-drag and flash-grab illusions. Adopted from Kohler (2014)

1.3.6 Flash-jump

If a moving object suddenly changes one of its features, for instance its color, the location of the feature change is perceptually shifted in the direction of motion, or jumped ahead of its physical position (Cai & Schlag, 2001). Originally this was explained by asynchronous feature binding. The color change takes time to be processed and is eventually assigned to a later position of the moving stimulus. However, Eagleman and Sejnowski (2007) suggested that the position of the object at the moment of the change is dragged in the direction of motion because the transient of the change triggers the position averaging mechanism.

This illusion has interesting implications for the interpretation of the Fröhlich effect. If a feature change happens right after motion onset, within the portion of the trajectory normally covered by the Fröhlich effect, this feature change is nevertheless perceived, although shifted ahead to the start of the visible motion path. This means that the initial positions of the moving stimulus are not masked early in the processing stream.

1.3.7 Flash-grab

Flash-grab illusion occurs when an object is briefly presented on top of the moving background just as it reverses direction (Figure 1.5C). This illusion has two components: the shortened trajectory of the moving object and the perceptually shifted flash. Sinico et al. (2009) first demonstrated that when an object follows a linear or a circular trajectory in a repeating back and forth motion, the observers significantly underestimate the apparent extent of this trajectory. At the speed of $8°/s$ this underestimation reaches 35% of the total trajectory length. Cavanagh and Anstis (2013) showed that when a flash is presented at the location and at the time of the reversal, it is grabbed to the perceived location of the reversal (Figure 1.6). This illusory shift is larger than any of the effects described above; the flash can be shifted up to several degrees of visual angle and multiple times its size. Cavanagh and Anstis (2013) compare this illusion to the flash-drag effect and notice a few differences, the most important being that the flash-grab has sharp temporal tuning around the time of the reversal, whereas the flash-drag shows broad temporal tuning.

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Figure 1.6 Illusory trajectory shortening and the flash-grab illusion. Green dot represents a moving object. Red dots represents flashes presented at the endpoints of the trajectory. Black arrows represent the direction of motion, grey arrows – the direction of the illusory shift. Figure from Cavanagh & Anstis (2013)

1.4 Neural correlates of motion-induced position shifts

An important question about motion-induced position shifts is when and where in the brain the physical position of objects is altered by the motion signal. A number of physiological and neuroimaging studies addressed the time course and the locus of this interaction.

Some studies demonstrated motion-position interactions at the very early stages of visual processing. Berry et al. (1999) found that a moving wave of spiking activity in the population of rabbit retinal ganglion cells travels near the leading edge

of the moving stimulus, effectively anticipating its future positions. Spatiotemporal predictive mechanisms were also found on the retinal level in salamanders and mice (Schwartz, Harris, Shrom, & Berry, 2007). This anticipatory mechanism shifts the receptive fields of the neurons in early visual cortex along the motion trajectory (Fu, Shen, Gao, & Dan, 2004), possibly explaining shorter latencies for moving compared to the flashed stationary stimuli (Jancke, Erlhagen, Shöner, & Dinse, 2004; Subramaniyan et al., 2015). Hogendoorn et al. (2015) applied multivariate pattern classification to electroencephalography recordings in order to reveal the time course of the motion-position interaction in flash-grab effect. The results showed that the direction of the illusory shift is evident in the very first cortical response to the stimulus, suggesting very fast interaction.

Another group of studies suggests that key events responsible for motion-induced position shifts happen further along the processing pathway. In an fMRI experiment Maus et al. (2013) compared patterns of activity produced by flash-drag stimuli and by physically shifted flashes in the absence of motion. They demonstrated a motion-induced change in areas MT and V3A but not in V1-V3, suggesting a relatively late locus of interaction (Figure 1.7). As previously shown, area V3A is also involved in predictive processing of motion. Activation in this area is higher for motion toward the region of interest than for the motion away from it, indicating a predictive shift in the representation of the moving object (Maus, Weigelt, Nijhawan, & Muckli, 2010). Additionally, disrupting processing in area MT by the means of transcranial magnetic stimulation (TMS) reduces the size of motion-induced position shifts, whereas applying TMS to V1 does not affect the illusion (McGraw, Walsh, & Barrett, 2004; Maus, Ward, Nijhawan, & Whitney, 2013).

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Figure 1.7. Correlations between the neural representations of the motion-induced shift and the neural representation of the physically shifted flash. High correlation values indicate that the neural representation is biased in the direction of the perceptual shift. Figure from Maus et al. (2013)

It is not always clear whether and how motion-induced changes in neural activity correspond to the perceptual effects. For instance, motion-induced position shift can affect the location of tilt aftereffect, a process known to be driven by V1 cells (Kosovicheva et al., 2012). However, this shift, although reliable, is much smaller than the corresponding perceptual mislocalization. Sundberg et al. (2006) reported a shift in the receptive field of V4 neurons associated with the flash-jump illusion. However, this shift was present even in the flash-terminated condition, where the position of the flash is perceived veridically. Finally, position shifts driven by internal motion (De Valois & De Valois, 1991) produce systematic displacements in the retinotopic representation of stimuli seen in fMRI activation patterns, however, the direction of these shifts is opposite that of internal motion (Whitney et al., 2003).

Overall, the train of neural events leading to motion-induced position illusions remains a mystery. Although the early anticipatory mechanisms have been explored in more detail, they do not seem to correspond to the perceptually observed effects. On the other hand, the evidence for the involvement of areas MT and V3A is abundant, but the time course of this interaction and whether the motion signal is a part of the feedforward or the feedback stage of processing (Lamme & Roelfsema, 2002) remains unclear.

1.5 Attention and motion-induced position shifts

The role of attention in illusory displacements has been discussed almost as long as the illusions themselves. There are two main lines of research using attentional manipulations to uncover the mechanisms of motion--position interactions. The first, historically earlier, idea is that at least some of the motion-induced position shifts are created by the shifts of spatial attention. This explanation is purely temporal, implying that the shifts of attention delay perception, which, given a dynamic scene, results in a dissociation between the physical and the perceived position of the attention-grabbing object. As mentioned in the previous section, attention-shifting explanations have been explicitly proposed for the Fröhlich effect (Müsseler & Aschersleben, 1998) and the flash-lag illusion (Baldo & Klein, 1995). Besides, attention shifts could be a driving mechanism behind more general processes

underlying, for instance, the differential latency hypothesis (Whitney, 2013). The second line of attention-related research is concerned with the contribution of attentional tracking to the motion-induced shifts. In these studies, the illusions are measured either under the conditions where attention tracking is unavailable, or, conversely, where it is the only possible source of the displacement (i.e. in the absence of low-level motion). The underlying motivation here is to link the illusion to the high-level or the low-level motion and infer the origin of the effect based on the involvement of attention. These two definitions of attentional influence produced largely non-overlapping sets of studies. The main findings related to both of them are reviewed below and summarized in Table 1.1

1.5.1 Are motion-induced position displacements caused by the shifts of attention?

The ability to orient in space is an important feature of attention, allowing us to efficiently distribute limited attentional resources throughout the visual space. There are several metaphors describing the focus of visual attention: spotlight (Posner, 1980), zoom lens (Eriksen & Yeh, 1985), Gaussian gradient (Downing & Pinker, 1985). Although different metaphors highlight different features of attention, there is a general agreement that attention enhances processing of stimuli within its scope, and that the focus of attention can flexibly change its location and size (Carrasco, 2011). The shifts of attention can be active/voluntary or passive/involuntary. The explanations of motion-induced position illusions depend on involuntary (or exogenous) shifts triggered by a salient object, in this case, a flash. Exogenous attention is characterised by the fast deployment towards the target and quick decay, with a peak of enhancement at around 100 ms after stimulus onset (Muller & Rabbitt, 1989; Johnston, & Yantis, 1992).

In order to estimate the contribution of attention shifts to motion-induced mislocalizations, a number of studies used paradigms that force attention to predictively relocate towards the future position of the target. This can be accomplished either by presenting cues that reveal the location of interest before the onset of motion, or by using highly predictable stimuli and always showing targets where they are expected to be. The idea is that if attention is already shifted to the area where the target will appear, the attentional delay and the resulting

mislocalization will be minimised. To preview, in the majority of studies these procedures indeed result in the reduction of motion-induced position shifts.

Namba and Baldo (2004) measured the flash-lag effect in three probability conditions: when the target was always presented at the same location, when it alternated between the two locations in a predictable way, or when it appeared at random positions. The results showed that in the two former conditions the flash-lag was smaller than in the latter. In the next experiment a cue indicated with 80% validity the hemifield where the target would subsequently appear. The flash-lag effect was smaller following the valid compared to the invalid cue. Similar pattern of results was demonstrated in a number of different flash-lag stimuli (Brenner & Smeets, 2000; Rotman et al., 2002; Shioiri et al., 2010). Müsseler and Aschersleben (1998) tested the attention-shift component of the Fröhlich effect by cueing the hemifield where the motion onset should be expected. They found that the apparent shift of the motion onset was equally large in the conditions where the cue was invalid and where no cue was presented. However, when the cue indicated the correct hemifield, the illusion was reduced. Another argument in favor of the attention-shifting explanation is that flash-lag increases with the distance between the moving stimulus and the target, suggesting that longer shifts result in larger illusion (Baldo & Klein, 1995; Baldo, Kihara, Namba, & Klein, 2002; Kanai et al., 2004).

In a related group of studies attention is manipulated in a different way: instead of misdirection, attention resources are limited by adding distracting stimuli or tasks. Representational momentum increases in the presence of irrelevant distractors (Hayes & Freyd, 2002; Munger & Owens, 2004). Similarly, flash-lag effect is larger when subjects perform multiple tasks or attend to multiple targets (Sarich et al., 2007; Shioiri et al., 2010). The modulation by attention load suggests that accurate localization is not automatic and requires allocaton of processing resources.

Overall, these studies suggest that delayed attention shifts result in larger position illusions, as predicted by attention-shifting explanation. However, there is an important caveat: valid cues or predictability reduce the illusions but do not eliminate them completely. Both flash-lag and Fröhlich effect are observed even when the need for attentional shift is minimised. Of course, there could always be a corrective attention shift or an additional time-consuming reallocation process explaining the residual illusion, however, it is not clear whether attention shifts are the primary cause of perceptual shifts, or if they just modulate the illusions.

1.5.2 Do motion-induced position shifts require attention?

As discussed in the previous section, attentional tracking is an independent mechanism responsible for the selection and individuation of targets. Attentional tracking maintains the representation of objects while they change and move around (Pylyshyn, 1989; Cavanagh, Hunt, Afraz, & Rolfs, 2010). Multiple targets can be tracked together (Pylyshyn & Storm, 1988), however, there are limits on the number of targets as well as on their speed (Alvarez & Franconeri 2007). The temporal limit of tracking is about 4-8 Hz (Verstraten, Cavanagh, & Labianca, 2000).

Studies measuring separate contributions of low-level and high-level / attentional motion to the illusory displacements fall into two categories. The first group of studies is testing whether the illusions require low-level motion, or the high-level motion can produce them on its own. For instance, Watanabe, Nijhawan, and Shimojo (2002) demonstrated that an object moving behind a narrow, one pixel wide, slit, could produce the flash-drag effect. Watanabe, Sato, and Shimojo (2003) reported flash-drag induced by a moving object completely invisible behind an occluder. Flash-drag also occurs during apparent motion (Shim & Cavanagh, 2004) or transformational apparent motion (Whitney, 2006). In all these cases the low-level motion signal is minimized, and attentional tracking predominantly drives the illusion. Importantly, when the direction of motion is ambiguous, the illusory shift follows the attentively selected direction. This was demonstrated using a bistable apparent motion (Shim & Cavanagh, 2005) and a stimulus containing superimposed transparent textures rotating in opposing directions (Tse, Whitney, Anstis, & Cavanagh, 2011, Figure 1.8).

The second group of studies asks a complementary question: whether the motion-induced position shifts require attentional tracking, or they can happen preattentively. Murakami (2001) was the first one to use random motion sequence for answering this question. In the random motion stimulus, moving bars are displaced randomly and at a very rapid rate, thus the direction and the velocity of motion are completely unpredictable and impossible to track or attend to. Without attentional tracking, random motion can produce a flash-lag effect (Murakami, 2001) as well as a flash-drag effect (Fukiage, Whitney, & Murakami, 2011).

Figure 1.8. Flash-grab produced by voluntary attentional tracking. (a) Two transparent textures are superimposed and rotate in the opposite directions, observers track either white or black spots. (b) Physical position of the target flashes. (c) Perceived position of the targets if black spots were tracked. (d) Perceived position of the targets if white spots were tracked.

Linares and Lopez-Moliner (2007) measured flash-lag in a display containing a large number of dot pairs where half of the dots were moving continuously, and half of the dots were flashed. When the observers were asked to judge the global structure of the stimulus, flash-lag was not observed, whereas judging the structure of local dot pairs led to illusory displacement. This result contradicts the findings of Murakami (2011) and Fukiage et al. (2011), by suggesting that the presence of motion is not sufficient for producing position shifts. Similarly, Cavanagh and Anstis (2013) found that motion-induced shifts observed for individual motion trajectories are larger than those seen when multiple trajectories are presented together. Their interpretation was that position shifts require attention: when the individual trajectories cannot be tracked, the illusion disappears. Finally, de Vito et al. (2015) studied the flash-grab illusion in visual neglect patients. These patients demonstrate attention deficit in the left visual field. When the flash-grab stimulus was presented in their top, right or bottom hemifield, neglect patients experienced illusion of the same size as controls. However, in their affected, left hemifield the flash was perceived at its veridical location, suggesting that attention is crucial in generating motion-induced position shifts.

Overall, the majority of studies agree that preallocation of attention to the target reduces the motion-induced position shifts, and that attentional tracking is capable of producing the mislocalizations even in the absence of real directional motion. However, the extent of attentional contribution to the motion-induced position shifts remains controversial. Some studies suggest that attention is a requirement, and without it the displacements are not perceived. Other studies demonstrate the illusions even under the conditions where attentional involvement is impossible. The present work attempted to a) evaluate the contribution of attention to

motion-induced attention shifts and b) examine the relationship between attention-shifting and attentional tracking.

Table 1.1. Summary of the attentional studies of motion-induced position shifts

Illusion	Is attentional tracking sufficient?	Is attentional tracking required?	Does allocation of attention modulate the illusion?
Flash-lag	Yes (Schlag, 2000)	No (Murakami, 2001) Yes (Linares & Lopez-Moliner, 2007)	Yes (Brenner & Smeets, 2000; Rotman et al., 2002; Shioiri et al., 2010; Namba & Baldo, 2004)
Representational momentum	Yes (Freyd & Finke, 1984)	Yes (Kerzel, 2003)	Yes (Hayes & Freyd, 2002; Munger & Owens, 2004)
Fröhlich effect	Yes (Watanabe, Matsunaga & Kitaoka, 2010)	*Yes (Section 2.1)*	Yes (Müsseler & Aschersleben, 1998)
Flash-drag	Yes (Shim & Cavanagh, 2004; Whitney, 2006; Watanabe et al., 2002, 2003)	No (Fukiage et al., 2011)	--
Flash-grab	Yes (Tse et al., 2011)	Yes (Cavanagh & Anstis, 2013; De Vito et al., 2015)	*Yes (Section 2.2)*
Flash jump	Yes (Eagleman & Sejnowski, 2007)	–	--

1.6 Overview of the experimental contributions

Based on the evidence reviewed in the introduction, the following questions were formulated and addressed in the empirical part of the dissertation:

1. **Are motion-induced position displacements created by the shifts of attention?**
Previous studies suggest that attention modulates illusory displacements, but even when the need for attention shifting is minimized, the illusions, although smaller, are perceived. Experiments 1 and 2 of the section 2.1 explore how attention shifts influence the Fröhlich effect. In Experiment 1 we replicate previous findings by Müsseler & Aschersleben (1998) with a novel stimulus, confirming that attention shifts contribute to the Fröhlich effect. In Experiment 2 we parametrically modulate the delay of attention's arrival to further test the predictions of attention-shifting hypothesis. We demonstrate that the later attention arrives to the moving target, the the more the onset position is shifted along its path. Section 2.2 extends these findings to the flash-grab illusion.

2. **Is attentional tracking required for motion-induced position shifts?**
Previous studies have yielded contradictory results. Experiments using stimuli with multiple elements suggest that targets need to be individuated in order to be predictively shifted. However, experiments using random motion sequences demonstrate flash-lag and flash-drag illusions produced by unexpectedly moving stimuli. Additionaly, if focused attention is the cause of motion-induced shifts, how can this be reconciled with the reduction of the illusion when attention is validly cued? In Experiment 3 of section 2.1 we modify the stimulus tested in the previous experiments and compare the Fröhlich effect produced when the targets are observed individually and as a group. This manipulation allows testing the involvement of attentional tracking using a stimulus that is as similar as possible to the one in the cueing experiments, and in the absence of attention shifts. We find that attention to

the group dramatically reduces the Fröhlich effect, suggesting that motion-induced shift is an active process that operates on an individually tracked target.

3**. Where does the motion-induced shift occur in the processing stream?**

Studies offer evidence for both early and late involvement of motion in determining where the target will be perceived. In section 2.3 we test whether the motion-induced shift operates equally on all components of a visual form. We incorporate canonical shapes in a flash-grab stimulus and ask whether the shift is uniform for all the features of the shape. This procedure demonstrates that the shift operates early in the processing stream, before the shape binding is completed.

Part II. Experiments

2.1 Fröhlich effect and delays of visual attention

Abstract

In the Fröhlich effect, the initial position of an object that suddenly appears in motion is perceived as being shifted in the direction of its motion. Here we establish that this shift is not an obligatory consequence of motion, but it is driven by focused attention. In Experiment 1 using different cueing conditions, we found that invalid cues produced larger perceptual shifts, although the Fröhlich effect was still present for valid and neutral cues. These results support Müsseler and Aschersleben's (1998) proposal that the Fröhlich effect is the result of the time it takes to shift focal attention to the moving stimulus. In Experiment 2 we found that the Fröhlich effect increased when the valid cue arrived more than 100 ms after the start of motion, suggesting again that a delay in attention's arrival shifted the location of the perceived motion onset. In Experiment 3 we compare the motion-induced shifts when the subjects attended to a set of moving stimuli as a group and when they attended to an orientation singleton. We showed that Fröhlich effect was only present when the target was individuated and disappeared when the stimulus was perceived globally. We conclude that the Fröhlich effect is a predictive spatial shift produced and modulated by focal attention.

2.1.1 Introduction

Localizing objects in space is one of the central functions of the visual system. When an observer or a target is moving, the motion of the eye or the object can be

taken into account to compute the current object locations. Indeed, it has been shown many times that visual motion can strongly influence the perceived position of an object. For example, a stationary patch containing moving texture (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990), a flash presented on (Cavanagh & Anstis, 2013) or next to (Whitney & Cavanagh, 2000) a moving texture, and even the onset and offset positions of the moving targets (Fröhlich, 1923; Freyd & Finke, 1984) are perceived as shifted in the direction of motion. In this paper we address attention's role in producing these motion-induced position shifts.

