THE INFLUENCE OF VISUAL TRANSIENTS ON THE PERCEPTION OF SPACE AND TIME

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CONTENTS

CHAPTER 1: Introduction

Perception takes time. In the primate visual system for example, there are delays on the order of 50-100 ms between light stimulating a location on the retina and the response of cortical neurons tuned to the corresponding location (Schmolesky, Wang, Hanes, Thompson, Leutgeb, Schall, & Leventhal, 1998). Although, it is an unresolved question where visual perception occurs (Ress, Kreiman, & Koch, 2002), nobody casts doubt upon that it involves cortical mechanisms (Crick & Koch, 1995). Thus, the visual perception of events inevitably lags behind their physical occurrence. This could suppose a difficulty for individuals to correctly perceive the environment and interact with it. Below, I will describe two non trivial problems associated to neural delays and two related visual illusions that have been used to study these problems.

The first problem involves the perception of moving objects. Judging the location of moving objects is important for avoiding obstacles or predators and for catching prey. But, considering a neural delay of 100 ms, for example, an object moving at a speed of 5 km per hour would be seen more than 10 cm behind its actual position. How are then interceptive behaviours, which require temporal accuracy to within several milliseconds, possible? The prevalent view is that the observed behavioral success is due to compensation at the higher cortical levels participating in motor output (Jordan, 1995). However, several investigators (Ramachandran & Anstis, 1990; De Valois & De Valois, 1991; Nijhawan, 1994), given the biological significance of visual motion, raised the possibility that in addition to motor compensation, neural delays may also be compensated at sensory levels. This problem has been extensively discussed in the context of the flash-lag effect (Nijhawan, 1994). In this illusion, a flashed object presented aligned to a moving object is perceived to lag the moving object.

The second problem arises if one considers brain modularity. It is commonly accepted that different visual attributes are processed in distinct cortical areas (Livingstone & Hubel, 1988). These different attributes may have different processing latencies. Assuming that the conscious experience of one attribute is related to the neural activity of the area that processes this attribute (Zeki, 2003) this could lead to a failure in experiencing a unified visual awareness. This problem is traditionally known as the binding problem (Wolfe & Cave, 1999). Does the brain compensate for differences in processing time, such that a unified percept is recovered that mirrors the synchrony of real-word events? This question has been studied among others by means of the color-motion asynchrony illusion. In this illusion, a stimulus that changes its color and motion direction, the change in color has to lag behind the change in direction in order to perceive both changes in synchrony (Moutoussis & Zeki, 1997a).

In the last ten years more than a hundred of investigations have been published in refereed journals about the flash-lag effect. In the first section of the Introductory Chapter, we will summarize the more important results. Afterwards, in the Introduction section of every chapter concerning this illusion (*Chapters 2, 4 and 5*) we will explain in more detail the findings related to the experiments we have conducted. For the color-motion asynchrony illusion, the amount of research done is smaller. So, the previous research about this illusion will be summarized in the Introduction section of the chapter describing color-motion asynchrony experiments (*Chapter 3*).

1. The flash-lag effect

1.1. Motion extrapolation explanation

In 1994, Romi Nijhawan reported a mislocalization effect which termed as the 'flash-lag' effect (Nijhawan, 1994; for a review see Krekelberg & Lappe, 2001; Nijhawan, 2002; Ögmen, Patel, Bedell, & Camuz, 2004). Several related effects of mislocalization had been reported before (MacKay, 1958; Mateeff & Hohnsbein, 1988), but the motion extrapolation hypothesis he proposed to solve the problem of neural delays renewed the interest on it.

Nijhawan (1994) presented observers a rotating bar made of three light segments. The inner segment was continuously visible and the two outer segments were flashed. Observers fixated the center of the bar. They saw that the two flashed segments appeared to lag behind the middle one. This is the flash-lag effect. The spatial lag increases linearly with the speed of the moving object (Nijhawan, 1994). Thus, the spatial lag divided by the speed is a temporal constant magnitude. Nijhawan found a value of 80 ms for this magnitude. This means that in order for the flash to be perceived aligned with the moving object the flash must be presented 80 ms before the moving object arrives at the position of physical alignment.

Interestingly, Nijhawan has also shown that the illusion is so strong that can produce visual decomposition of colors (Nijhawan, 1997). As expected, when a red bar is flashed overlapping a static green bar is perceived as yellow. But, when the green bar is in motion, not only the flashed bar is perceived to lag the moving green bar (flash-lag effect), but also is perceived as red.