One of the most basic and longest known motion-induced position shifts – a shift of the perceived onset position of a moving stimulus – is now referred to as the Fröhlich effect (Fröhlich, 1923). The original finding showed that a strip of light travelling across a screen is not seen first at the edge of the screen, but farther into it. Over the decades a number of explanations for this effect have been presented, including attention delay (Müsseler & Aschersleben, 1998) and metacontrast masking (Kirschfeld & Kammer, 1999; see Kerzel, 2010 for a review). The attention delay explanation claims that the Fröhlich effect results from the lack of conscious representation of the stimulus before attention arrives so that any delay in shifting attention to the moving stimulus creates a displacement in its perceived starting location. To test this, Müsseler and Aschersleben cued one of two locations briefly (120 ms) before motion onset and then presented a moving stimulus at only one of the locations. A valid cue decreased the Fröhlich effect compared to an invalid cue and a no-cue condition. Note that Müsseler and Aschersleben (1998) do not assume that the invalidly cued location is unattended, but instead that attention is delayed in getting there as it starts first at the cue location and then switches to the uncued location. Their result was therefore in line with attention delay explanation. Additionally, Whitney and Cavanagh (2000) showed that when a static object is presented for 2500 ms, then removed for 30 ms and immediately presented in motion, the "invisible" part of its trajectory is significantly reduced. Both these results suggest that if attention is already at the position where the motion is about to start, there is less motion-induced position shift.

Nevertheless, some studies of motion-induced position shifts show a different effect: smaller or no illusion in the case where attention is not focused either initially or eventually on individual moving stimuli. For instance, Linares and López-Moliner

(2007) tested mislocalizations of moving dots relative to static ones (flash lag) when attention was directed to the global shape created by a field of many dot pairs. In each dot pair of the 400 that were presented one dot was in motion and the other one was static and flashed briefly. When their participants attended to the global shape created by all the dot pairs, they did not report any illusory misalignment. Cavanagh and Anstis (2013) reported a similar loss of motion-induced position shift with multiple stimuli. When observers had to judge the length of the trajectory of a single moving dot, they consistently underestimated it. However, when this same judgment was made about multiple, asynchronously moving dots that could not be individually tracked, no such underestimation happened. Both of these studies compared focused attention to an individual item to attention distributed across a group of items and both reported improved localization performance (decreased illusion) with distributed attention. These results suggest that the effect of motion on position is not obligatory but arises only when attention is focused on individual trajectories. This would seem to be at odds with the results of the cueing experiment where a longer delay in attention's arrival at the motion onset position leads to more motion-induced position shift. With global attention to a set of trajectories, attention never actually focuses on any individual motion path and one prediction might therefore be that a very large position shift should be seen in this case, rather than the absence of any shift that is observed.

Given these apparently contradictory results, the question of whether and how attention modulates the localization of motion onset remains open. The current paper attempts to reconcile the two accounts by exploring how the Fröhlich effect varies as a function of attentional delay and as a function of group versus individual attention using the same stimuli for both manipulations. In Experiment 1 we replicate the cueing results of Müsseler and Aschersleben (1998), showing that invalid cues produce a stronger Fröhlich effect, supporting the attention delay hypothesis. In Experiment 2 we vary the delay between the cue and the motion onset, showing a larger Fröhlich effect for cues arriving more than 100 ms after the motion onset. Finally, in Experiment 3 we test multiple Fröhlich stimuli and show that with attention to the group of stimuli, no motion-induced position shift is seen whereas with attention to one of the stimuli, the effect is present.

Based on our results, we suggest that the shift in the perceived onset of a moving stimulus is an active process that is engaged only when attention is directed to an individual target in motion. We will link this to the corrections in position necessary whenever eye movements must be made to a moving stimulus. We call this the "saccade intercept hypothesis" where every attended target is naturally a potential saccade target, linking covert attention to overt attention. As a practical detail, any eye movement to a moving target must compensate for the movement of the target after the saccade has been programmed, as the target keeps moving during the saccade. So its position representation must be extrapolated ahead along the path of movement.

We assume that this extrapolation along the motion path is made for each tracked target whether or not a saccade is eventually made to it. Previous studies of simple moving targets have shown that the perceived location of, and saccades to the target both show this extrapolation effect (Nijhawan, 1994; Khurana & Nijhawan, 1995; Etchells, Benton, Ludwig & Gilchrist, 2010). This predictive shift extrapolates the perceived location to match the position to which the saccade must be targeted in order to accurately intercept the moving object. We assume that this extrapolation is the origin of the Fröhlich effect. When attention is delayed in reaching the target to begin tracking it, additional extrapolation is required and the Fröhlich effect increases. In contrast, when attention is directed to a set of moving stimuli, none of the trajectories is attentively tracked, none of them can be individual saccade targets without further processing, and the predictive shift is not engaged. These suggestions and the evidence behind them are presented in more detail in the General Discussion section.

2.1.2 Experiment 1.

Müsseler and Aschersleben (1998) showed that delay of arrival of endogenous attention at the location of the motion shifted the visible onset of the motion ahead along its path. Here we extend this finding using the stimulus based on the one used by Kirschfeld and Kammer (1999), namely, a rotating rod inside a circular placeholder. We arranged eight placeholders in a circle, as shown in Figure II.1.1, which allowed us to cue the placeholder where the stimulus was about to appear (by briefly changing the color of the ring) without cueing the onset angle itself. Independent control over the to-be-reported feature (onset angle) and the direction of

cueing is a major advantage of this stimulus. We tested the onset localization accuracy with valid, invalid and uninformative cues. In line with the attention-shifting explanation we predicted that invalid cues would yield larger localization errors than valid and neutral cues.

2.1.2.1 Method

Participants

Eight healthy adults took part in the experiment (three male, mean age = 26.2 years, SD = 2.4, with a range of 22 to 34), including one author (S3). Two subjects (S3 and S5) were experienced psychophysical observers.

A power analysis was carried out in order to determine the sample size we used for the experiments. On the basis of the mean effect size (in the attentional manipulation) from the study of Müsseler and Aschersleben (1998) and our own pilot data ($\eta2$ = .5) a minimal sample size of 4 is required to obtain statistical power of .95 in a within-subject ANOVA with 4 levels of dependent variable. However, since we also planned to run pairwise comparisons of conditions, we chose a sample size of 8, which allowed us to detect the expected effect (dz = 1.6) in a two-tailed t-test with the power of .95.

All participants in this and following experiments reported normal or corrected-to-normal vision. All participants gave informed consent in writing prior to participation and the protocols for the study were approved by the Université Paris Descartes Review Board, CERES, in accordance with French regulations and the Declaration of Helsinki. They were compensated 10€ per hour for their time.

Stimuli

In all the experiments stimuli were displayed on a gamma-corrected LaCIE Electron monitor (100 Hz, 1024*768 resolution) controlled by a Mac Pro running MATLAB 7.1 (The MathWorks, Inc.) using Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Head position was held constant using a chin rest and a forehead bar at a viewing distance of 57 cm. Experiments were conducted in a darkened room. On each trial participants fixated a small point in the middle of the screen filled with black background (CIE Yxy 2.3 cd/m^2, .2, .19), and covertly monitored eight white circles

(placeholders) each subtending 5° of visual angle evenly distributed around the fixation point at an eccentricity of 8° (CIE Yxy 75.6 cd/m^2, .28, .30). After a random delay (500-700 ms) either none, one, or all placeholders briefly (for 50 ms) changed color from white to pink (CIE Yxy 13.0 cd/m^2, .35, .22). After a 50 ms blank period, a target – a sector covering 1° rotation – appeared inside one of the placeholders and rotated clockwise. The starting position of the target varied from -60° to 60° relative to the upper vertical radius of the placeholder, and the target disappeared once it reached the lower vertical radius. With the rotation speed of 0.9 revolutions per second, the average target presentation time was 450 ms. A response screen appeared immediately after target offset. Participants indicated whether they saw the target appearing to the left or to the right of the upper vertical (regardless of the placeholder) by choosing one of two response keys on the standard keyboard.

Procedure

We tested four conditions – Valid Cue, Invalid Cue, All Cued and None Cued. All Cued and None Cued conditions were presented as separate experimental blocks, while the trials with Valid and Invalid Cues were presented in a randomly permuted order as one block. The trial sequence is shown in Figure 2.1.1. During the Valid/Invalid cueing block, only one placeholder was cued on a given trial. In 75% of the trials the cue was valid, that is, the target subsequently appeared in the cued placeholder. In 25% of the trials the cue was invalid, and the target appeared in one of the seven uncued placeholders. In All Cued condition all eight placeholders were simultaneously cued on each trial, followed by only one target. In None Cued condition no cues were presented. Given that the initial fixation period was jittered (500 to 600 ms), our None Cued condition represented the situation when neither location nor timing of the motion onset was cued. It is important to note that the cues only specified information about the location of the target, not about its onset angle.

For all conditions the target position (one of the eight placeholders) and the onset angle (-60° to +60° off the vertical in 20° increments) were counterbalanced within blocks. Following a two-alternative forced choice (2AFC) method of constant stimuli, observers were asked to judge whether the target appeared to the left or to the right of the upper vertical radius, regardless of the position of the target on the screen. Conditions were presented in separate blocks within one testing session, the order of

the blocks was randomized between subjects. In total, participants ran 280 trials per condition for the Invalid Cue, All Cued and None Cued conditions, and 840 trials for Valid Cue condition. Participants were encouraged to take short breaks between the blocks and every 40 trials.
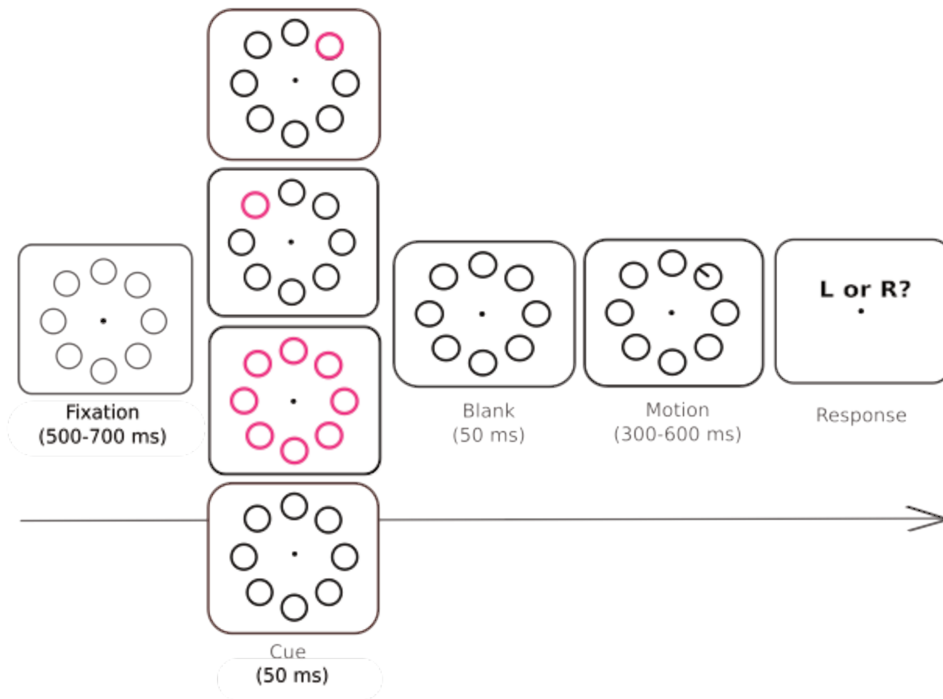
Figure 2.1.1. Experiment 1 trial schematic. Each trial started with a jittered fixation period, followed by a cue (a brief change in color of one or more placeholders). The cue could be predictive of a future target location (valid cue, 75% trials) or invalid (25% trials). In the separate blocks, the cue could be uninformative (all placeholders cued) or absent (no change in any of the placeholders). Following a 50 ms blanking period, one rotating target was presented, its onset angle varied according to the method of constant stimuli. The target was on until it reached the lower vertical radius of the placeholder, after that it disappeared and subjects were asked to judge the onset angle of the target. Stimuli are not drawn to scale; in the real experiment the contrast was reversed (white stimuli on black background).

2.1.2.2 Results

The perceptual onset shift (Fröhlich effect) was measured individually for each condition, resulting in four estimates: a) Valid Cue, b) Invalid Cue, c) All Cued, d) None Cued. Participant responses as a function of onset angle were fitted with logistic functions using *quickpsy* package for R (Linares & López-Moliner, 2015), and points of subjective equality (PSEs) were calculated for each condition. Here we assume that PSE reflects the onset angle that is perceived as vertical (although see Weiß & Scharlau, 2011, for a discussion of whether PSEs are an accurate measure of temporally uncertain percepts).
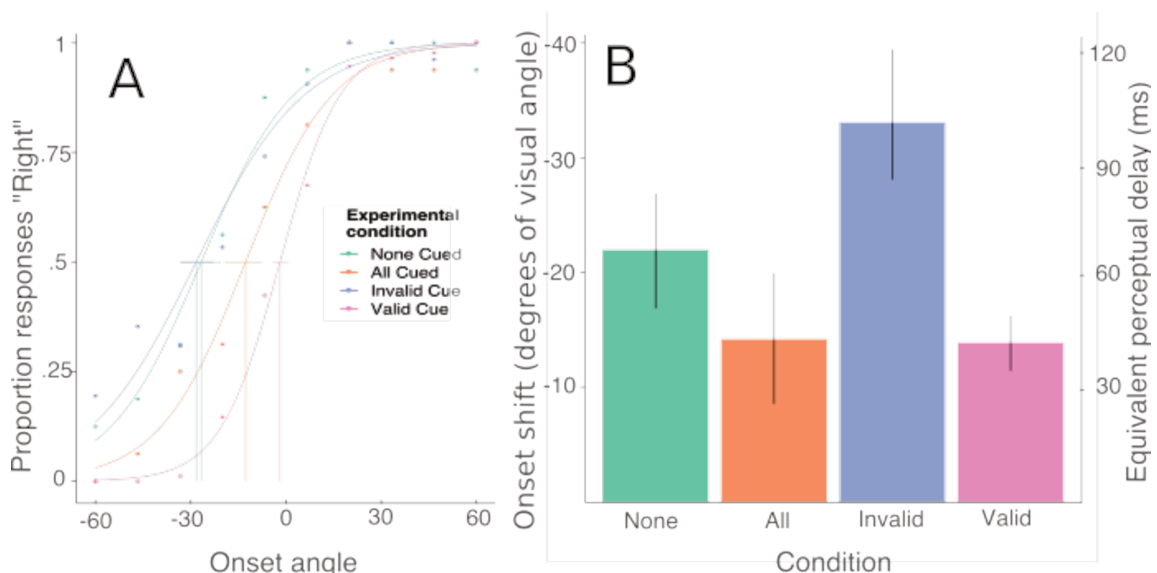
Figure 2.1.2 Results of Experiment 1. Panel A shows example Fröhlich effect measurement data from one subject, Panel B shows Fröhlich effect sizes for all conditions (n=8). The shift (error) in degrees is the distance travelled by the target at the speed of 0.9 revolutions per second. Error bars on both panels represent 95% CIs.

Figure 2.1.2A shows individual data from one observer. All but one of the 8 observers demonstrated the same pattern of results. If attention shifts are a part of the mechanism generating Fröhlich effect, the localization error should be larger (PSE will be shifted further away from zero) in the Invalid Cue condition compared to the Valid Cue condition and baseline conditions (All Cued and None Cued), and/or smaller (PSE closer to the zero) in the Valid Cue condition compared to the baseline.

As shown on the figure 2.1.2B, the "Invalid Cue" condition yielded the largest localization shift. A one-way repeated measures ANOVA revealed a significant difference between conditions ($F(3,21) = 9.54$, $p < .001$, $\eta^2 = .58$). Post-hoc pairwise comparisons confirmed that invalid cues resulted in larger Fröhlich effect compared to valid cues, and to "All Cued" (but not "None Cued") baseline conditions ($p = .009$, $p = .007$ and $p = .65$ respectively, with Bonferroni corrections). The magnitude of shift in the Valid Cued condition did not differ significantly from either of the baselines ($p = .72$, $p = .99$ for "None Cued" and "All Cued" respectively), however, it did differ significantly from zero ($M = -13.94$, $t = -3.65$, $p < .001$). These findings replicate the original Müsseler and Aschersleben (1998) results, providing additional information regarding the source of the attentional effect. Taking the uninformative cue ("All Cued" condition) as baseline, we confirm that it is the cost of the invalid cue rather than the benefit of the valid cue that drives the observed difference. Additionally, the "None Cued" condition demonstrates that temporal predictability of motion onset is an important factor in localization accuracy — when the start of the trial is not well defined temporally, localization is shifted. However, even in the Valid Cue condition Fröhlich effect was still present.

2.1.2.3 Discussion

We find that invalid cues increase the magnitude of the Fröhlich effect compared to the neutral (All Cued) condition. We reproduced the attentional effect first reported by Müsseler and Aschersleben (1998) in a paradigm that allowed cueing of spatial location (placeholder) but not the exact representation (onset angle) of the upcoming stimulus.

Alongside the cue-to-baseline comparisons, we replicated another previously reported finding. Although reduced by the cueing manipulation, the Fröhlich effect was not eliminated in any of the conditions. Even a validly cued target onset was perceived as shifted by about 14° of rotation (equal to a perceptual delay of 35 ms). If the delay of attention's arrival is the cause of the shift in the moving target's onset, our result suggests that this delay is longer than 100 ms (the cue-target stimulus onset asynchrony, SOA, that we used). Since our placeholder cue only indicates the region of the moving stimulus but not its actual start position, there may be a small additional delay as attention moves in from the overall region to the specific start location. As

explained in the introduction, we assume that the critical delay in producing the Fröhlich effect is not just the delay of attention in arriving at the target but also the time a saccade would then need to land on the target, if one were executed. This extra delay to compensate for (potential) saccade programming is in addition to any attentional delay in selecting the target and may be part of the explanation of the residual Fröhlich effects when the target is already attended. To examine the time course of attention-modulated position shifts, we next manipulate the timing of attention shifts by the means of different cue-to-motion onset intervals. According to the strict attention delay hypothesis, the later attention arrives, the larger the portion of the trajectory that will be omitted.

2.1.3 Experiment 2

In Experiment 2 we measured the Fröhlich effect as a function of cue to motion onset SOA. Having established in Experiment 1 that invalid cues increase the shift in localization, we now explore whether this effect is linearly associated with attentional delay using only validly cued targets. We manipulated cue-target SOAs such that the cues could appear both before (pre-cues) and after (post-cues) the target onset. If the Fröhlich effect is the result of the delay in attention reaching the cued moving stimulus, it should also increase with the additional cue-motion delay, now for the validly cued target.

2.1.3.1 Method

Participants

Nine healthy adults took part in the experiment (two male, mean age = 23.9 years (SD = 2.36) with a range of 18 to 30). Three subjects (S1, S3 and S4) were experienced psychophysical observers, but were naive to the purposes of the experiment, two subjects (S1 and S2) also participated in Experiment 1. Data of two subjects were removed because of the self-reported failure to understand the instructions, leaving data of seven subjects for analysis. As noted in the Participants section of Experiment 1, this sample size allowed us to detect the effect of attention with enough statistical power.