According to the motion extrapolation hypothesis (Nijhawan, 1994), the visual system uses the motion signals to extrapolate the position of the moving object and in this way compensates for neural delays. So, according to this hypothesis the moving object is seen at its true position. However, the extrapolation cannot occur for the flash because of its short duration –which causes the flash-lag effect.

The major problem of the motion extrapolation explanation arises if one consider the so called flash-terminated cycle. In this condition the pre-flash trajectory of the moving object is indistinguishable from that of the standard display. However, simultaneously with the disappearance of the flash the moving object also disappears. The key result is that in this situation there is not flash-lag effect[1] (Eagleman & Sejnowski, 2000a). This finding is not compatible with the motion extrapolation account. As the disappearance of the moving

[1] Exceptions will be discussed in Chapter 6.

object is registered after a delay, compensation should cause the moving object to perceptually overshoot the termination point. Nijhawan proposes (Nijhawan, 2002) that the lack of overshoot in the flash-terminated condition could be due to a second mechanism that provide accurate position information at motion-termination. He thought that this second mechanism could be backward masking[2] (Bachmann, 1994; Enns & DiLollo, 2000).

A second problem of the motion extrapolation arises when one takes into account the effect of luminance on the illusion. It has been shown that neural latency increases when the stimulus luminance decreases (Lennie, 1981; Maunsell & Gibson, 1992). It has been also shown that when the latency of the moving object is increased by decreasing its luminance, the flash-lag decreases (Lappe & Krekelberg, 1998; Ögmen, Patel, Bedell, & Camuz, 2004; Purushothaman, Patel, Bedell, & Ögmen, 1998) and can even turn into flash-lead effect (Ögmen, Patel, Bedell, & Camuz, 2004; Patel, Ogmen, Bedell, & Sampath, 2000; Purushothaman, Patel, Bedell, & Ögmen, 1998). Contrary to this, the motion extrapolation hypothesis predicts that the flash-lag effect should remain constant because the perceived position of the moving object should coincide with its physical position.

1.2. Processing time differences explanation

According to the processing time differences explanation (Murakami, 2001; Ögmen, Patel, Bedell, & Camuz, 2004; Purushothaman, Patel, Bedell, & Ögmen, 1998; Whitney & Murakami, 1998), the flash-lag effect is explained because the visual system processes moving objects more quickly than flashed objects and these differences have a direct consequence in terms of perceptual experience.

The processing time explanation provides a natural explanation for the linear dependence on speed (Nijhawan, 1994) and the effect of luminance on the flash-lag effect. Decreasing the luminance of the moving object increases the latency to perceive it and so the flash-lag effect is reduced. For the same argument, the latency explanation is also compatible with the finding that the flash-lag effect is enlarged when the luminance of the flash is decreased (Ögmen, Patel, Bedell, & Camuz, 2004; Purushothaman, Patel, Bedell, & Ögmen, 1998).

In addition to the flash-terminated cycle there is another condition of interest: the flash-initiated cycle. In this condition there is not motion stimulus before the flash, i.e. the moving object appears simultaneously with the flash. The important finding (Baldo & Klein, 1995; Eagleman & Sejnowski, 2000a; Nijhawan, Watanabe, Khurana, & Shimojo, 2004) is that in the flash-initiated condition the flash-lag effect has the same magnitude as the one obtained in the standard condition[3]. It has been suggested that this result is not compatible with the processing time explanation because the moving object would suffer

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[2] Backward masking has also been considered as an explanation of the standard flash-lag effect. It will be explained in the point 1.4 of this chapter.

[3] Exceptions will be discussed in Chapter 5.

from the same delay as the flash, as it appears suddenly (Eagleman & Sejnowski, 2002). But, it has been pointed out that this criticism oversimplifies the spatio-temporal dynamics of visual processing (Krekelberg & Lappe, 2002; Ögmen, Patel, Bedell, & Camuz, 2004). In the time period between when light impacts in the retina and when observers become aware, there is a chance for neural processing to speed up the response. A similar argument has been put forward (Khurana & Nijhawan, 1995) to explain the compatibility of the flash-initiated cycle result with the motion extrapolation explanation. Khurana and Nijhawan considered that during this period the lag-correction occurs because the change in position of the moving object triggers the motion signal of the fast magnocellular stream.

It has been pointed out that the performance in temporal order judgments between flashes and moving objects is inconsistent with the processing time explanation (Eagleman & Sejnowski, 2000b). Eagleman and Sejnowski used a display like that used by Nijhawan (Nijhawan, 1994). At some time before or after the flash, the moving bar halted movement. They asked observers to report if the flashes occurred before or after the halting of the bar and showed that temporal order judgments were made accurately. But, it has been argued (Krekelberg & Lappe, 2002) that this situation is not illustrative because in fact corresponds to a flash-terminated condition for which it has been shown that there is not flash-lag effect (Eagleman & Sejnowski, 2000a). Temporal order judgments, however, have been also studied in the flash-initiated cycle situation (Nijhawan, Watanabe, Khurana, & Shimojo, 2004) for which a flash-lag effect like that corresponding to the standard situation occurs. Contrary to the processing time explanation, it has been shown that the flash was perceived a little before than the moving object. Reaction times to the flash and to the onset of the moving object were also measured (Nijhawan, Watanabe, Khurana, & Shimojo, 2004) and the small differences found were again not consistent with the processing time explanation.

The criticisms to the processing time explanation concerning temporal order judgments and reaction times are based on the tacit assumption that these tasks and the relative position task corresponding to the flash-lag effect are based on the same neural mechanisms. So, it has been suggested (Ögmen, Patel, Bedell, & Camuz, 2004) that the processing time explanation can avoid these problems without considering this assumption: different tasks would engage different mechanisms, each one with their characteristic processing times. This proposal is has been also suggested to explain the findings related to flash-lag effect generalizations which usually are claimed to rule out the processing time explanation. Below, I will describe two flash-lag effect generalizations: the flash-lag effect for feature changes and the cross-modal flash-lag effect.

It has been shown that the flash-lag effect not only applies to motion but also to other dimensions of the stimulus (Sheth, Nijhawan, & Shimojo, 2000). In one experiment, a spot gradually changed color from green to red. At some time, another spot was flashed with exactly the same color of the changing spot. Observers reported that at the moment of the flash, the changing spot was more reddish than the flashed spot. Interestingly, the flash-lag effect for this situation was greater than 400 ms. This large value has been considered unlikely to be caused by differences in processing time (Durant & Johnston, 2004; Krekelberg & Lappe, 2001; Schlag & Schlag-Rey, 2002). Similar results, but with different temporal lags, were obtained for changes in luminance, spatial frequency and pattern entropy (Sheth, Nijhawan, & Shimojo, 2000).

In another study (Alais & Burr, 2003), it has been shown that the flash-lag effect can occur in audition and cross modally. A briefly presented auditory stimuli lag behind a translating sound source. In addition, both, a visual moving object presented with a briefly sound and a translating sound presented with a visual flash also result in flash-lag effects. Since latencies in audition are shorter than those for vision (Heil, 1997; Nowak, Munk, Girard, & Bullier, 1995), these results are regarded as being inconsistent with the processing time explanation (Alais & Burr, 2003). Alais and Burr, for example, argued that, according to a processing time account, in the crossmodal version in which they found a large flash-lag effect for a briefly sound presented instead of a visual flash, a flash-lead effect would be predicted. One must be cautious, however, interpreting this result because in another study (Hine, White, & Chappell, 2003) indeed a significant flash-lead effect was found in this crossmodal condition.

1.3. Attentional explanation

The extrapolation hypothesis was first questioned by Baldo and Klein (1995), who showed that increasing flash eccentricity increased the magnitude of the flash-lag illusion. According to the motion extrapolation hypothesis, the effect should depend only on the kinematics of the moving object. To explain this result, Baldo and Klein proposed a version of the processing time explanation according to which the differential time delay between the moving object and the flash depends on shifting visual attention from the flashed to the moving stimulus (Baldo and Klein, 1995).

The attentional explanation was questioned (Khurana, Watanabe, & Nijhawan, 2000) using a cost-benefit cue paradigm (Posner, 1980). Observers viewed two moving objects. A flash was presented near one of the moving objects. An arrow presented 500 ms before the flash cued, with 80% validity, the position of the flash. Against the attentional account, it was found that the measured flash-lag did not depend on the validity of the cue. Demonstrating, that the cue actually influenced the allocation of attention, when observers were asked to respond as quickly as possible to flash onset, reaction times were significantly shorter on the valid-cue trials. This suggests that the quicker responses to validly cued locations are more likely to be due to facilitation of motor responses rather than to perceptual facilitation (Goodale & Milner, 1992).