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Stimuli
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Stimuli were the same as in Experiment 1 with the following changes. As shown in Figure 2.1.3, moving bars appeared in all the placeholders on each trial. However, only one of them was the target, the others served as distractors. The target placeholder was cued at one of the tested SOAs (-300 ms to 300 ms relative to motion onset in the increments of 100 ms), signaling to the subject which of the moving objects they have to report.
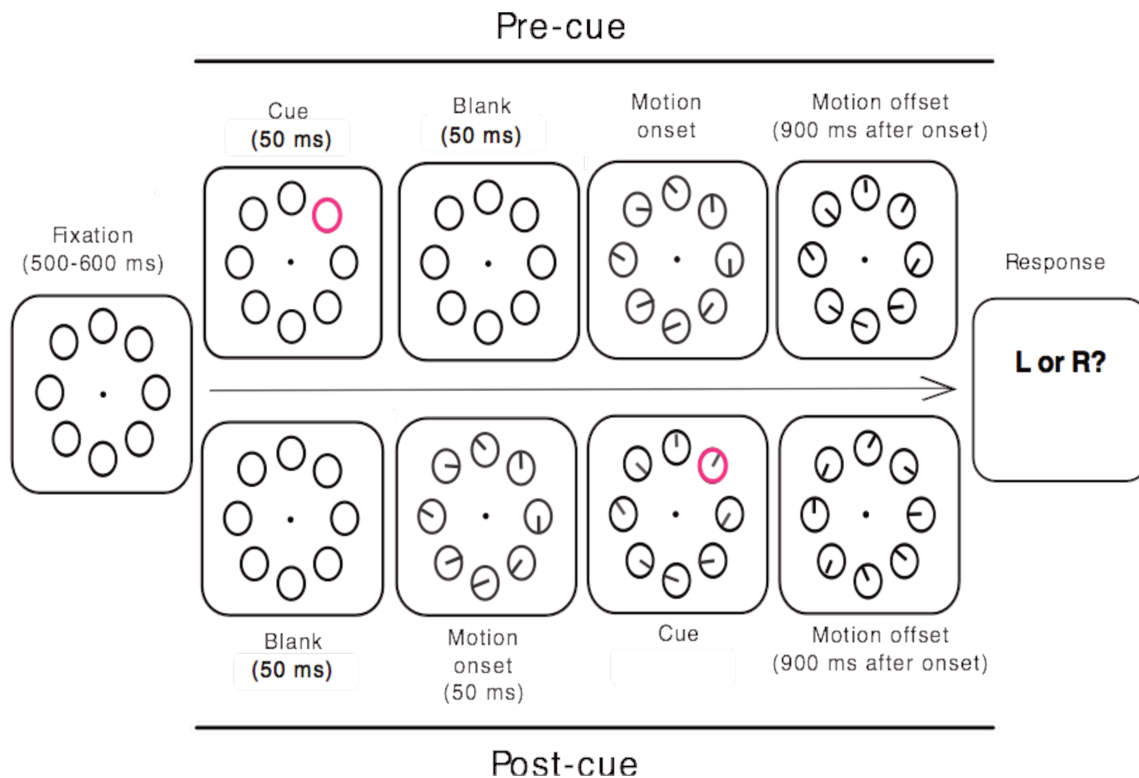

Figure 2.1.3. Experiment 2 trial schematic. Upper row shows the "pre-cue" cases, lower row shows the "post-cue" cases. In all the trials the task was to report the onset angle of the cued target. In the pre-cue cases, the cue (identical to Experiment 1) preceded the onset of eight moving targets by a fixed SOA, thus allowing to selectively attend to one item. In the post-cue condition the to-be-attended target was revealed only after the motion onset (again, after a fixed SOA).

Negative SOAs mean that the cue was presented before motion onset, which is identical to the cueing used in Experiment 1. However, with the positive SOAs the cue appeared after the motion onset, which means that observers had to attend to all eight stimuli for some time before being able to focus on the target. Onset angles

varied from -80° to 80° relative to the upper vertical of the placeholder, whereas in Experiment 1 we used the range of -60° to 60°. The expanded range was necessary for the more difficult late SOAs, where the participants' responses covered a larger range of angles. Another difference from Experiment 1 was that all stimuli disappeared from the screen simultaneously 900 ms after the motion onset (having travelled 290°), and not when they reached the lower vertical position. Thus, the duration of motion was not predictive of the onset angle.

Procedure

The procedure was similar to Experiment 1. On each trial subjects were asked to fixate the central dot, observe the rotation and then respond with the button press whether the cued stimulus started moving from the left or from the right relative to the upper vertical radius of the placeholder. Subjects were aware that the timing of the cues varied unpredictably. Trials with pre- and post- cues were presented in a pseudo-random order. On average, subjects had 1700 trials, with 240 trials per SOA.

2.1.3.2 Results

The size of the Fröhlich effect was estimated in the same way as in Experiment 1. Individual PSEs were then plotted against the SOAs to reveal the time course of attentional modulation of Fröhlich effect.

Figure 2.1.4B represents the average time course of the Fröhlich effect modulation. Overall, SOA had little effect on the perceived onset position except at the two late SOAs (+200 and +300 ms) where the Fröhlich effect increased compared to the other SOAs ($F(6, 36) = 53.1$, $p < .001$, $\eta 2 = 0.87$). This pattern of results was shared by all subjects.
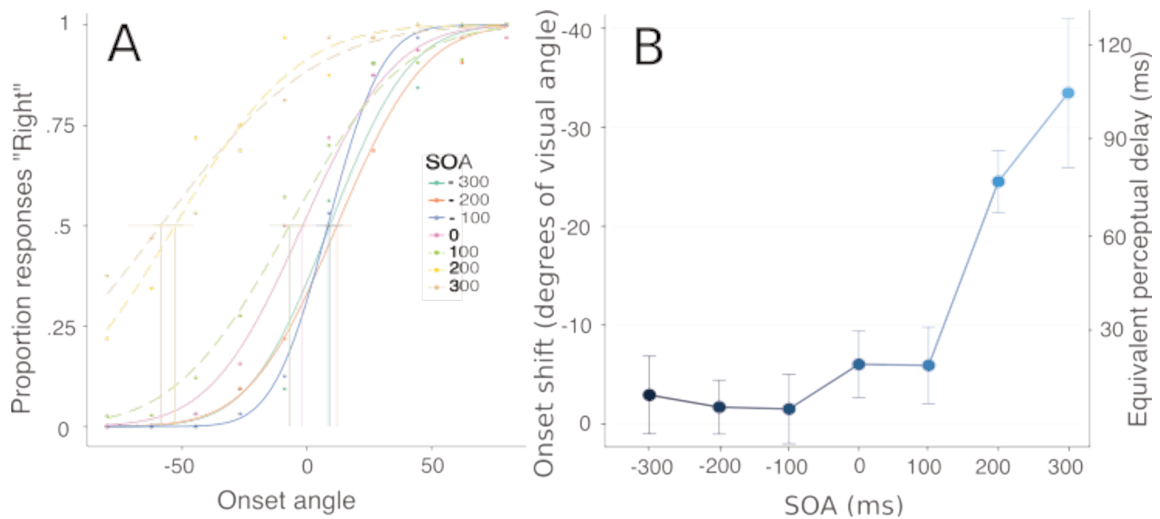
Figure 2.1.4. Results of Experiment 2. Panel A shows example data from one participant across the 7 SOAs. Negative SOA conditions are plotted in dashed lines, positive SOA conditions – in solid lines. Panel B shows average Fröhlich effect size as a function of SOAs for all subjects (n=7). Error bars represent 95%CIs.

This increase is consistent with the attentional explanation of the Fröhlich effect, as the later attention arrives at the moving target, the bigger the mislocalization. As in Experiment 1, the mislocalizations after pre-cues (-300, -200, and -100ms) although smaller than seen in Experiment 1 were still significantly greater than zero ($M = -4.12$, $t(20) = -2.26$, $p = .04$), again confirming that Fröhlich effect was present even when attention was shifted towards the target area prior to motion onset. Note however, that in Experiment 1, a valid cue at -100 ms SOA yielded mislocalization of -22° in Experiment 1 but only -3.9° in Experiment 2. A few differences between the tasks may account for this reduction of the position shift. First, the range of starting angles was larger in Experiment 2 (-80°:80° compared to -60°:60°), possibly helping the discrimination performance. Second, in Experiment 2 the stimuli were simultaneously presented in all the placeholders, whereas in Experiment 1 stimuli were presented one at a time. This presence of irrelevant but perceptually similar distractors could enhance the effectiveness of the cue. Additionally, the irrelevant stimuli could provide references for the judgement about the starting angle of the target. Third, the offset angle of the stimulus was predictive of its onset angle, since the motion duration was fixed. However, participants were not aware of this association and never received response feedback.

We also analyzed the slopes of the psychometric curves as a function of SOAs (Figure 2.1.5). Slopes were calculated by fitting logistic functions to participants' responses as a function of onset angle for each SOA condition. Cueing delay could affect not only the magnitude of the perceptual effect, but also the memory of the percept, making the onset locations at later SOAs more difficult to report. In this case we would expect the slope of the psychometric functions to be shallower for the later
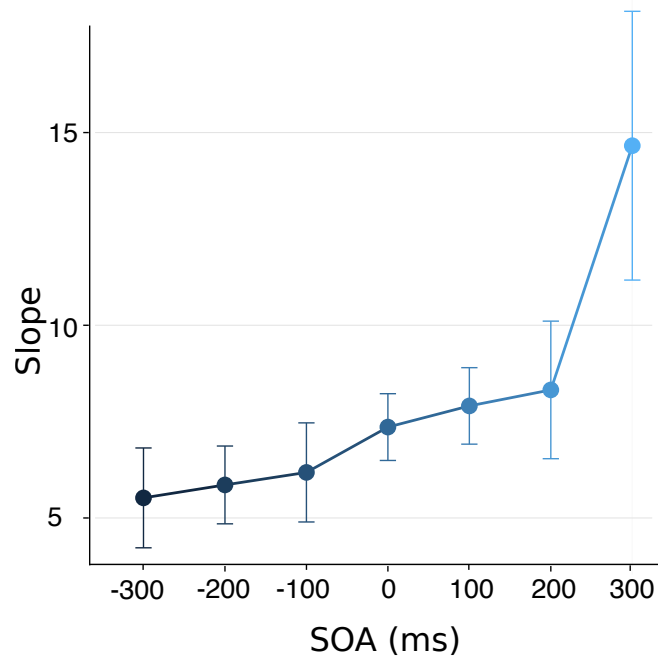
cues. One-way repeated measures ANOVA with SOA as a factor did show a significant main effect ($F(6,36) = 19.2$, $p < .001$, $\eta2 = .58$), meaning that the task indeed became more difficult with increasing SOA.

Figure 2.1.5. Slopes of the psychometric curves as a function of SOAs, averaged across all participants (n=7). Error bars represent 95%CIs.

2.1.3.3 Discussion

The results of this experiment showed that the Fröhlich effect increased when cues arrived after motion onset, as would be predicted by a delayed attention explanation. The later attention arrives at the moving target, the more the start position is shifted along its path. However, participants were surprisingly good at reporting the onset location of one of the eight simultaneously attended moving targets even when the cue indicating which to report came 100 ms after the onset of

the motions. The results suggest that the simultaneous onsets may be held in iconic memory and the cued motion trajectory can be retrieved if the cue arrives soon enough. If this interpretation is correct, it suggests that iconic memory is not simply a static memory but a dynamic one. This is in line with the previous accounts of multiple layers of iconic memory (Rensink, 2015) or multiple systems of visual memory (Sligte, Vandenbroucke, Scholte, & Lamme, 2010).

The increasing shifts with more delayed post-cues (>100 ms) might be caused by factors other than simple delay of attention. A late SOA implies a longer memory retention period and that means that the reported shifts could arise from working memory limitations and might not be perceptual in nature. This could explain why the Fröhlich effect observed with late cues is much bigger than one observed with simple invalid cue in Experiment 1 and why, as evident from the analysis of slopes (Fig. 5), the task is harder with late SOAs.

Additionally, these data again suggest that the Fröhlich effect is not solely explained by the delay in attention reaching the cued position from the fixation point. The size of the Fröhlich effect is largely unchanged for pre-cues, and we can safely assume that attention would reach the cued location at or prior to motion onset if the cue preceded the motion onset by 300 ms (Posner, 1980; Egeth & Yantis, 1997, although see Purushothaman, Patel, Bedell & Ogmen, 1998). Rather than the absence of Fröhlich effect, we still see a significant shift. If there were an additional delay as attention moves from the general area cued by the flashed ring toward the actual start location of the motion, it might explain part of this Fröhlich effect for the pre-cues as attention cannot make this final move until the motion actually starts. Another additional shift is required with the saccade intercept hypothesis (see General Discussion) even if attention is already at the moving target. Programming a saccade to accurately intercept the target requires a position extrapolation to account for the unavoidable delays in taking the eye to the target.

Overall, this experiment showed that attentional shifts modulate Fröhlich effect within a specific time frame. If attentional selection of the target happens before the motion onset, a minimal (but significant) shift in the perceived motion onset is reported. If attention is shifted to the target later, this shift progressively increases, as expected from attentional delay account. However, in all these cases one target out of the group had to be selected at some point.

Both Experiment 1 and 2 show that there is a residual Fröhlich effect even when attention is already at the location of the target. We next examined whether the motion-induced shift depended on the mere presence of attention alone or if attention had to track individual targets to produce the shift. To address this we compared two modes of attention to the target: either a distributed attention to several targets or a focused attention on one.

2.1.4 Experiment 3

Experiment 1 and Experiment 2 confirmed the basic predictions of attention delay explanation. However, this explanation assumed a tight focus of attention that was either on the individual target or elsewhere. What would happen if attention were directed to several targets at once? Is the presence of distributed attention sufficient to generate the Fröhlich effect? Cavanagh and Anstis (2013) used multiple and single dots travelling back and forth to test the role of attention in illusory trajectory shortening. In a trajectory shortening stimulus, a dot travels back and forth along a linear path and there is a Fröhlich-like shift of the beginning of the visible path at both ends of the trajectory, shortening its apparent length. Importantly, when multiple stimuli are presented, moving asynchronously along parallel paths, they are not unattended, but rather attended as a group, which allows reporting of the end-points of all the trajectories without engaging focused attention on individual trajectories. It was shown that trajectory shortening only exists for individually attended trajectories, but not for those attended as a group. This is similar to the finding by Linares and López-Moliner (2007) where flash lag was eliminated with a group display. Here we use this logic to test the occurrence of the Fröhlich effect with distributed attention to multiple rotating line segments.

For this experiment we created a new stimulus display and a new task. First, we added more items to the display and increased the eccentricity (as shown in Figure 2.1.6B). To ensure distribution of attention to all items throughout the trial, we presented synchronised motion in all the placeholders simultaneously and we asked subjects to report a feature of the display created by all the items on the screen — their alignment. At the moment when all the stimuli were aligned, they are grouped together as three distinctive lines, either vertically (Figure 2.1.6B, top left panel) or horizontally (Figure 2.1.6B, bottom left panel). Vertical and horizontal configurations

were tested in separate blocks. We took advantage of this momentary grouping to probe motion perception under distributed attention. If the Fröhlich effect persists for each individual rotating segment, all of their perceived onset angles will be shifted. Therefore, if the segments start from alignment, this alignment would not be perceived, as the Fröhlich effect would render them visible with some additional rotation (Figure 2.1.6A). By estimating the maximal onset angle that results in perceived alignment we were able to measure the simultaneous Fröhlich effect for the entire group of elements.

For our control condition, we introduced focused attention to a single moving element in this display (Fig. 2.1.6B right hand panels). To do so, we took advantage of another well known phenomenon — attentional capture (Yantis, 1994). We rotated one of the items of the display relative to the others making it an orientation singleton, and asked participants to report whether this singleton is seen as either horizontal or vertical at any point during the trial. This question is essentially the same as the one we asked about the group alignment (since the alignment was only present when the segments were either all vertical or all horizontal), only here the judgment had to be done on a single, attended item.

2.1.4.1 Method

Participants

Eight healthy adults took part in the experiment (four male, mean age = 21.8 ± 2.2 years with a range of 19 to 28), three of them (S3, S5 and S7) participated in Experiments 1 or 2. Two participants (S3 and S4) were experienced psychophysical observers, but were naive to the purposes of the experiment.
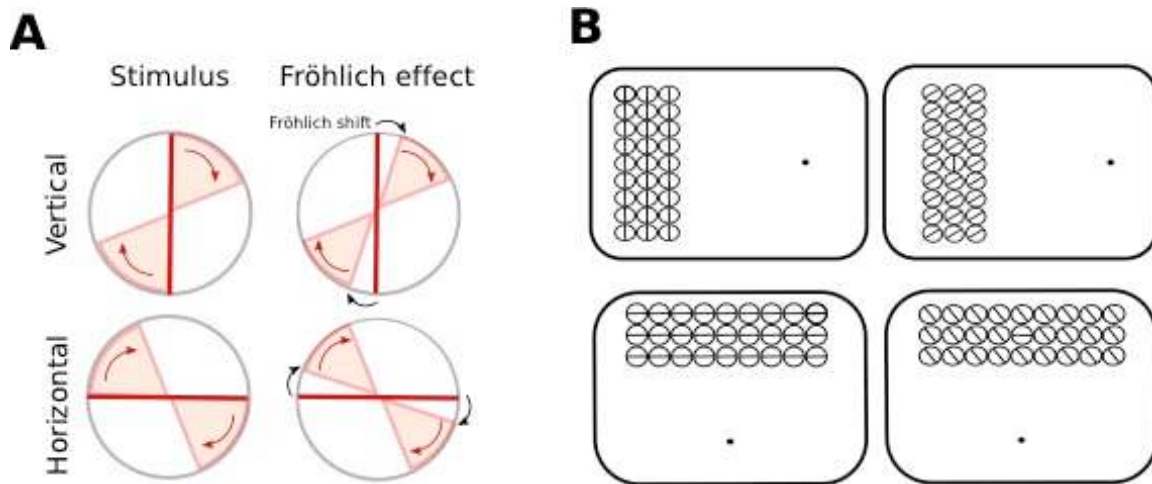
Figure 2.1.6. Panel A. A schematic showing the orientations covered by a single rotating line starting at vertical (top left, 0° onset trial) or horizontal (bottom left). To the right of each is the hypothetical range of perceived orientations given a 15° Fröhlich shift. The thick red bar within each circle (not actually shown on screen) indicates the to-be-detected orientation, either vertical (top) or horizontal (bottom), respectively. Physically, the stimulus contains the to-be-detected orientation right at the start of the motion (left), but the illusion then renders it invisible (right). Panel B. Stimuli arrangements at the to-be-detected orientations in Experiment 3. The upper row shows the Vertical condition, lower row shows the Horizontal condition. The left column shows the alignment to be detected in the "Group" condition. The right column shows the orientation of the singletons to be detected in the "Single target" condition

Stimuli

The stimulus consisted of 27 placeholders lined up in the periphery as shown in Figure II.1.6B, arranged in three rows of nine. Each placeholder was 2.5° wide. The whole stimulus set was 22.5° long and 7.5° wide, and its center was 21° away from the fixation point. Targets (bars covering placeholders' diameters, 0.2° thick) were presented in all the placeholders simultaneously, and moved in the same direction and in synchrony. Motion started at a randomly selected angle from -30° to 36° relative to the vertical or horizontal (in respective blocks) in the increments of 6°, and rotated 60° clockwise with the speed of 0.83 revolutions per second.

In the Group condition, all the targets had the same onset angle. In the Single condition, one random target was rotated 45° counterclockwise relative to the rest of the targets, thus becoming an orientation singleton and breaking the alignment. The

stimuli were presented in two spatial arrangements, with the stimuli in the upper visual hemifield (Vertical condition) and in the left visual hemifield (Horizontal condition). Stimuli for Horizontal condition were created by rotating the stimuli from the Vertical condition 90° counterclockwise.