Other studies, however, using different stimuli showed that attention can certainly influence the flash-lag effect (Baldo, Kihara, & Namba, 2002; Eagleman & Sejnowski, 2000c; Namba & Baldo, 2004; Vreven & Verghese, 2005). Nevertheless, as the flash-lag effect does not disappear even when attention is firmly focused on the target stimulus, in the more recent view (B

Baldo, Kihara, & Namba, 2002; Namba & Baldo, 2004) attention is considered a modulating rather than a causal factor.

1.4. Backward masking explanation

Backward masking was first proposed together a with cue-induced focal attention mechanism to account for both the Fröhlich and the flash-lag effect (Kirschfeld & Kammer, 1999). It is worth mentioning that a similar explanation has been proposed to explain the flash-lag effect for feature changes like color (Sheth, Nijhawan, & Shimojo, 2000). The Fröhlich effect refers to the observation that the initial position of a moving object that abruptly appears in the visual field is perceived shifted forwards in the direction of motion (Fröhlich, 1923).

The cue-induced focal attention mechanism is related to the processing time explanation. According to it, when a location in visual space is cued, a focus of attention surrounding the cue is created so that the latency to perceive a subsequently presented stimulus is reduced. This phenomenon is also known as attentional prior entry (Titchener, 1908; Shore, Spence, & Klein, 2001). The line-motion illusion (Hikosaka, Miyauchi, & Shimojo, 1993) has been considered an example of this mechanism in action. The illusion consists in perceiving that when a brief lateral cue precedes an instantaneously presented horizontal line, observers report a sensation of motion in the line propagating from the cued end toward the uncued end. The original interpretation is that the cue creates a gradient of attention that decreases with increasing the distance from the cue. The movement illusion would result from the fact that the latency-shortening effect is less pronounced for parts of the line farther away from the cue. This explanation, however, has been questioned by several investigations (Downing & Treisman, 1997; Schneider & Bavelier, 2003; Tse & Logothetis, 2002).

Backward masking in general describes the phenomenon in which a briefly visual stimulus that is clearly visible when presented alone can be hidden by the subsequent presentation of a second visual stimulus (Enns & Di Lollo, 2000). The explanation of the phenomenon is still a matter of debate (Bachmann, 1999; Enns & Di Lollo, 2000; Enns, 2004). When the second stimulus is presented near the first stimulus, but there is not spatial overlap backward masking is usually referred to as metacontrast masking (Enns & Di Lollo, 2000). This term, indeed, was the one used by Kirschfeld and Kammer (1999).

In the case of a moving object, it has been proposed that cue-induced focal attention and metacontrast mechanisms act in the following way (Kirschfeld & Kammer, 1999). On the one hand, the moving object is perceived with shorter latency because it is itself the cue indicating the position it will occupy next. On the other hand, the moving object also acts as a mask for itself suppressing the trailing signals. The first mechanism, as a version of the processing time explanation, has similar advantages and problems to explain the flash-lag effect. But, although the existence of neural delays is undeniable, the effect of attention accelerating neural processing (prior entry) is questionable (McDonald, Teder-Sälejärvi, Di Russo, & Hillyard, 2005; Schneider & Bavelier, 2003; Shore, Spence, & Klein, 2001). Regarding metacontrast, the suppression of the trailing signal is in good agreement with the lack of visibility of the onset trajectory of a moving object (Fröhlich effect). In addition, it can also account for the misperception involving a moving object that reverses direction. Like in the flash-terminated cycle condition and, again inconsistently with the motion extrapolation hypothesis (Whitney & Murakami, 1998), it has been shown that the perceived point of reversal of a moving object does not overshoot the physical point of reversal (Whitney & Murakami, 1998). Indeed, the moving object appears to change motion direction before it arrives at the physical point of reversal (Whitney & Murakami, 1998) which is compatible with the signal suppression of the metacontrast mechanism (Kirschfeld, 2006).

1.5 Position sampling explanation

In flash-lag experiments observers must ascertain the position of the moving object in a given moment. The flash gives this moment, so the flash acts as a time marker. According to the position sampling explanation (Brenner & Smeets, 2000) the flash-lag is caused because sampling the position of the moving object in response to the flash takes time. Hence, according to this explanation the flash-lag effect is a temporal error rather than a spatial error. It must be noted, however, that the sampling explanation is different from the differential processing time explanation for which the error is caused by the differences in the processing delays of the moving object and the flash.

The linear dependence of the spatial lag with speed (Nijhawan, 1994) so that the flash-lag effect magnitude expressed in temporal terms is constant, as in the case of the processing time account, is well accommodated by the sampling explanation.

The major challenge for the sampling explanation concerns the reported flash-lead effects. As described previously, when the luminance of the flash is much larger than the luminance of the moving object, observers perceive the flash to lead the moving object (Ögmen, Patel, Bedell, & Camuz, 2004; Patel, Ogmen, Bedell, & Sampath, 2000; Purushothaman, Patel, Bedell, & Ögmen, 1998). In the cross-modal study of Hine and cols. (2003) a significant flash-lead effect was also found. In this study, observers had to report the position of a moving object with respect to a fixation point. The flash was replaced by a briefly presented sound as a time marker. When the brief sound was displayed just when the moving object reached the fixation point, observers perceived the moving object in an earlier position. Since in the sampling explanation the mislocalization is due to the time taken to complete the process of spatial localization of the moving object in response to the flash, it never could predict flash-lead effects. Indeed, according to the sampling model, events occurring before the flash should not change the magnitude of the flash-lag effect. Contrary to this, it has been shown that when in a flash-initiated condition, the moving object is pre-exposed as a stationary stimulus before the flash occurred, the flash-lag effect is significantly reduced (Chappell & Hine, 2004).

1.5. Temporal integration explanation

The temporal integration explanation claims that the visual system collects information over a time period in order to make a judgment about the position of an object (Lappe & Krekelberg, 1998; Krekelberg & Lappe, 1999; Krekelberg & Lappe, 2000a). According to this model, the flash-lag effect occurs because the persistence of the flash is larger than the persistence of the moving object, possibly due to motion deblurring (Burr, 1980) and then the position estimate is biased towards the last seen position of the flash. A version of this model was also proposed to act in combination with the processing time difference model (Whitney, Murakami, & Cavanagh, 2000).

Inconsistently with a differential visible persistence playing a role in the flash-lag effect it has been shown that when the flash is masked (Whitney, Murakami, & Cavanagh, 2000) or is replaced by the onset of a static object (Baldo, Kihara, & Namba, 2002) the flash-lag effect does not change. To explain these results, it was proposed that the position judgments are based on the persistence of the position which is distinct from the visible persistence (Krekelberg, 2001). Another weakness of this account is that the time window of 500 ms proposed (Krekelberg & Lappe, 1999) is unlikely long. A lot of reaction time tasks, for example, are performed in less time.

1.6. Postdiction explanation

The motion extrapolation hypothesis proposes that the visual system account for neural delays by extrapolating the position of moving objects forward in time. Hence, it asserts that visual awareness is predictive. The processing time differences explanation assumes that awareness is an on-line phenomenon. The awareness of an event occurs when analysis are concluded in specific regions of the brain. According to the postdiction explanation (Eagleman & Sejnowski, 2000a) visual awareness is neither predictive nor on-line, but instead postdictive, such that the percept attributed to the time of an event depends on what happens in a temporal window of around 80 ms following the event.

According to the postdiction explanation, the flash-lag effect is explained because the flash resets motion integration and then, the new position of the moving object is calculated by integrating its position signals after the flash and postdicted to the time of the flash.

The postdiction explanation, as the temporal integration explanation, proposes some form of temporal recruitment, although in a smaller temporal window (80 ms versus 500 ms). For the temporal integration explanation, however, the flash does not reset the integration and there is no need to postdict perception to the time of the flash (Krekelberg & Lappe, 2000b).

In the original report (Eagleman & Sejnowski, 2000), a flash-initiated cycle in which the flash was presented before the moving object was used to test the processing time differences explanation. It was proposed that against the latency explanation the flash-lag effect was not reduced. But, as it has been pointed out (Krekelberg & Lappe, 2002; Ögmen, Patel, Bedell, & Camuz, 2004; Patel, Ogmen, Bedell & Sampath, 2000; Whitney & Cavanagh, 2000a) due to methodological issues, they did actually not measure the flash-lag effect, but the Fröhlich effect. Indeed, the same mechanism underlies the Fröhlich and the flash-lag for the postdiction explanation (Eagleman & Sejnowski, 2000a). This assumption is not supported, however, by researchers that advocates for the processing time explanation (Ögmen, Patel, Bedell, & Camuz, 2004; Whitney & Cavanagh, 2000a). Providing evidence against the claim that the Fröhlich effect and the flash-lag effect are two expressions of the same phenomenon, Whitney and Cavanagh (2000) showed that a stationary cue presented before the onset of the moving object reduced strongly the Fröhlich effect but not the flash-lag effect. They also argued (Whitney & Cavanagh, 2000a) that if the flash has the same effect as the onset of motion in the Fröhlich effect, it would be predicted that a series of flashes presented aligned with the moving object in rapid succession would mask the moving object impairing its visibility (Lappe & Krekelberg, 1998). This did not turned out to be the case (Krekelberg & Lappe, 1998). It must be said, however, that in this situation the flash-lag effect is reduced which is also not consistent with the processing time differences explanation.