Procedure

Each combination of conditions (Single/Group and Horizontal/Vertical) was tested in a separate block of 360 trials. The order of the blocks was counterbalanced across subjects. On each trial, subjects had to fixate, then observe the motion and respond by key press. Trials were separated by 500 ms to 600 ms jittered ITI.

In the Group condition subjects had to report whether the targets were perceived in alignment at any point during the trial. In Single Target condition they had to report whether the stimulus that was different from the rest of the set was at horizontal (or vertical, in respective blocks) at any point during the trial. The to-be-detected orientation of the stimuli/stimulus was present at some point in all the trials with the starting angle lower or equal to 0°. Importantly, the to-be-detected orientation could only appear once per trial, since motion was restricted to 60° of rotation and so only passed through either horizontal or vertical (for starting angle of 0° or less), depending on the block. The singleton location changed from trial to trial.

To test our hypothesis that the Fröhlich effect is reduced in the Group condition, i.e. that alignment will be detected when the stimulus starts at 0° in the Group trials, we first calculate participants' performance on trials with 0° onset. We then performed the analysis of the full psychometric curve to estimate the Fröhlich effect in both conditions in the same way that we did in Experiments 1 and 2.

2.1.4.2 Results

Psychometric curves were fitted individually for each observer and condition, and PSEs were estimated as the onset angle of motion that produced 50% reports of a horizontal or vertical alignment (Group conditions) or a horizontal or vertical singleton (Single condition). Therefore, negative PSEs reflect a shift in the perceived onset location in the direction of motion (Fröhlich effect).

The analysis of 0° onset trials showed that the starting angle was correctly detected as aligned to the vertical or horizontal on average in 78% (± 10.5) of the trials in the Group condition suggesting that the orientations of the line segments were perceived almost veridically with little if any shift when reported as a group. In contrast, only 7% (± 8.2) of Single trials were reported as aligned to vertical or horizontal. The analysis of the psychometric functions confirms these results. Figure 2.1.7 shows that PSEs were shifted to the left in the Single condition compared to the Group condition both in vertical and horizontal layouts, meaning that perceived onset locations were shifted further in the direction of motion in the Single condition. This pattern of results was observed in all participants. One-way repeated measures ANOVA revealed a significant main effect of condition ($F(3,21) = 14.35$, $p < .001$, $\eta2 = .32$). The PSE shift was significantly larger in Single compared to Group condition ($M_{Group} = -0.44$, $M_{Single} = -11.84$, $t = 3.05$, $p = .005$). The pattern of results was the same if vertical and horizontal cases were analyzed separately. Overall, the onset shift was significantly different from zero in the Single condition ($t(15) = - 4.51$, $p < .001$, JZS $BF_{10} = 6.38$) but not in the Group condition ($t(15) = - 0.17$, $p = .87$, JZS $BF_{10} = 0.26$).
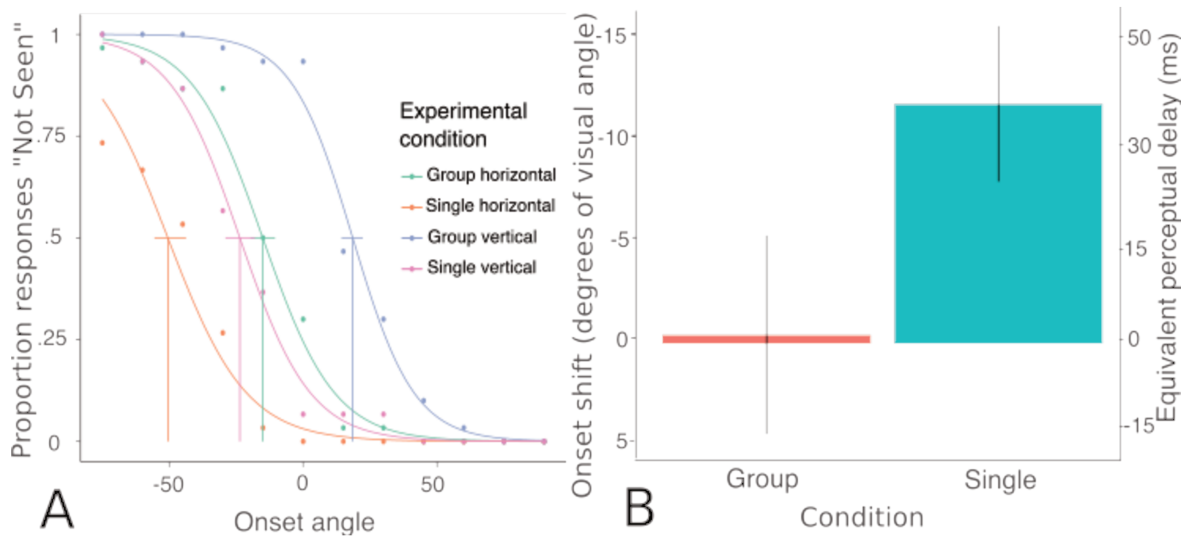

Figure 2.1.7. Results of Experiment 3. Panel A shows data from one participant. Panel B shows the average Fröhlich effect for Group and Single conditions for all participants (n=8). Error bars represent 95% CIs.

2.1.4.3 Discussion

The main finding from this experiment is that Fröhlich effect is greatly reduced when the moving stimuli are attended as a group. Equally important, the effect was restored when focal attention was directed to an orientation singleton within the group. While it is true that distributed attention is enough to detect the presence of a singleton item, focal attention is then necessary to analyze its features (Sagi & Julesz, 1985), for example, as in our case, its orientation. The presence of focal attention then allows the motion of the target line segment to be individuated and tracked. By contrast, in the Group condition moving bars were attended as a group in order to detect the emergence of the global shape (alignment) and although the motions were clearly visible, no single trajectory could be isolated and tracked. This condition reveals that the full motion trajectory is not masked by some low level property of the stimulus motion.

We propose that it is this focal attention to a specific trajectory that engages a predictive mechanism for that trajectory, advancing the location of the motion onset for purposes of targeting, as we explain in the General Discussion section that follows. With multiple stimuli attended as a group, no one stimulus can be a saccade target without further processing. We suggest that when saccade programming is not possible, the predictive position shift is not engaged.

This result is in line with the finding by Cavanagh and Anstis (2013) who showed that attention to multiple trajectories does not result in trajectory shortening (a Fröhlich effect at both ends of a reversing trajectory), but attention to the individual trajectory does lead to the illusory shift. Here we show that focal attention shifts localization not only for motion reversals, but also for motion onsets. Again, this suggests that the Fröhlich effect is not an unavoidable consequence of motion, but it is driven by focused attention.

One important feature of the Single target task is that the target changed its position from trial to trial. Müsseler and Kerzel (2004) argued that Fröhlich effect is only observed when stimuli appear at a predictable position, possibly because moving targets require attentional disengagement from the previously attended space. However, our data show that although the orientation singleton had 27 possible locations, it still produced a Fröhlich effect, casting doubt on this hypothesis.

There are alternatives to our distributed attention explanation for the reduction of Fröhlich effect with multiple stimuli. It is possible that a summary or ensemble representation of all of the orientations is generated by a fast, automatic mechanism (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Alvarez & Oliva, 2009). This ensemble representation would always be more accurate than the representation of a singleton, and possibly available earlier. Additionally, the to-be-detected alignment in Group condition was a property of a much larger stimulus, involving all the elements, than the single item, and this could also affect the speed of processing (Vogels, 2009). However, previous studies using comparably large stimuli (Kirschfeld & Kammer, 1999) successfully demonstrated large Fröhlich effect.

2.1.5 General Discussion

In this series of experiments, we set out to disentangle the evidence regarding the role of attention in Fröhlich effect. Experiments using cueing paradigms (Müsseler & Aschersleben, 1998; Whitney & Cavanagh, 2000) report that validly cued stimuli show less of a Fröhlich effect than invalidly cued stimuli. Müsseler and Aschersleben (1998) proposed a delay hypothesis wherein the later attention arrived at the stimulus, the further it was seen shifted along its path. In contrast, other experiments showed that the Fröhlich effect is absent when attention is directed to a group of moving stimuli (Linares & López-Moliner, 2007; Cavanagh & Anstis, 2013) and not to individual targets within the group. The group result indicates first that the position shift of the Fröhlich effect is not an obligatory consequence of stimulus movement. However, the group result does not easily match with what the attentional delay hypothesis would predict. Here we used similar stimuli in both cueing and group attention situations and we replicated these previous findings. We consider an alternative explanation of the Fröhlich effect based on the preparation of saccade programming to moving targets. This interceptive saccade conjecture is consistent with both results.

In Experiments 1 and 2 we varied the delays with which attention reaches the target with invalid vs valid cuing (Experiment 1) and with cue-motion onset delays for valid cues (Experiment 2). In both cases, we found increases in the Fröhlich effect associated with longer delays. Critically, following Müsseler and Aschersleben's

(1998) proposal, we interpret the invalid cue condition as causing a delay in attention reaching the target rather than a condition of inattention or lack of attention. Our finding of a modulation of Fröhlich effect with attention cues is consistent with the previous research using single targets. Specifically, Müsseler and Aschersleben (1998) as well as Whitney and Cavanagh (2000) showed that the Fröhlich effect could be increased by invalid attention cues.

We also found, in line with the previous cueing experiments, that the Fröhlich effect is small, but always present and significant when the location of the upcoming motion onset is attended. In some stimuli, including ours, part of this residual Fröhlich effect could be attributed to the additional delay of transferring attention from the cue to the actual start location of the motion within the cued area, as well as to the hypothetical execution delays of a potential saccade.

The execution delays refer to the "saccade intercept hypothesis" we propose to link covert attention to overt attention by treating every attended target as a potential saccade target. Any accurate eye movement to a moving target requires compensation for the distance travelled by the target after the saccade has been programmed but before it lands on the target (Ludwig, Mildinhall, & Gilchrist, 2007). Given how closely linked attention and saccade systems are (Corbetta et al., 1998; Krauzlis, 2014) we assume that this extrapolation along the motion path is engaged for every tracked target, whether or not it eventually engages a saccade. As long as the target is attentively tracked, we assume that its perceived location is extrapolated to match the location where the saccade will intercept it, the position to which the saccade must be targeted. Several studies with motion-induced position shifts with simple moving targets show evidence for a similar extrapolation for perception and saccades. All of these show matched shifts in perceived location and saccade landings (Nijhawan, 1994; Etchells et al., 2010). The one exception is for a stimulus with two motion components (double drift, Lisi & Cavanagh, 2015) where the internal motion of the stimulus appears not to be registered by the saccade system.

Note that this proposal has the target shifted in position so that its initial appearance is *displaced*, not masked as some have proposed (Kirschfield & Kammer, 1999). Evidence in favor of this shift as opposed to masking is clear when the initial target position is marked in some way, for example, with a unique color. In this case, that brief unique color does not disappear, as it should if the initial portion of the trajectory were masked to produce the Fröhlich effect. Instead, the color flash is seen

displaced, still at the beginning of the trajectory, but that trajectory now starts further along the motion path (Cai & Schlag, 2001; Eagleman & Sejnowski, 2007; Cavanagh & Anstis, 2013, Fig 13b, flash at start of trajectory).

The saccade intercept hypothesis provides a possible explanation for the residual Fröhlich effect seen with advanced cues in Experiment 2 as well as in other studies where the target is fully attended, including the original observation by Fröhlich (1923). Even if attention is already deployed to the upcoming target location, any potential saccade will only reach the target after a delay, which could be compensated in a predictive manner by perceptual extrapolation. Additionally, when attention is delayed in reaching the target to begin tracking it, more extrapolation is required and the Fröhlich effect increases, as demonstrated by several cueing experiments.

In contrast, when attention is directed to a set of moving stimuli, as in the Group condition of Experiment 3, no Fröhlich effect is seen. In this case, none of the trajectories is attentively tracked and none of them can be individual saccade targets without further processing, and the predictive shift is not engaged. There are other examples in the literature showing that motion-induced position shifts disappear with attention to the group (Cavanagh & Anstis, 2013), attention to the global shape (Linares & López-Moliner, 2007) or attention to a large space (Müsseler and Tiggelbeck, 2013). All of these conditions required a spatial spread of attention (20-30° visual angle) to all items of the display, not to a few locations or objects within it. In other words, they implied diffusion of attention where no particular stimulus is attended individually and none could be targeted by a saccade without further processing to single them out.

However, once focal attention is directed to an individual target in the same group (Single condition), it becomes a potential target and the predictive shift is again seen. This result strongly suggests that whatever the mechanism creating the perceptual shift in position, it requires focal attention. When the target engages focal attention on one particular location, a moving object there gets shifted forward. Once attention is narrowly focused, the magnitude of the Fröhlich effect is determined by the time it takes to arrive at the moving object as well as, we suggest, any additional execution delay for a potential eye movement to it.

2.1.6 Conclusion

The findings of this study are two-fold. Our data confirm that attention delays are important predictors of the magnitude of the Fröhlich effect. More importantly, we show that focused attention by itself is a requirement — without it the Fröhlich effect disappears completely. We suggest that focused attention tracks the target motion and adjusts the perceived location to match the necessary targeting location for an accurate saccade, even if one is not made. When attention is deployed to a group of targets, they are not tracked individually and they could not be individual saccade targets without further processing, and so the position shift that produces the Fröhlich effect is not engaged. In this case, the initial portions of the motion traces are clearly seen showing that the Fröhlich effect is not an obligatory consequence of any motion, only of motion that is attentively tracked.

2.2 Spatial predictability reduces the flash grab shift

Abstract

When a stationary target is briefly presented on top of the moving background as it reverses direction, the target is perceptually displaced in the direction of the upcoming motion (flash grab effect). This illusion requires attentional tracking of motion (Cavanagh & Anstis, 2013). To determine the role of target-related attention, we investigate whether spatial and temporal predictability of flash grab targets modulates the illusion. First we establish that flash grab is weaker for spatially predictable targets. Next, we show that flash grab decreases as a function of spatial spread of attention before the onset of the target. Finally, we show that temporal predictability doesn't influence the illusion as effectively as spatial predictability. Together these results suggest that when attention is allocated elsewhere, the increased delay in reaching the target increases the shift (attentional delay hypothesis, Müsseler & Ascherschleben, 1998; section 2.1) relative to conditions when attention is already focused on the predictable target location.

2.2.1 Introduction

Localization of objects is one of the most important functions of vision yet it remains poorly understood, especially when a location has to be assigned to a moving object or an object surrounded by motion. A range of motion-position illusions including the flash-drag (Whitney & Cavanagh, 2000), flash lag (Nijhawan, 1994), and flash-jump (Cai & Schlag, 2001) illusions vividly illustrate that motion information plays a crucial role in determining where objects are perceived, and show that motion and position are not independently processed. One particularly powerful example of motion induced position shifts is the flash grab – an illusory position shift seen when a target is briefly flashed on top of a moving background that abruptly changes direction (Cavanagh & Anstis, 2013).

The flash grab illusion has two components. The first is the apparent shortening of the motion trajectory between successive reversals, possibly explained by location averaging or predictive position extrapolation (Sinico et al., 2009; Nijhawan & Khurana, 2010). The second is a position shift of the briefly presented stationary stimulus (flash), which is "grabbed" to the perceived location of the reversal. The illusion is the strongest when the transient of the flash coincides with the transient of the motion reversal (Cavanagh & Anstis, 2013, Exp. 2), suggesting that flash grab requires an assumption that the flash belongs to the moving stimulus. Another important feature of flash grab is the involvement of attentive tracking of the motion. Cavanagh and Anstis (2013) tested if the trajectory shortening that underlies flash grab is also perceived when multiple trajectories are attended as a group. They found that the shortening only happens when a single trajectory can be individually tracked, suggesting that flash grab requires attention. Tse et al. (2011) used a flash grab stimulus composed of two transparent layers of opposed motion. Subjects could switch their attention from one layer of motion to another, and the direction of flash grab was found to follow the direction of the attended motion. This result proved that attention to motion is sufficient for generating flash grab even in the absence of net low-level motion energy.

The studies described above manipulated attentional tracking of motion. Less is known about the role of target-related attention in the flash grab. It is well established that focused spatial attention improves performance compared to the distributed attention (Posner, 1980; Mangun and Hillyard, 1988), and that attentional

benefits decrease with increasing distance from attended location (Downing & Pinker, 1985; Handy, Kingstone & Mangun, 1996). Motion-induced position shifts such as the Fröhlich effect (Müsseler & Ascherschleben, 1998) and flash lag (Namba & Baldo, 2004; Vreven & Verghese, 2005; Shioiri, Yamamoto, Oshida, Matsubara & Yaguchi, 2010) have been shown to be reduced by valid attentional cueing. That is, the perception of physically unchanged stimuli depended on preparatory allocation of attention to the space containing or not containing the upcoming target. However, in both these illusions the moving object and the target object are two separate but spatiotemporally bound stimuli. In case of the Fröhlich effect, the motion and the target are represented by the same object, and in case of flash lag the location of the target is always judged relatively to the location of the moving element. In flash grab, the target can be manipulated independently from the motion, allowing a measurement of the effect of target-related attention.

Here we examine the attentional modulation of the flash grab illusion by varying the spatial and temporal predictability of the target. In all the experiments, the task is to observe the rotating texture and report the location of the flash presented at the moment of the reversal by clicking on it (Figure 2.2.1). In Experiment 1, we manipulate spatial predictability by presenting the flash at the same location one or multiple times. The first flash appears at an unexpected position, but serves as a valid cue to the location of subsequent flashes. In the Experiment 2, participants are cued to the narrow or broad spatial area where the flash would subsequently appear. The cue allows participants to focus or spread their attention in anticipation of the target. In Experiment 3, participants are cued to the timing of the flash in order to evaluate the contribution of temporal attention. In agreement with previous studies on motion-induced position shifts, we hypothesize that decreased predictability will reduce the flash grab illusion. Furthermore, we expect the magnitude of the illusion to depend on the distance between the focus of attention and the target.

2.2.2 Experiment 1.

This experiment measures the flash grab illusion when the flash appears at expected and unexpected locations. To manipulate spatial predictability of the target we presented the flash at the same location multiple times within the same trial, and

66

asked participants to report the position of the last flash in the trial. We then compared the flash grab of targets presented once (unexpected location) to the flash grab of repeated targets (expected location). We also included a control condition to measure the contribution of temporal expectations.

2.2.2.1 Method.

Participants

Ten healthy adults took part in the experiment (four male, mean age = 23.2 years, SD = 2.1, with a range of 18 to 29). All participants in this and the following experiments reported normal or corrected-to- normal vision. All participants gave informed consent in writing prior to participation and the protocols for the study were approved by the Université Paris Descartes Review Board, CERES, in accordance with French regulations and the Declaration of Helsinki. They were compensated 10€ per hour for their time.

Stimuli and apparatus

The stimulus was an annulus of 18 degrees of visual angle (dva) outer radius and 14 dva inner radius filled with five octave 1/f noise texture. A new texture was generated for every trial. The annulus was presented against a mid-gray background (10.2 cd/m2). A black (2.1 cd/m2) centrally located fixation dot remained on screen throughout the experiment. During the trial the annulus rotated back and forth at 270° per second and changed direction after a variable amount of time (500-900 ms, uniformly distributed between trials). Importantly, within each trial the time to reversal was stable, creating a rythmic back and forth rotation. Motion continued for 1-3 pairs of reversals depending on the condition. The starting direction and duration of rotation was chosen randomly for each trial. Once per motion cycle (i.e. on every odd-numbered reversal) the motion stopped for 20 ms, and during that pause a target — a green (19.5 cd/m2) disc 2 dva in diameter — could appear on top of the annulus at 15.5 dva eccentricity.

The experiment took place in a darkened room. Stimuli were presented on a gamma-corrected LaCIE Electron monitor (100 Hz, 1024*768 resolution). Participants were seated 57 cm from the monitor with their heads resting on a chin- and headrest. Eye fixation was controlled using an EyeTribe eye tracker (The Eye

Tribe Aps, Copenhagen, Denmark). The experiment was programmed in MATLAB 8.4 (The MathWorks, Inc.) using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997) for presentation and the Eyetribe toolbox (Dalmaijer, 2015) for eye tracking. Statistical analyses were performed using R 3.1.2 (Ihaka & Gentleman, 1996).

Procedure and design

Participants performed 240 trials in six blocks, 60 trials per condition (see the description below). Before the experiment, subjects performed 20 trials identical to the experimental trials as a practice. The eyetracker was calibrated using a standard nine-point calibration procedure prior to starting the experiment. Gaze position was collected throughout the trial at 60Hz (binocularly), and a trial was aborted and rerun later if the gaze was detected outside of the fixation window (1 dva around fixation).

The procedure for the experiment is shown in Figure 2.2.1. The beginning of each trial was triggered by participants directing their gaze on the fixation point. Then the textured annulus appeared on the screen and immediately started back and forth motion.

There were four conditions. In the First Flash condition the target was presented at a random location during the first reversal of the texture. Thus, neither the location of the target nor the exact timing of the reversal was known by the participant beforehand. In the Second Flash and Third Flash conditions, the target was presented two or three times respectively, without a change in location, during consecutive motion cycles. In these conditions both the time of the reversal and the location of the target became expected after the first motion cycle. In the Time Control condition there were three back and forth rotations of the texture, but the target was only presented in the last one, at a random location. Thus, the timing of the reversal but not the location of the flash could be anticipated, since participants were aware of the structure of the trials. Trials were presented in a random order.

Participants reported the perceived location of the last target of the trial using a mouse cursor which could be moved around the screen at the same eccentricity as the target. Participants were aware that the targets within the trial are presented close in space to each other.
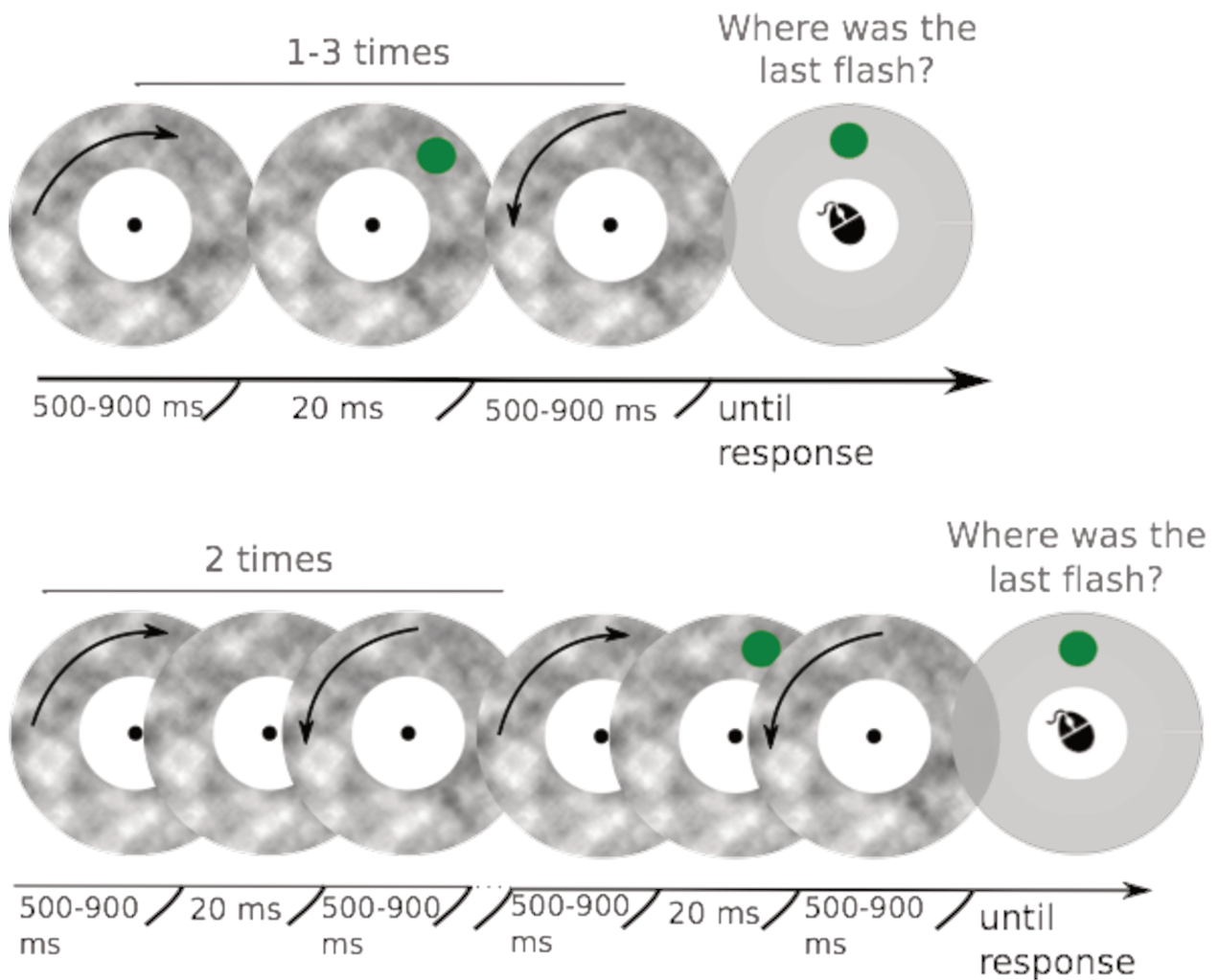
Figure 2.2.1 Schematic representation of the procedure used in Experiment 1. Top row corresponds to the trials in First Flash, Second Flash and Third Flash conditions. Bottom row corresponds to the trials in Time Control condition.

2.2.2.2 Results

The magnitude of flash grab effect in each trial was computed as the smallest difference between the physical position of the target and the position reported by the subject, in degrees of arc. Trials with deviant responses were removed using the Median Absolute Deviation approach (Leys et al., 2013) resulting in removal of 4% of trials. Results from trials with counterclockwise (negative) direction of expected position shift were flipped in sign. The reported direction of the illusion matched the expected direction in 96% of the trials, suggesting that the stimulus successfully produced the flash grab illusion.

Condition means were submitted to a repeated-measures ANOVA. Beyond the overall effect of target expectancy, we were interested in the following pairwise

comparisons: First Flash vs Second Flash as well as Second Flash vs Third Flash to capture the effect of spatial predictability, and First Flash vs Time Control for temporal predictability. Figure 2 shows the mean illusion values for each condition.

The results show that the flash grab magnitude was significantly affected by the condition, $F_{(1.1, 9.9)} = 115.4$, $p < .001$, $\eta^2 = .5$ (degrees of freedom corrected using Huynh-Feldt estimates of sphericity, $\varepsilon = .36$).

Post-hoc pairwise comparisons with Holm's correction showed that the illusion decreased after the first presentation of the target (First Flash vs Second Flash, $t_{(9)} = 9.6$, $p < .001$) as well as after the second presentation of the target
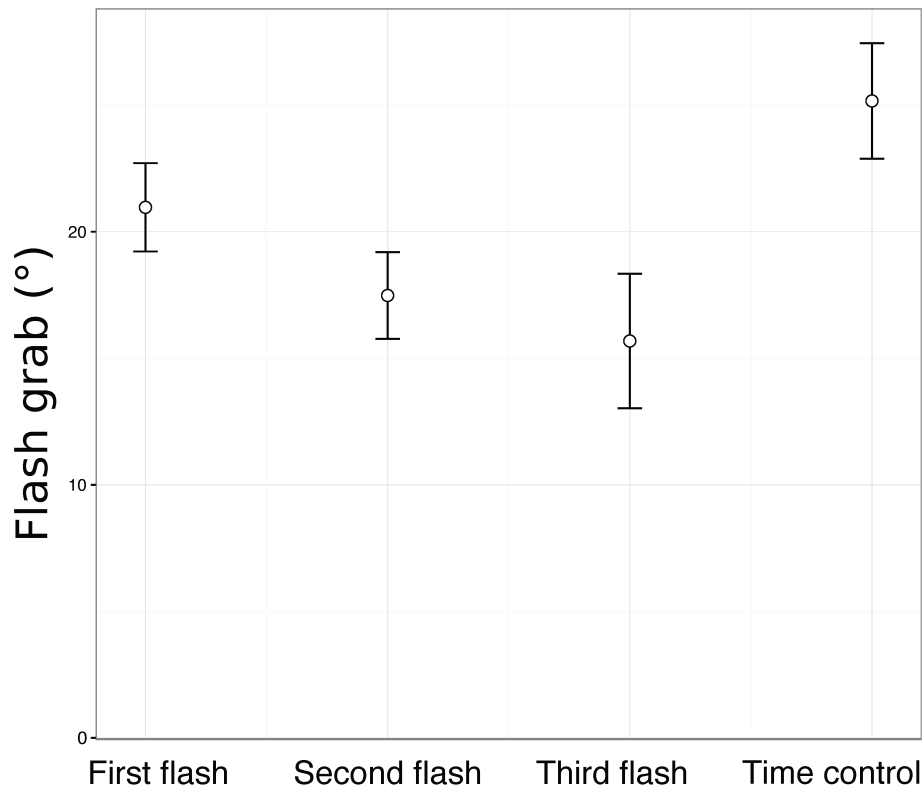
Figure 2.2.2 Averages of flash grab illusion for different conditions in Experiment 1. Error bars represent between-subjects 95%CI.

(Second Flash vs Third Flash, $t_{(9)} = 2.5$, $p = .035$). Unexpectedly, the illusion increased when the timing of the flash was known (First Flash vs Time Control, $t_{(9)} = -3.8$, p = .0087).

2.2.2.3 Discussion

Experiment 1 explored how the flash grab illusion depended on the available spatiotemporal information about the upcoming target. We manipulated spatial predictability by presenting the target once or multiple times at the same location, and we manipulated temporal predictability by presenting the target either at the first, unexpected reversal, or after a few identical back and forth oscillations of the background.

The main finding here is that a flash presented at an unexpected location is shifted or grabbed more than a flash whose location is known in advance. In other words, narrowing the focus of attention reduced the motion-induced shift of the flash. A narrower distribution of the targets results in shorter delays of attention's arrival at the target and consequently in smaller illusion. This is in line with a number of studies showing a decreased flash lag (Namba & Baldo, 2004; Vreven & Verghese, 2005; Shioiri et al., 2010) or Fröhlich effect (Müsseler & Ascherschleben, 1998) where valid spatial cues were used.

Although the position of the target was always constant within the trial and thus fully disclosed after one appearance, the illusion was further reduced at its third presentation compared to the second presentation. This pattern of results indicates the modulation of attentional distribution in between the consecutive presentations of the flash even after the initial narrowing of position uncertainty. One possibility is that narrowing of the attentional focus continues as more information about the position of the target is accumulated after each consecutive presentation. Additionally, shifting the focus of attention towards the new, more veridical perceived location of the target could also incrementally decrease the illusion. This dynamic is explored in more detail in Experiment 2.

Finally, we unexpectedly observed a significant increase of the flash grab illusion when a single flash was presented after several back and forth oscillations of the background. This control condition was aimed to separately measure the contribution of expected timing to the reduction of the illusion, however, the observed effect was the opposite. This could be potentially explained by the reallocation of attention to motion tracking. When spatial selection becomes irrelevant, the targets could be misplaced even more than when the focus of attention is far from the target.

71

The role of the temporal variability of flash grab targets is further tested n Experiment 3.

2.2.3 Experiment 2a.

Experiment 1 demonstrated that targets at unexpected locations have a larger flash grab illusion. Here we extend this finding by asking whether the strength of the illusion is modulated by the spatial uncertainty of the target. In this experiment, trials with the flash grab illusion were presented in blocks of eight. Before each block a cue indicated a range of possible target locations, prompting subjects to focus or distribute their attention in order to better anticipate the target. We expect the flash grab illusion to increase within the blocks with less precise attention cues. This paradigm also allows us to test the hypothesis that the magnitude of the illusion depends on the distance between the target and the centre of attentional focus.

2.2.3.1 Method.

Participants

Fifteen healthy adults (6 male, mean age = 20.9 years, SD = 2.2, with a range of 18 to 26) were recruited for Experiment 2a. All gave written informed consent prior to the start of the experiment and received monetary compensation for their time. Five participants were experienced psychophysical observers, two of them also participated in Experiment 1.

Stimuli and apparatus

The equipment was identical to that of Experiment 1. The flash grab stimulus was similar to the one used in Experiment 1 with the following changes. In all the trials, the motion duration was fixed: motion reversed direction after 500 ms (having travelled 135° of rotation). There was one reversal per trial, always coinciding with the target presentation. The starting direction of motion was randomly chosen on each trial.

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Figure 2.2.3. Examples of spatial cues used in Experiment 2a

0° range   45° range   90° range   180° range   360° range
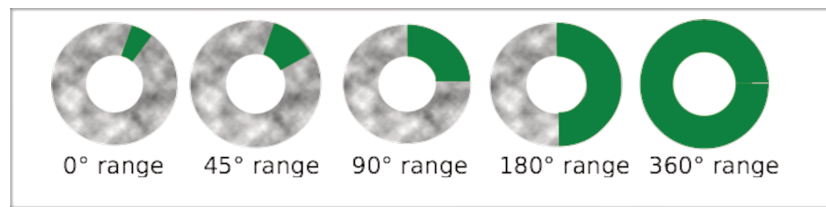
Procedure and design

Trials were presented in blocks of eight. The pre-block cue indicated the area where the targets could appear in the particular block (Figure 2.2.3). The exact physical position of the target was randomly selected from a uniform distribution within the cued range on each trial. There were five ranges for the cue: 1) 360°, targets appear anywhere along the circular background; 2) 180°, all targets appear either in the left or in the right hemifield, 3) 90°, all targets appear within one of the quadrants of the visual fieldЖ upper left, lower left, upper right or lower right; 4) 45°, all targets appear along a 45° arc centered within one of the quadrants; 5) 0°, all targets appear at a fixed location. Targets were presented with a fixed eccentricity of 15.5 dva.
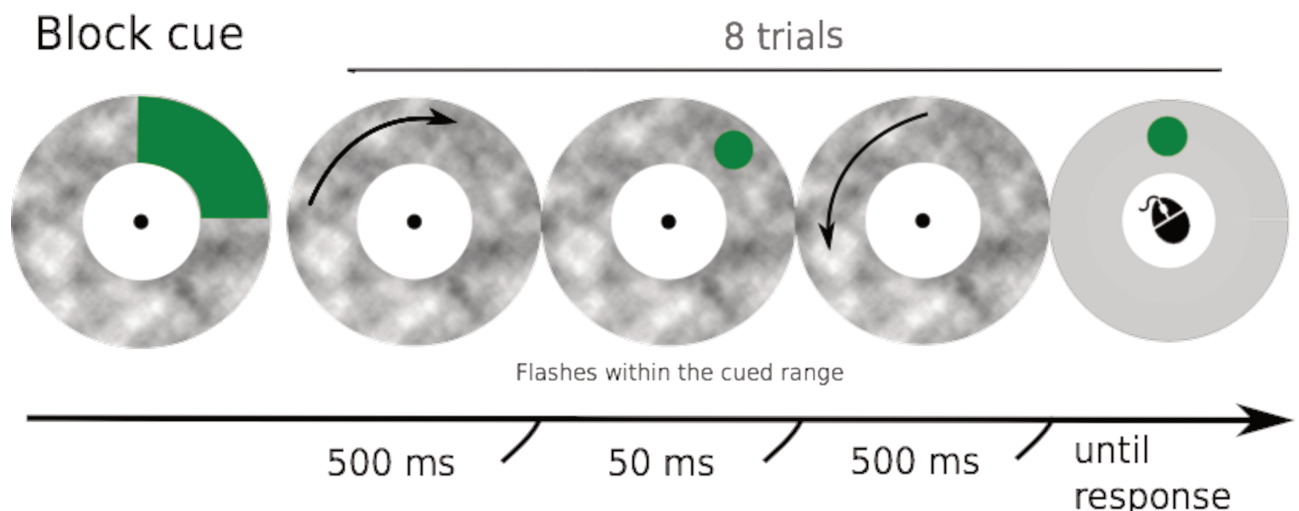
Figure 2.2.4. Schematic representation of the procedure used in Experiment 2a and Experiment 2b. Each block of eight trials begins with the presentation of a spatial cue. Green area of the cue indicates the range of possible target locations in the following block. Cues could cover 360°, 180° (left or right hemifield, 90° (upper left, lower left, upper right, lower right quadrants), 45° (in the middle of each quadrant) or 10° (precisely indicating the location of the target). Each trial consists of 1000 ms of motion reversing direction after 500 ms. At the reversal motion stops for 50 ms during which the target is presented.

73

Participants were asked to attend to the cued area while maintaining central fixation and report the location of the target on each trial. They were instructed to report the perceived location of the target even if it fell outside the cued range.

There were eight blocks per condition totaling 320 trials. Across all blocks, each hemifield and quadrant was represented with equal probability.

Data analysis

Main analysis. As in Experiment 1, responses were converted into flash grab estimates by subtracting the physical positions of the target from the reported positions in each trial and reversing the sign in those trials where negative (counterclockwise) shift was expected. For the analysis of flash grab magnitude as a function of cueing condition, outliers (3.5% of all the trials) were removed using the Median Absolute Deviation approach (Leys et al., 2013). Of the remaining 4634 trials 96.8% showed the illusion in the expected direction.

Intertrial distance. In order to test whether flash grab is modulated by the distance between the target and the focus of attention on the previous trial, we computed intertrial distances between successive targets in two ways, based on the physical and on the perceived target location on the previous trial. The physical distance between the two targets on successive trials simply shows how far away the target presented on the current trial is from the target *presented* on the previous trial. Perceived distance shows how far away the target presented on the current trial is from the *perceived* target location (reported) on the previous trial. Since the direction of motion (and, consequently, of the illusion) varied from trial to trial, this perceived distance could be shorter or longer than the corresponding physical distance. Physical and perceived distances were normalised within each cueing condition by rescaling raw distance values between 0 and 1. The first trial of each block was removed because they were not preceded by another target, hence intertrial distance could not be calculated. The condition with a perfectly predictable cue (0° range) was excluded from this analysis because the physical distance between the targets had no variance. In order to estimate the role of physical and perceived intertrial distances on the flash grab a total of 3054 trials were subjected to linear mixed effects modeling implemented in R via the lme4 package (Bates, Mächler, Bolker, & Walker, 2014). We constructed two separate linear mixed-effects models for physical and perceived intertrial distances. Both models included a fixed effect of spatial range as well as a

random intercept for participant and a by-participant random slope for spatial range. The highest spatial range (360°) was set as the reference level, therefore all reported estimates are relative to the flash grab magnitude in this condition.

Model 1 included physical intertrial distance as a fixed effect, and Model 2 included perceived intertrial distance instead. Model 0 with the same structure of random effects and only spatial range as a fixed effect was used as a baseline. All models were fitted by maximum-likelihood. Physical distance and perceived distance were not included as separate fixed effects into a single model because of the high correlation between the two variables ($r = .66$). Instead, both Model 1 and Model 2 were separately compared to the baseline model via the likelihood ratio test, then Models 1 and 2 were compared to each other with Akaike information criterion (AIC: Akaike, 1974). Lower AIC values indicate a better model fit.

Control analysis: response bias. In order to confirm that the effect of intertrial distance isn't confounded by response bias, namely, the tendency to bias reported locations towards the previously chosen ones, we analysed trials from the blocks where the target was always presented at the same location (0° range). These blocks were excluded from the analysis of intertrial distances, therefore providing an independent check.

Because the direction of motion was chosen on a trial-by-trial basis, there were trials in which the direction of motion happened to be the same as on the previous trial, or the opposite. If participants biased their responses towards the locations reported on the previous trial, with the change in the direction of motion they would report the target more veridically. For instance, consider the target presented at a location A. On trial (n-1) the target is perceived at the location A+15° (the flash grab shift). On trial (n), with the reversed motion direction, the same target should be perceived at A-15°. However, the bias towards the previous reported location (A+15°) would bring the response closer to the veridical location of the target. To rule out that such bias is responsible for our results, we compared mean magnitude of flash grab on trials where the direction of motion was (n=334) or wasn't (n=430) changed compared to the previous trial.

2.2.3.2 Results

The increase in spatial range of targets resulted in the increase of the illusion, as shown in Figure 2.2.5 ($F_{(2.2, 30.24)}$ = 7.34, p = .001, η^2 = .09, degrees of freedom corrected using Huynh-Feldt estimates of sphericity, ε = .63).
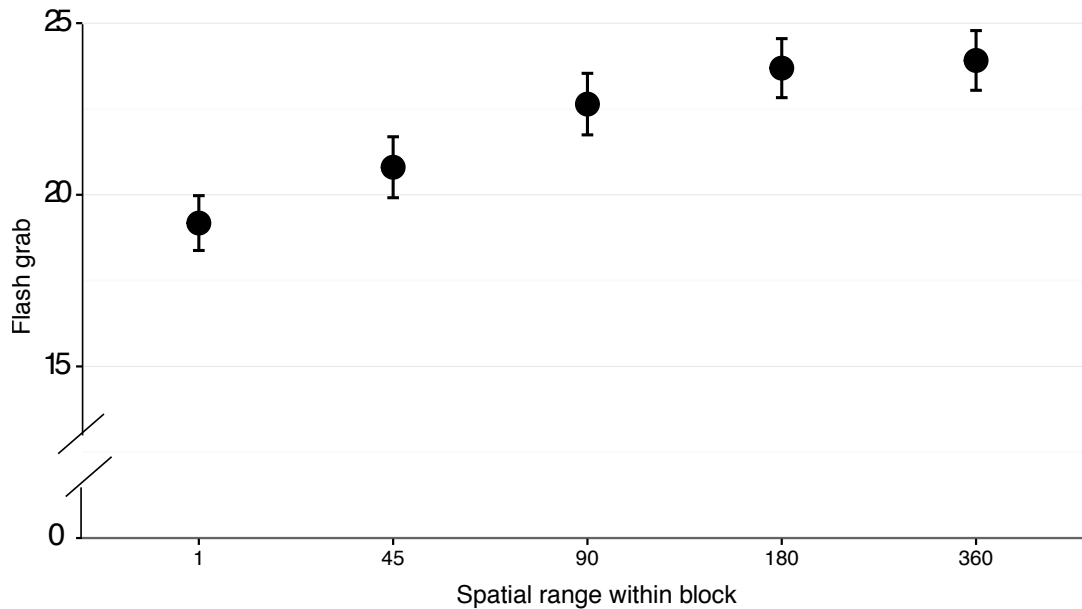

Figure 2.2.5. Mean flash grab magnitude in each cueing condition. Error bars: between-subjects 95%CI

Intertrial effects. Consistently with attention-shifting explanation, the flash lag was larger when the new target appeared farther away from the previous one. A comparison of the models' log likelihood ratios showed that including either the physical or the perceived distance significantly improved the fit to the data (physical: $\chi^2_{(4)}$ = 13.25 , p = .01; perceived: $\chi^2_{(4)}$ = 46.21 , p < .01). Model based on the perceived distance fits the data better ($AIC_{perceived}$ = 23245, $AIC_{physical}$ = 23284). In both models, the effect of intertrial distance varies with the spatial range. On a basis of bootstrapped 95% confidence intervals, we observed significant effect of distance at the spatial range of 90° ($\beta_{perceived}$ = 5.4 [2.23 8.6]) and 45° ($\beta_{perceived}$ = 9.36 [6.14 12.59]; $\beta_{physical}$ = 3.76 [0.91 6.62]). For a full overview of the estimated parameters, see Supplementary Table 1. Overall, the data show flash grab scaling with intertrial distance within the spatial range of 90° or lower (Figure 2.2.6).
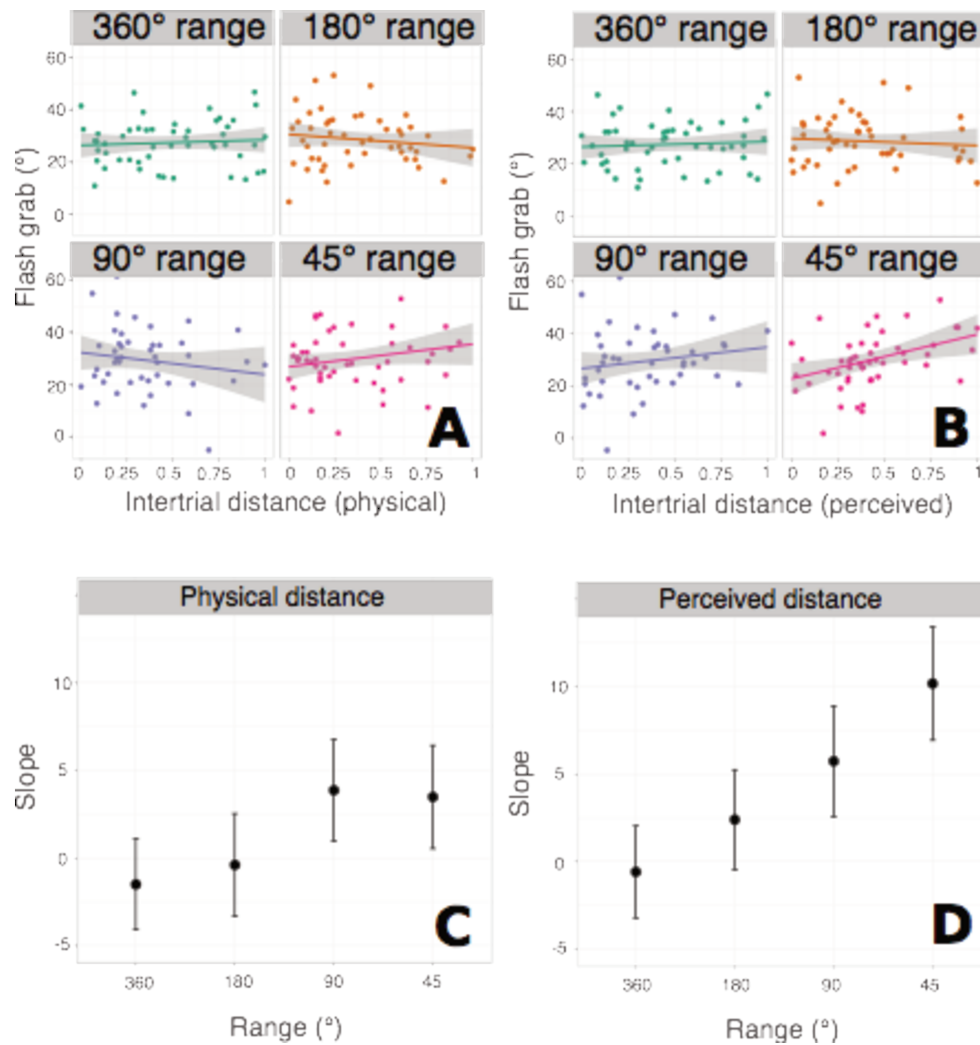
Figure 2.2.6. The results of intertrial distances analysis in Experiment 2a. Panels A and B show example data from one subject. Dots represent flash grab illusion as a function of intertrial distance in each trial. Panel A uses physical intertrial distance, Panel B uses perceived intertrial distance (see text for details). Lines and shaded areas represent linear fit and corresponding confidence intervals. Panels C and D show the estimates of fixed effect of Range in linear mixed-effects models. Panel C represents Model 1 (physical distance), Panel D represents Model 2 (perceived distance). For the full description of both models, see Supplementary Table 1.

Control analysis: response bias

We did not observe a difference in the magnitude of flash grab between the trials with repeated and changed motion direction (Table 2.2.1, $F_{(1,14)} = 0.003$, $p = 0.96$).

Motion	Flash Grab(°)	n	SE	CI
Same	19.60	430	0.59	[18.44 20.75]
Different	18.63	334	0.50	[17.64 19.63]

Table 2.2.1. Results of the response bias analysis

2.2.4 Experiment 2b

If flash grab illusion depends on the distribution of attention, it could also be susceptible to the asymmetries in this distribution. For instance, it is known that attention shifts within one quadrant of the visual field more easily than across the horizontal and vertical meridians (e.g. Rizzolatti et al. 1987; Reuter-Lorenz & Fendrich, 1992). Experiment 2a showed a weaker flash grab illusion when attended area was narrowed to 90° compared to 360°. Here we compare flash grab within 90° spatial range located within the quadrants defined by the vertical and horizontal meridians or centered on the meridians. If flash grab illusion reflects a slowing of attention shifts, the illusion should be larger when the attended range included the meridian.

2.2.4.1 Method.

Participants

Twelve healthy adults (5 male, mean age = 22.4 years, SD = 2.4, with a range of 16 to 30) were recruited for Experiment 2b. All gave written informed consent prior to the start of the experiment and received monetary compensation for their time. None of them participated in the previous experiments.

Stimuli and apparatus

Stimuli and experimental set up were identical to the Experiment 2a.

Procedure and design

Trial structure was identical to the Experiment 2a. In all the blocks the target range was 90°. There were two types of blocks depending on the position of the 90° area on the circular background (Figure 2.2.7). Blocks of the first type were identical to the 90° condition of Experiment 2a. Target ranges were located within the quadrants of the visual field, starting at 0°, 90°, 180° and 270° (where 0° is the top). Target ranges of the second type were centered on the vertical meridian (90° starting at 135° and 315°) or horizontal meridian (90° starting at 45° and 225°). There were 160 trials per condition, delivered in blocks of 8 trials. Data were treated in the same way as in Experiment 2a.
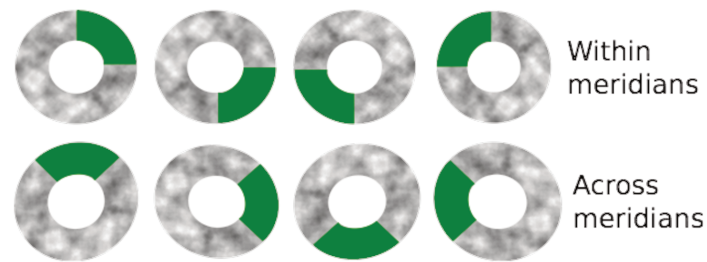
Figure 2.2.7. Block cues used in Experiment 2b.

2.2.4.2 Results

We did not find an effect of range position on the flash grab illusion (Table 2.2.2, $t_{(11)} = 1.6$, $p = 0.13$). Additionally, there was no significant difference in the flash grab between the blocks involving horizontal and vertical meridians ($t_{(11)} = -1.6$, $p = 0.14$).

Condition	Flash Grab(°)	n	SE	CI
Within Quadrant	25.79	1876	1.2	[23.78 27.77]
Across Meridians	26.71	1939	1.3	[24.56 28.78]

Table 2.2.2 Results of Experiment 2b.

2.2.4.3 Discussion

In Experiment 2 we manipulated the spatial range of attention to quantify the reduction of the flash grab illusion for expected targets. A similar paradigm has been previously used to demonstrate that decreasing certainty regarding the location of the target results in slower reaction times and decreased accuracy in a detection task (Mangun & Hillyard, 1988; Voytek et al., 2016), consistent with the effects of endogenous spatial attention. Our results confirmed that narrow attentional distribution results in a weaker flash grab. We further showed that this attentional benefit is mediated by the size of the attention shift required to move from one target to another, and this effect cannot be explained by response bias.

The influence of target predictability was previously demonstrated in other motion-induced mislocalizations. Baldo and Namba (2002) showed that spatial predictability of the flash reduced flash-lag effect. In their study, the stimulus was a pair of dots rotating around the fixation point. A third dot (target) was flashed at one of the two possible locations in a predictable (fixed or alternating between the two) or unpredictable (randomly chosen) manner. In terms of distribution of attention, their design compared narrowly focused attention with attention distributed between the two locations, 180° from each other. The flash lag was observed in all conditions, and the illusion was the smallest with the fixed target position. Our results confirm this finding for flash grab, and show the possibility of more fine-tuned attentional modulation.

The second part of our findings concerns the increase of flash grab as a function of the distance between the targets in successive trials. This result suggested that on each trial attention was to some extent refocused to the perceived location of the target, and if the subsequent target was further away, it increased the attentional delay to reach the new target. Interestingly, intertrial distance predicted the magnitude of the illusion only when the focus of attention was 90° or lower, indicating that the distance affected delay only over short distances. In fact, the flash grab was not significantly reduced when attention was directed to one hemifield compared to 360° condition.

Attentional explanations of motion-induced position shifts usually relate the effects of distance to the time it takes for attention to shift its focus to the target (Kirschfield & Kammer, 1999; Müsseler & Ascherschleben, 1998; Baldo & Klein,

1995). It is assumed that this shift takes time, during which the target itself (Fröhlich effect) or its moving counterpart (flash lag) continues to move, creating the mislocalization. In the case of the flash grab, the flash could be preattentively bound to a specific location on the moving texture and perceptually shifted towards this location after the attention shift is completed (e.g. Humphreys, 2001; Blaser, Papathomas & Vidnyanszky, 2005). We attempted to test this proposal in Experiment 2b by measuring flash grab under the conditions where attention shifts are expected to be slower (across meridians), but we did not observe the expected increase in illusion. However, it is not clear whether our manipulation was effective in slowing down attention shifts, since the meridian crossing effect is not always present with exogenous attention shifts (Egly & Homa, 1991; Reuter-Lorenz & Fendrich, 1992; Chica, Bartolomeo & Lupiánez, 2013).

An alternative explanation of distance-dependent attention effect on flash grab comes from the evidence that attention is directed towards a specific location in a graded fashion, with attentional benefits typically weakening with the distance between the cue and the target (LaBerge, 1983; LaBerge & Brown, 1986). In case of flash grab, attention could downweight irrelevant motion signal in favour of position information, thus protecting the target from motion-induced shift. The closer the target is to the current focus of attention, the more effective is the filtering out of motion and the less illusion is experienced. This is similar to modulation of flash lag by attention set, where asking participants to attend to the stationary flash instead of the moving object reduces the illusion (Gauch & Kerzel, 2009). These two explanations are not mutually exclusive and both mechanisms could independently modulate flash grab.

2.2.5 Experiment 3

Experiment 1 unexpectedly showed an increase in flash grab when the target appeared at a predictable time but at an unpredictable location. It has been demonstrated many times that attention can be intentionally drawn to the moment of target onset, facilitating perception (e.g. Coull and Nobre, 1998; Naccache et al., 2002; Correa, Lupiáñez, Madrid & Tudela, 2006; Vangkilde, Coull & Bundesen, 2012). Here we test if the temporal variability of the target event (and the background

reversal) affects the flash grab magnitude. To explore the possible interaction between spatial and temporal attention, we tested the effect of temporal variability with predictable (360° range) and unpredictable (0° range) target locations.

2.2.5.1 Method

Participants

Eight healthy adults (4 male, mean age = 23.2 years, SD = 2.7, with a range of 19 to 29) participated in the experiment. All gave written informed consent prior to the start of the experiment and received monetary compensation for their time. Three of them participated in the Experiment 2a.

Stimuli and apparatus

Stimuli and experimental set up were similar to the Experiment 2a with the following changes. Motion duration (i.e. the time from motion onset to its reversal and target presentation) was variable between trials. Within each block, the average duration of motion before the reversal was 700ms (190° rotation). The exact duration of motion was drawn from a uniform distribution with a mean of 700 ms and a range determined by the type of the block (see the description below).

Procedure and design

Trial and block structure was similar to the Experiment 2a with the following changes. Only two spatial conditions were tested (0° range and 360° range) in different sessions. In both sessions, block cues indicated the temporal predictability of targets for the current block (± 0 ms; ± 80 ms; ± 150 ms; ± 300 ms). These values were chosen to match the spatial ranges tested in Experiment 2a (e.g. with the speed of 270°/s, motion travels 45° in approximately 160 ms). In the 0° range session the cue also indicated the physical position of the target for the block. The spatial location of the target was randomly chosen for each trial in 360° range session, and for each block in 0° range session. The duration of motion in each trial was randomly chosen from a uniform distribution within the cued range. There were 8 blocks per condition, totalling 512 trials per subject.

Before the experiment, subjects practiced the task with all temporal ranges (at least 4 blocks), to make sure they understood how long the interval of interest was in each case.

2.2.5.2 Results

The data were treated in the same way as in Experiment 2a. A total of 3840 trials (4% of trials removed as outliers) were submitted to a two-way repeated measures ANOVA with temporal variability (4 levels) and spatial variability (2 levels) as factors. Figure 2.2.8 shows the results of the experiment.
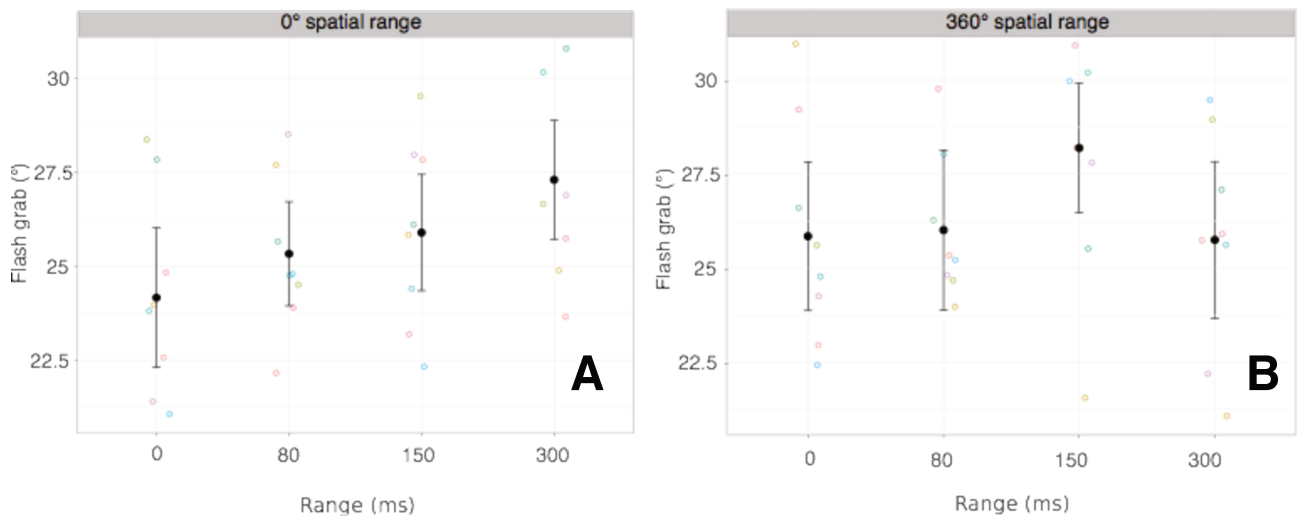
Figure 2.2.8. Results of Experiment 3. Panel A shows flash grab measurements across all temporal ranges for the sessions with 0° spatial range, Panel B — with 360° spatial range. Colored dots show individual participants, black dots are sample averages. Error bars are between-subjects 95% CIs.

Neither factor was found to modulate the magnitude of the flash grab illusion (Temporal range: $F_{(3, 21)} = 1.48$, $p = .247$, $\eta^2 = .08$; Spatial range: $F_{(1, 7)} = 0.48$, $p = .509$, $\eta^2 = .005$). Their interaction also did not show significant effect on the illusion ($F_{(3, 21)} = 2.47$, $p = .009$, $\eta^2 = .13$). Interestingly, the mean illusion values in this Experiment are slightly higher than the ones found in similar conditions in Experiment 2a. Specifically, when both target position and timing are stable within the block, mean flash grab magnitude was 19°(±12°) in Experiment 2a, and 25°(±18°) in Experiment 3. With a random target position and stable time, the flash grab was

24°(±13°) in Experiment 2a, compared to 26(±15°) in Experiment 3. Although these comparisons are exploratory, this is a similar trend to that observed in Experiment 1, where a target presented at an unexpected location was subject to more flash grab when its timing was expected (Time Control Condition).

2.2.5.3 Discussion

This experiment was aimed at manipulating temporal predictability of flash grab targets. We used a method similar to Experiment 2, varying the size of the temporal window where the target was expected. We hypothesised that similarly to spatial attention, narrowing the focus of temporal attention would reduce the flash grab illusion. This effect was not observed in the data. Moreover, we failed to replicate the main finding of Experiment 2: spatial predictability of the targets (perfectly predictable, 0°, vs unpredictable, 360°) did not affect the magnitude of flash grab. Finally, the illusion was on average larger in this experiment than in the comparable conditions of Experiment 2, especially for the spatially cued targets.

Previous studies investigating temporal predictability of targets with motion-induced position shifts found inconsistent results. Vreven and Verghese (2005) studied temporal predictability of the flash lag illusion. They cued the occurrence of the target by presenting a series of beeps, one of which coincided with the flashed object. They found that flash lag effect was smaller when the timing of the flash was cued, compared with the no cue condition. They also found that spatial cue combined with the temporal cue reduces the illusion more than either of the cues presented separately. A similar technique was used by Rotman, Brenner and Smeets (2002) to study target shifts during smooth pursuit eye movements. In their study subjects pursued a moving target that flashed somewhere along its trajectory. The flash could be temporally cued by rhythmic warning beeps, but these beeps had no significant effect on the motion-induced shift. By contrast, spatial cuing influenced the illusion. Overall, the effect of temporal cues, even if detected, is usually smaller than the effect of spatial cues. In our procedure the temporal cues were not explicit, as is the studies described above.

We manipulated the length of the temporal interval containing the flash, which could be a less effective way to control temporal attention. Also, temporal cues may have inadvertently drawn participants' attention to the moving part of the stimulus. A region of space can be attended to independently from tracking the motion. By contrast, a period of time can't be independently selected without attending to the surrounding stimulation. This side effect of temporal cueing also explains why the illusion becomes larger when time is attended to. Any attentional benefits coming from target predictability can be superseded by the effect of motion tracking.

2.2.6 General discussion

The goal of this study was to determine if target predictability decreases the effect of flash grab illusion. Experiment 1 showed that flash grab is smaller for targets appearing at expected locations. Experiment 2 showed that the flash grab changes with the distribution of attention, with a narrower attention focus resulting in smaller illusion and stronger dependence on the distance between the focus of attention and the target. Finally, Experiment 3 showed that temporal predictability doesn't modulate the flash grab illusion.

Overall, these results are in line with a number of studies investigating target predictability in the other motion-induced position shifts. Spatial predictability or cuing of spatial attention attenuates most illusions of this family: flash lag (Namba & Baldo, 2004; Vreven & Verghese, 2005), Fröhlich effect (Müsseler & Ascherschleben, 1998), representational momentum (Hayes & Freyd, 2002). Our results add the flash grab illusion to this list. It has been argued that time-consuming attention shifts to the moving object are responsible for flash lag and Fröhlich effects (Müsseler & Ascherschleben, 1998; Baldo & Namba, 2002), and it is possible that a similar mechanism is implicated in the flash grab illusion.

A separate line of studies on motion-induced position shifts is concerned with attentional tracking of motion. Motion processing literature suggests that there are at least two types of motion perception (Julesz, 1971; Anstis, 1980; Braddick, 1980; Cavanagh & Mather, 1989). A low-level motion system is based on the responses of directionally selective cells in the early visual areas when they are stimulated by the motion energy in their receptive fields. High-level motion system, also sometimes

called attentional tracking (Verstraten, Cavanagh, & Labianca, 2000), is based on the analysis of position (Seiffert & Cavanagh, 1999). It has been demonstrated many times that high-level motion is sufficient to produce motion-induced mislocalisations even in the absence of low-level motion (Watanabe, Sato, & Shimojo, 2003; Shim & Cavanagh, 2004; Tse, Whitney, Anstis & Cavanagh, 2011). Moreover, it has been suggested that at least some of the motion-induced shifts only happen when high-level, attentional mechanism is involved (Cavanagh & Anstis, 2013; Section 2.1.4 of this thesis). Based on our results, motion tracking and target predictability counteract each other, with the former creating the illusion and the latter modulating its magnitude. However, the effect of attentional tracking is much larger that any possible attenuation provided by the spatial cues, therefore some flash grab is perceived even when the target is perfectly predictable and fully attended.

De Vito et al. (2015) presented flash grab stimuli to the patients with left visual neglect and demonstrated that the illusion is significantly reduced when it is presented in the neglected space, where attention is impaired. This result confirms that attentional processing is crucial for flash grab. Importantly, neglect patients demonstrate prominent deficits of exogenous, but not endogenous attention (Bartolomeo et al. 2001). They can attend to a certain location and locate the target, but their impaired exogenous attention doesn't allow them to fully perceive the motion surrounding the target, resulting in weaker flash grab. In a way, our results mimic the same imbalance in healthy observers. Narrow focus of attention moves the attentional resources towards the perception of the target, weakening the impact of background motion and attenuating flash grab.

Whitney (2002) proposed that possible explanations of motion-position interactions roughly fall into two categories. The first suggests that the timing of perception determines the perceived position, and the second suggests a purely spatial mechanism that takes into account motion signal. Attention to target and attention to motion can represent both these classes of explanation. Attention to target likely involves transient shifts of attention that underlie temporal differences in processing, while attention to motion involves continuous tracking, possibly resulting in the predictive shift of the coded location of the object.

2.3 Motion induced distortion of shapes

Abstract

Motion, position and form are intricately intertwined in perception. Motion distorts visual space, resulting in illusory position shifts such as flash-drag and flash-grab effects. The flash-grab displaces a test by up to several times its size. This lets us use it to investigate where the motion-induced shift operates in the processing stream from photoreceptor activation to feature activation to object recognition. We present several canonical, highly familiar forms and ask if the motion-induced shift operates equally on all components of the form. If it did, we could conclude that the effect occurred after the elements of the form are bound. However, we find that motion-induced distortion affects not only the position, but also the appearance of briefly presented canonical shapes (square, ellipse and letter T). The results showed that motion asymmetrically distorted both contoured and filled shapes. Features of the flashed target that were orthogonal to the background motion were shifted in the direction of motion more than those parallel to the background motion. Contoured shapes were affected more than filled shapes, and the strength of the distortion depended on the contrast of the moving background. This not only supports an orientation specificity in the motion–induced shift but also indicates that the shift operates before the features are bound, even for highly familiar shapes like squares and circles.

2.3.1 Introduction

Successful interaction with a dynamic environment requires rapid integration of information about form, motion and position of objects. Psychophysical studies offer clear evidence that such interactions exist. For instance, motion biases the perceived location of stationary (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990) and moving (Fröhlich, 1923; Freyd & Finke, 1984) stimuli, as well as stimuli briefly presented some distance away from the motion (Whitney, 2002; Whitney & Cavanagh, 2000). One of the largest known motion-induced position shifts occurs when an object is flashed on top of the moving background as it reverses direction (flash-grab, Cavanagh & Anstis, 2013). Flash-grab shifts the perceived the position of the object in the direction of motion after the reversal by up to several degrees of visual angle.

A number of studies indicate that motion not only shifts the perceived position of objects, but also alters their appearance, such as size and shape (Ansbacher, 1944; Anstis, Stürzel & Spillmann, 1999; Zanker, Quenzer & Fahle, 2001). Often these perceptual deformations accompany motion-induced position shifts. For instance, Shim and Cavanagh (2004, 2006) reported that apparent motion can shift the perceived position of the stationary flash presented near the motion path. Khuu, Phu and Khambiye (2010) using similar conditions revealed that concurrently with the position shift, apparent motion distorts the shape of an object presented in its way, such as the shape appears elongated along the axis of motion. Another example of simultaneous position shift and deformation is found in the stationary Gabor pattern that contains sinusoidal grating motion. The perceived position of such stimulus is biased towards the direction of motion (De Valois & De Valois, 1991), and its perceived shape is elongated, with the leading edge extended in the direction of motion (Tsui, Khuu & Hayes, 2007).

The studies described above used spatially uncertain Gaussian-profile stimuli, however, perceptual distortions also affect well-defined shapes. Zanker et al. (2001) measured the perceived deformation of continuously moving contours and found that a straight line appeared bent in the center towards the direction of motion, with its endings trailing the central segment. This result was interpreted as a bottleneck in the

mechanism determining the position of the moving stimulus, causing a distortion between coherently moving parts of the single object.

The purpose of the current study is to determine whether the flash-grab illusion is also accompanied by perceptual deformation of the shifted stimulus. Specifically, we are interested whether the parts of the briefly presented target are shifted by motion equally, or, as in case of Zanker et al. (2001), certain parts of the stimulus will be shifted stronger than others. One possibility is that motion shift is uniformly applied to the different parts of an object, or to the object as a whole. In this case the spatial relationship between the parts will be preserved, and the target will appear shifted, but not distorted. Alternatively, the amount of illusory shift could depend on the particular feature of the shape. In this case, the target will appear both shifted and distorted.

2.3.2 Method

Participants

Ten observers (6 female, 1 author, mean age 26, standard deviation 3) participated in the experiment. All observers had normal or or corrected-to-normal vision. Study protocols were approved by the Université Paris Descartes Review Board (CERES) in accordance with French regulations and the Declaration of Helsinki. Informed consent was obtained in writing prior to participation. Participants were reimbursed for their time. All observers (except for one author) were naïve to the exact purposes of the experiment and weren't familiar with the flash-grab illusion.

Apparatus and Stimuli

Participants were seated in a quiet dimly lit room. Participant's head was positioned on a chin rest with a forehead stabilizer at 130cm of the projection screen that subtended 60 by 34 degrees of visual angle [dva]. Stimuli were displayed with a PROPixx projector (VPixx Technologies Inc.) at 120Hz. The experiment was programmed and presented with MATLAB using Psychtoolbox (Brainard, 1997; Pelli, 1997) and Eyelink toolbox (Cornelissen, Peters, & Palmer, 2002) and was run on an Apple computer. The right eye was monitored using an Eyelink 1000 Plus desktop mount (SR Research Ltd.) at 1000Hz.

Figure 2.3.1. Target shapes and their adjustable parameters. Middle column corresponds to the reference shape. Assuming that motion changed direction from clockwise to counterclockwise, left column corresponds to the distortion in the direction of motion before the reversal, right column – to the distortion in the direction of motion after the reversal (flash-grab).

All stimuli were presented against a mid-gray background. A black fixation point (0.25 dva in diameter) was always presented in the middle of the screen. The stimulus consisted of an annulus (10 dva inner radius, 7.5 dva outer radius) divided into four alternating light and dark sectors. The contrast of the annulus varied from trial to trial and could take one of the five values: 0%, 20%, 40%, 60%, 80%. The annulus rotated at a speed of 135°/s and reversed direction every 90° (80 frames). The polarity of the annulus and the starting direction of motion were counterbalanced within each condition. Every second reversal, motion stopped for 50 ms (6 frames) and a green ellipse (2.5° wide and 4° long) with a black target on it was presented on

90

the top sector edge. The precise position of the sector edge during the reversal was jittered from trial to trial (±23.5° of rotation). There were five conditions depending on the shape of the target: filled rectangle, contour rectangle, filled ellipse, contour ellipse, and T-shape.

Based on the pilot observations we developed a range of possible shape distortions (Figure 2.3.1). For each case we hypothesized a distortion that would be caused by shifting the leading edge of the shape in the direction of its motion. Such a shift would result in the square becoming a wider rectangular shape (Figure 2.3.1, rows 1 & 2); a circle becoming an asymmetric ellipse with the blunter side facing the direction of motion (Figure 2.3.1, rows 3 & 4); and a T becoming an inverted L (Figure 2.3.1, row 5). We mirrored these distortions to create a full range of adjustments. Therefore, the reference shape was in the middle of the adjustment range and was separated from each end of the range by 40 steps.

Contours were always 0.2 dva thick. Rectangles were 1.5 dva high and had adjustable width (from 0.5 dva to 2.5 dva). Elliptical shapes were created by merging two complementary halves of ellipses with the same minor axis (1.5 dva) and variable major axes. The width of the resulting asymmetric "egg"-shape was always 1.5 dva, and the degree of asymmetry was adjustable. Finally, T-shape was constructed from a 1.5 dva wide horizontal segment, and a 1.5 dva long vertical segment. The horizontal segment was fixed in the middle of the green background ellipse, while the vertical segment could be moved in horizontal plane.

Procedure

Trials were self-paced. Before each trial, a reference shape (symmetrical, middle row of Figure 2.3.1) was shown in the middle of the screen. During the trial observers had to fixate in the middle of the screen and adjust the shape presented during motion reversals to match the reference shape shown before.

Motion was on screen continuously until the response was submitted. The initial appearance of the shape was randomly drawn from all its possible states. Eye position was controlled 300ms before and after the presentation of the target. If the gaze was detected outside the fixation window during this period (1 dva around fixation), the trial was interrupted. Although targets were on screen only briefly during reversals, participants could keep changing the shape in between presentations, evaluating the result of the adjustment when the target came up. Responses were

centered and normalized, so that 0 corresponded to the reference shape, negative responses corresponded to the distortion in the direction of motion before the flash, and positive responses – in the direction of motion after the flash (i.e. in the flash-grab direction).

Two factors were manipulated in the experiment: target shape and background contrast. The experiment was carried out in two sessions of approximately one hour each. Trials from different contrast and shape conditions were presented in a random
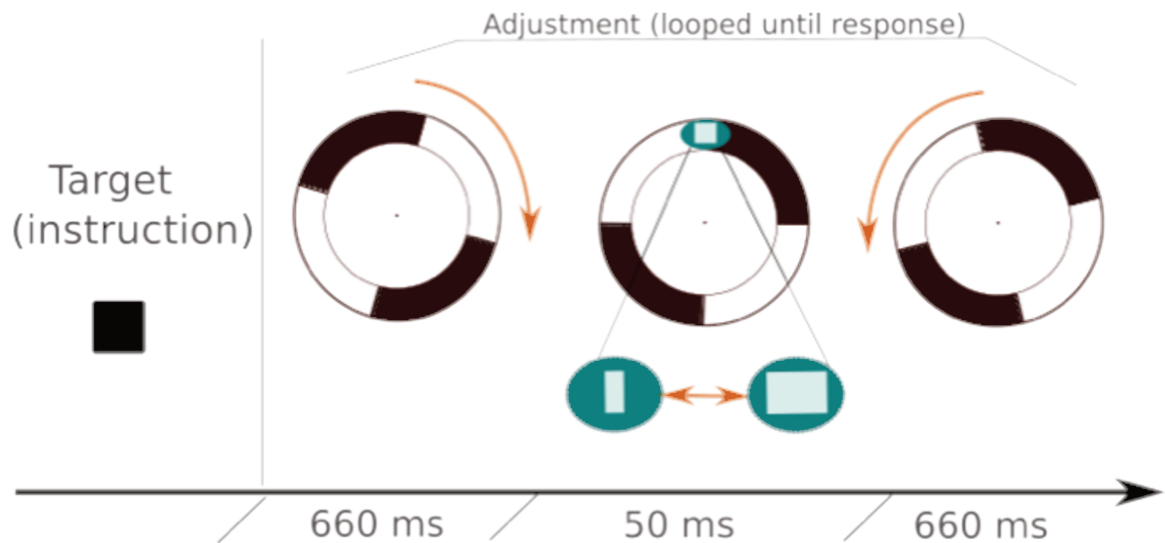
order.

Figure 2.3.2 Trial sequence. Each trial started with the presentation of the target shape. Stimulus was then presented in motion, with the adjustable target briefly flashed every second reversal.

2.3.3 Results

The analysis was aimed at two questions: a) whether each of the shapes is distorted by motion, and b) whether this distortion is mediated by the background contrast. Trials from different shape conditions were analyzed separately. Using single-sample t-tests, responses were tested against the zero point to determine whether the shape was subject to distortion. Means of the responses were then subjected to a one-way repeated measures ANOVA with background contrast as a factor. Data for each shape and contrast condition is presented on Figures 2.3.3-5.

Rectangle

Both filled and contoured rectangles were significantly expanded by motion (Figure 2.3.3; $t_{(9)} = 8.11$, $p < .001$). However, the distortion increased as a function of background contrast for contoured ($F_{(4,36)} = 10.69$, $p < .001$, $\eta^2 = .47$) but not for filled rectangles ($F_{(4,36)} = 1.2$, $p = .32$, $\eta^2 = .09$).

Figure 2.3.3 Distortion of rectangular shapes as a function of contrast. Top row represents the shape perceived as a square in each condition. Error bars represent ±SEM.

Ellipses

Both filled and contoured ellipses were distorted by motion such that the side of the ellipse leading after the reversal was pointier, and the opposite side was blunter than the physically presented shape (Figure 2.3.4; Contoured: $t_{(9)} = 16.02$, $p < .001$; Filled: $t_{(9)} = 5.34$, $p < .001$). Contoured ellipses were distorted more than filled ellipses ($t_{(9)} = 11.1$, $p < .001$) and ANOVA showed a linear increase of distortion with contrast for contoured ellipses only (Contoured: $F(4,36) = 5.34$, $p = .01$, $\eta^2 = 0.19$; Filled: $F(4,36) = 0.5$, $p = .67$, $\eta^2 = .056$).
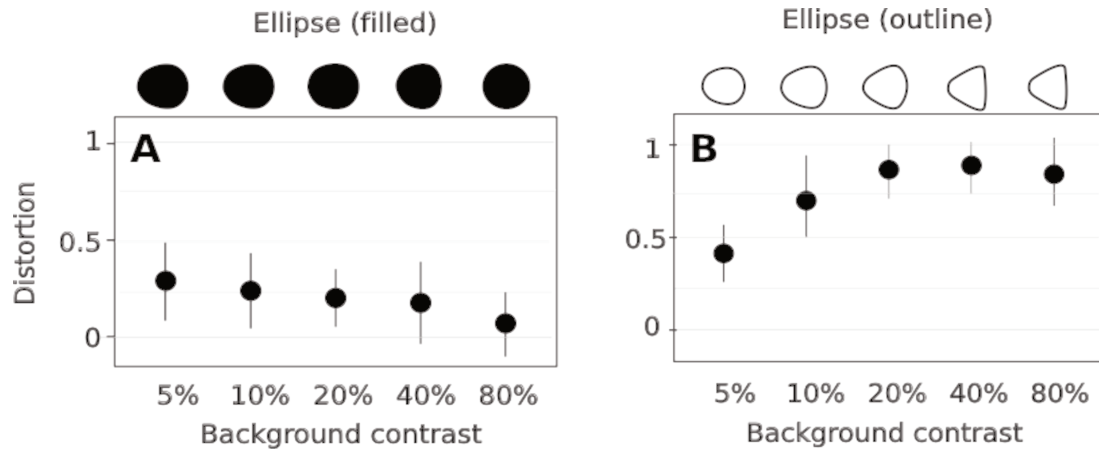
Figure 4 Distortion of elliptical shapes as a function of contrast. Top row represents the shape perceived as a circle in each condition. Error bars represent ±SEM.

T shape

The vertical segment of the T-shape was shifted towards the end of the horizontal segment which was leading after the reversal (Figure 2.3.5; $t_{(9)} = 9.5$, $p < .001$). There was a significant linear increase of distortion with contrast ($F_{(4,36)} = 2.9$, $p = .034$, $\eta^2 = 0.18$).

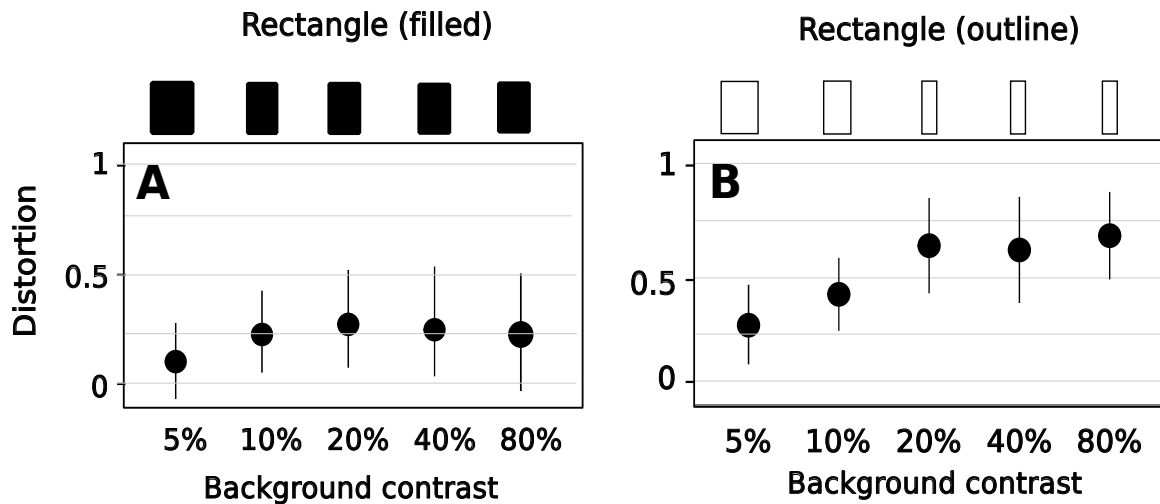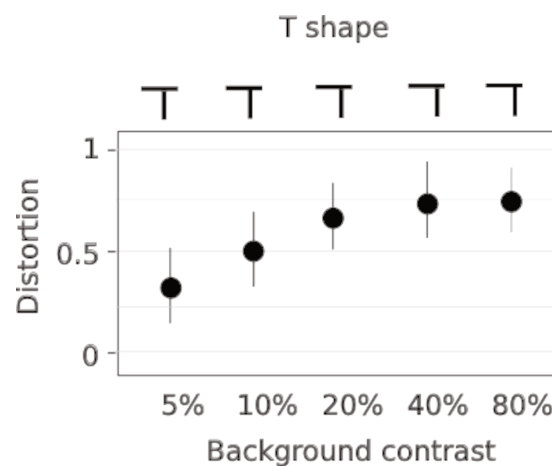*Figure 5 Distortion of letter T as a function of contrast. Top row represents the shape perceived as a T in each condition. Error bars represent ±SEM.*

Overall, we observed distortions of all briefly presented shapes. The distortion was driven by the position shifts of the features orthogonal to the background motion and aligned with the moving contrast edge of the background (vertical stem of the T, vertical sides of the rectangle, minor axis of the ellipse). These distortions were

94

stronger for contours than for filled shapes, and were mediated by the contrast of the moving edge.

2.3.4 Discussion

The experiment showed that when a briefly presented target is perceptually shifted by the background motion, it also becomes distorted, as different components of the target have different sensitivity to the motion-induced position shift. The observed distortions are consistent with the larger shifts of the features aligned with the moving contrast edge. This results in the asymmetric elongation of the shapes and a change in their proportions.

Interestingly, in most cases, the strength of the perceived distortion depended on the background contrast, showing a profile different from the flash-grab itself (Cavanagh & Anstis, 2013). The size of the flash-grab illusion increased with the contrast of the moving texture up to around 5% contrast, where it saturated. This property of the illusion was linked to the function of magnocellular pathway, which exhibits high contrast gain but saturates at fairly low contrast (Derrington & Lennie, 1984; Snippe, 1998). Distortions, however, show linear increase up to 20%-40% contrast, suggesting that the coding of local spatial configurations relies on a different processing route.

Any sudden displacement of a complex object results in a conflict between the strong motion signal of the overall shape, and the weak motion signal of its details. This conflict can be resolved by attributing the motion of the most salient feature to all the other features – a process termed "motion capture" (Ramachandran, 1981; Ramachandran & Anstis, 1983; Ramachandran & Inada, 1984). For instance, if a moving low-frequency grating is superimposed on a field of dynamic random dots, the dots will appear to move along with the grating, as if they were rigidly attached to it (Ramachandran & Cavanagh, 1986). Motion capture is the most effective if the two motion vectors are parallel. The distortion of flash-grab targets resembles this process. The motion of the salient contrast edge "captures" the features aligned with it but not the features orthogonal to it. According to the motion capture literature, the assignment of motion to a contour depends on whether the contour can produce motion signal in the background direction (Ramachandran, 1986). Since features orthogonal to the moving edge wouldn't produce a strong motion signal if they

95

continued moving, these features remained intact. This logic can also explain why filled shapes are less affected by distortion. Low spatial frequencies of filled shapes contain all orientations, preventing effective "capture" by the moving edge.

In accounting for the motion-induced position shifts such as flash-grab, a major issue is to determine the stage of visual processing at which the motion-position interaction occurs. A number of studies demonstrate that motion can influence coding of position early in the processing stream (Fu, Shen, Gao, & Dan, 2004; Kosovicheva et al., 2012; Hogendoorn, Verstraten & Cavanagh, 2015). However, another line of research suggests a much higher-level locus of interaction (Cavanagh & Anstis, 2013; Linares & Lopez-Moliner, 2007, Tse, Whitney, Anstis & Cavanagh, 2011; de Vito et al., 2015). In this study, we were able to demonstrate that motion-induced shifts operate on separate features of an object in an orientation-specific way, which points to the early motion-position interaction. Hayes (2000) reported that grouping of visual elements in the perceptual whole is based on the perceived, not veridical positions of the elements shifted by motion. Our result is in line with this finding, showing that motion-position interaction precedes feature binding.

Eye movements are a well-known source of perceived distortions and displacements. When a bar is briefly displayed immediately prior to the saccade, its position is shifted toward the saccade goal. Depending on the position of the bar, this shift can be in the direction of the saccade, or in the opposite direction compressed (Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). Similarly to this presaccadic shift, motion-induced distortion applies differentially to the orthogonal and parallel components. However, there is an important difference. Because of the presaccadic compression, observers tend to underestimate the number of elements when multiple bars are presented at the saccade goal just before the saccade. However, when a square of a matching width was presented instead of multiple bars, the width of the square was unchanged by the saccade, suggesting that presaccadic compression affects each element of the group separately as long as they are not bound into a global shape (Matsumiya & Uchikawa, 2001). According to our findings, even the elements of a highly familiar shape are distorted by motion, suggesting that global shape does not protect against this type of mislocalization. However, despite the relative shift of the components, stimuli in our experiment preserved their basic structure, and their elements were still perceived as belonging to a single shape. This illustrates that motion-induced distortions and contour binding /

object recognition mechanisms interact to support coherent representation of the word.

Part III. General discussion

At the beginning of the dissertation I set out three questions about motion-induced position shifts:

- Are they caused by the shifts of spatial attention?
- Do they require attentional tracking?
- Do they happen early or late in the processing stream?

Now I will summarise and discuss the findings related to each of these questions.

3.1 Shifts of attention

The first question was addressed by experiments described in sections 2.2 and 2.3. Section 2.2 includes two experiments on the Fröhlich effect. In the first experiment we replicated a previously reported result: invalid attentional cues produced larger perceptual shifts, although the Fröhlich effect was present even when the motion onset location was validly cued. In the second experiment we tested whether the illusion depends on the delay in attention's arrival. This hypothesis is the direct prediction of the attention-shifting explanation, which our data confirmed. Again, although the Fröhlich effect was small with valid cuing (in fact, smaller than normally reported in the literature), it was reliably observed in all subjects. In sum, these experiments support the attention-shifting exlanation of the Fröhlich effect, but do not offer a new insight on why it occurs even at a directly attended location.

The study reported in section 2.3 tested for the first time the effects of attention on the flash-grab illusion. The first experiment compared the flash-grab effect produced by spatially expected and unexpected targets, finding again that knowing where the target will appear reduces the motion-induced shift. This result suggests that the flash-grab may be produced by the same mechanism as the Fröhlich effect and the flash-lag. In the second experiment we wanted to test whether the flash-grab is affected by the distribution of attention before the target arrives. We found that if attention is focused over one quadrant of the visual field or narrower, the

flash-grab is smaller. Under these conditions we were able to capture very subtle differences in the magnitude of the illusion, correlating it with the distance between the consecutive targets from one trial to the next. It is highly likely that this variation is again caused by the shifts of attention, as a narrower target distribution limits the "search area" attention has to cover after the target onset. However, it is also possible that the attentional distribution changes the way positional information is processed even before any attentional shift is initiated. Attention is a tool the visual system uses to prioritise information and optimise processing. In case of the flash-grab stimulus it is faced with two streams of information: the flash itself and the moving background. The key to the veridical perception of the position of the flash is ignoring the information coming from the background. It is possible that narrower attentional focus allows the visual system to downweight the motion signal and to amplify positional information provided by the flash itself. This explanation can also accommodate the effect of the distance. If attention has a Gaussian-like distribution, attentional facilitation will gradually weaken with distance from its focus. Does attention come into play before the target onset, after or both? The experiments reported here cannot rule out either option. In future studies it would be informative to link the magnitude of the flash-grab illusion to the pre-target distribution of attention while controlling for shifts of attention.

In sum, we added evidence to the attention-shifting hypothesis of the motion-induced position illusions. Even if the shifts of attention are not the cause of mislocalisations, they are certainly a significant contributor. One of the theories of motion-induced position shifts suggests that they are driven by the differences in processing delays between moving and static stimuli (Whitney, 2002). It is possible that attention shifts, being able to delay the percept, contribute to this latency difference.

3.2 Attentional tracking

The question that was unanswered by the cueing experiments is why even expected targets are displaced by motion. Attention-shifting explanation is very tempting in that it is almost impossible to rule it out. It is rather easy to divert attention from the upcoming target and explain the resulting perceptual difference by

the larger attentional delay. However, the opposite manipulation – attracting attention to the future position of the target – proves to be more controversial. Even if attention is initially shifted towards the target, additional shifts may be required upon target onset. Therefore, to test the role of attentional tracking, we needed to carefully control for attention shifts. To do so we constructed a stimulus that requires global assessment of the visual scene (described in the Experiment 3 of the section 2.2, also see Supplementary demonstrations). Importantly, the building blocks of this stimulus come from the Fröhlich effect tested in the previous experiments, therefore we know that attentional cues attenuate the effect they produce. Our new stimulus also minimises the chances of individuating a separate target: it combines high eccentricity, crowding, and a global detection task. We showed that this global assessment of the scene leads to the loss of the Fröhlich effect, and this loss is more dramatic than in case of valid cueing.

Have we proved that attentional tracking is essential for motion-induced shifts? As Laplace famously said, "The weight of evidence for an extraordinary claim must be proportioned to its strangeness." Here we report one attention-reducing manipulation leading to the loss of the effect and contrast it to multiple cueing studies showing that reducing attention at the target site amplifies the effect. Besides, we considerably altered the paradigm and the task in order to prevent attentional tracking. However, when comparing the effects of different attentional manipulations one should carefully consider what exactly about attention is being changed. A Posner-like cue merely diverts attention, delaying its arrival at the target. It is primarily a temporal manipulation. A global attention task, on the other hand, makes individual elements inaccessible for attentional processing. It does not delay attention -- it changes its scope. In fact, in our group-Fröhlich stimulus motion was completely irrelevant to the task of the observers, their task was to detect a specific configuration. I mentioned above that attention to the motion and attention to the target may be competing and counteracting each other in the motion-induced position illusions. Here again we pushed the observers to look for the target, minimising the possibility of attention shifts and tracking of motion, and observed a large reduction or even absence of the Fröhlich effect. I believe that together with the results of other experiments suggesting attentional source of motion-induced shift (Kerzel, 2003; Linares & Lopez-Moliner, 2007; Cavanagh & Anstis, 2013; De Vito et al., 2015), this

creates a compelling case. How and why exactly attentional tracking is producing the shifts is an interesting question for future studies.

3.3 Stage of processing

The motion-induced position shifts may be a consequence of low-level motion or a product of attentional tracking and one goal of these experiments is to determine the level at which the effect arises. Specifically, where in sequence of visual processing stages does the physical position of the object get converted into its perceived position, shifted by motion signal. Studies reported in sections 2.2 and 2.3 suggest that this interaction takes place relatively late in the processing pipeline. Under the attention-shifting explanation, the only motion signal that counts is the one perceived between the target onset and the moment attention catches up with the target. Although exogenous attention shifts are rapid, most studies detect attentional benefits at least 100ms after the attention shift is triggered, allowing plenty of time for the analysis of the visual input. Attentional tracking is also a high-level process, so its involvement suggests late interaction. However, the experiment reported in section 2.4 adds to the evidence that motion influences the position somewhat early in processing, before visual features are bound together into an object. Are these two results in conflict?

Visual processing is usually pictured as a sequence of stages, where at each stage more complex features are processed and added to the final percept. Equally important is the timing of the processing. Lamme and Roelfsema (2002) proposed that the first, feed-forward sweep of visual information reflects preattentive perceptual stages, whereas feedback and recurrent processing are the basis of attentive vision. Given that frontal eye fields (FEF) and MT have short processing latencies, it is possible that during the motion-induced position shift feedback information coming from the higher areas 'clashes' with the information carried from the earlier stages, modulating the processing. Thus, the fact that motion-induced shifts produce shape distortions does not necessarily imply that this distortion is preattentive.

Kosovicheva et al. (2012) reported evidence of motion-induced shift in V1, however, this shift was several times smaller than the perceived illusion. They concluded that V1 represents the first step of the motion-induced shift, retaining much of the coding of the target's physical position. In our experiment although the shapes

are perceptually distorted, they still remain continuous, suggesting that global form has some influence over the percept. Together these findings may suggest that the site of the motion-position interaction is not located in a particular brain area or even at a particular processing stage. It is a gradual process of inferring the position of an object using diverse and often conflicting visual information.

In order to behave adaptively we need to react quickly and precisely to any changes in the environment. This necessarily involves the accurate perception of objects that are moving, appearing and disappearing. Given that we are remarkably good at interacting with this challenging environment, our visual and cognitive systems must have a solution for this task that overcomes processing, motor and other potential delays. This dissertation explored the link between motion processing and spatial attention using motion-induced position shifts as a diagnostic tool. We confirmed and added more details to the attention-shifting explanation of motion-induced position shifts and offered new evidence in favor of attentional source of these illusions. Nevertheless, much of the mystery of the motion-induced position shifts remains to be addressed.

Supplementary Table 1.

Linear mixed model fits (Section 2.2)

Formulas:

Model 1: FlashGrab ~ Range * PhysicalDistance + ((1 | Participant) + (0 + Range | Participant))

Model 2: FlashGrab ~ Range * PerceivedDistance + ((1 | Participant) + (0 + Range | Participant))

	Model 1			Model 2		
	B	*CI*	*p*	*B*	*CI*	*p*
Fixed Parts						
Intercept	**24.70**	**[21.77 27.62]**	**<.001**	**24.19**	**[21.27 27.10]**	**<.001**
Range 180°	-0.86	[-2.97 1.24]	.423	-1.03	[-3.11 1.06]	.335
Range 90°	-3.04	[-6.05 -0.03]	.056	-2.92	[-5.89 0.04]	.062
Range 45°	**-4.63**	**[-7.78 -1.48]**	**.007**	**-6.07**	**[-9.18 -2.96]**	**.001**
Physical Difference	-1.78	[-4.31 0.76]	.169			
Range 180° : Physical Difference	2.05	[-1.78 5.87]	.294			
Range 90° : Physical Difference	**5.54**	**[1.74 9.35]**	**.004**			
Range 45° : Physical Difference	**4.97**	**[1.12 8.82]**	**.012**			
Perceived Difference				-0.83	[-3.39 1.73]	.526
Range 180° : Perceived Difference				2.98	[-0.81 6.77]	.124
Range 90° : Perceived Difference				**6.22**	**[2.18 10.27]**	**.003**
Range 45° : Perceived Difference				**10.20**	**[6.09 14.30]**	**<.001**

	Model 1			Model 2		
	B	**CI**	**p**	**B**	**CI**	**p**
Random Parts						
Participants (n)		15			15	
Range (n)		4			4	
Observations		3054			3054	
AIC		23278.254			23245.291	

Supplementary demonstrations

In all the experiments reported here we used dynamic stimuli inducing illusory mislocalisations, which are best experienced in person. Unfortunately, videos are not supported by the current version of paper. Below are the links to some of the demonstrations available online.

Section 2.1 The Fröhlich effect

1. Fröhlich effect absent for a group: http://bit.do/FrohlichGroup
   Fixate on the dot in the bottom part of the screen. The motion seems to start the bars are horizontally aligned row-wise, which is consistent with their physical positions. This alignment indicated that the Fröhlich effect is not perceived.

2. Fröhlich effect observed for an individual item: http://bit.do/FrohlichSingle
   Fixate on the dot in the bottom part of the screen. Observe that bar which is oriented differently from the rest. At motion onset it seems to be tilted rightwards, although physically it is vertical.

Sections 2.2 & 2.3 The flash-grab effect

3. Flash grab is larger for unexpected stimuli: http://bit.do/FlashGrabShift
   Fixate in the middle of the screen.The flashes are presented in series of three: on the top, on the right, on the bottom and on the left. The location does not change inside the group, but the flash is perceived slightly shifted each time.

4. Flash-grab distorts shapes. http://bit.do/FlashGrabDistortion
   Fixate in the middle of the screen. The shape appearing inside the green disc is the letter T, however, most observers perceive an inverted L-shape.

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