The postdiction explanation, as the position sampling account, cannot explain flash-lead effects (Hine et al., 2003; Ögmen, Patel, Bedell, & Camuz, 2004; Patel, Ogmen, Bedell, & Sampath, 2000; Purushothaman, Patel, Bedell, & Ögmen, 1998) as well as the effect of events occurring before the flash presentation (Chappell & Hine, 2004). In order to avoid this type of difficulties, it was proposed (Eagleman & Sejnowski, 2000b, 2000c) that the resetting of the motion detectors is not an all-or-none process and instead depends on the salience of the flash: the visual system might use pre-flash signals if the flash is low salient. Finally, it is worth mentioning that in a more recent version, postdiction (Eagleman & Sejnowski, 2002) is described as very similar to the sampling explanation (Brenner & Smeets, 2000).

2. Outline and objectives of the thesis

While some investigators consider the flash-lag effect and the color-motion asynchrony illusion as the most striking psychophysical evidence of the existence of neural delays in the visual pathway, others think these visual illusions do not reflect neural delays. The experiments of this thesis can be framed within this debate. We address the following two questions. First, are these illusions compatible with the processing time explanation? Second, how does the processing time explanation have to be interpreted so as to be compatible with these illusions? These two main objectives are further elaborated next.

2.1. Are the color-motion asynchrony illusion and the flash-lag effect compatible with the processing time explanation?

A positive answer to this question supports the view that processing times in the brain have direct consequences at the perceptual level. In the case of the flash-lag effect, perhaps the most important evidence favoring the processing time account is the variation of the effect depending on the luminance of the flash. The flash-lag effect decreases as the luminance of the flash increases. According to the processing time account this is because increasing the luminance of the flash, the time for the flash to be perceived decreases. It has been also suggested that the time taken to perceive a visual event is shorter when the event is the consequence of a self-generated action. We reason, therefore, that if in the flash-lag effect the flash would be perceived as a sensory consequence of our action, the perception of it would be accelerated resulting in a reduced flash-lag effect. In *Chapter 2*, we demonstrate that this is the case. This finding suggests that the time needed to perceive an event, not only depends on its visual properties, but also on the internal dynamics of the brain associated to a motor response.

In the color-motion asynchrony illusion, the processing time explanation competes with the time marker and postdiction explanations to account for the illusion. In *Chapter 3,* we address the plausibility of these explanations. We demonstrate that a single direction changes suffices to obtain the perceptual asynchrony. While this finding is perfectly compatible with the processing time account, it supposes a challenge to the time marker explanation. Our simplified version of the illusion allows us to study the effects of the color presented after the color target of the task and, in this way, testing the postdictive predictions. We show, running counter to the postdiction account, that the asynchrony does not depend on the color presented after the target color. This finding is again compatible with the processing time explanation.

However, in *Chapter 3,* in addition to the perceptual asynchrony between color and motion we also found some effect of visual masking between colors. Although, it does not contribute to the measured perceptual asynchrony, this masking effect changes the percept. The effect could be compatible with postdiction or backward masking theories, but not with the processing time explanation. Hence, the processing time explanation is not enough to fully explain the percept.

In *Chapter 5,* we also show that in the case of the flash-lag effect, the processing time explanation is not sufficient to explain the whole effect. Firstly, we show that spatial mechanisms that work integrating motion signal contribute to the flash-lag effect. Secondly, we show that the flash interacts with the perceived position of the moving object. This last finding showing that the perception of the flash and the moving object cannot be considered independents not only challenges processing time accounts, but also the most of the explanations of the flash-lag effect.

2.2. How does the processing time explanation have to be interpreted in order to be compatible with the color-motion asynchrony illusion and the flash-lag effect?

In *Chapter 3,* we show that the asynchrony measured in the color-motion asynchrony illusion is only compatible with the processing time explanation. However, we also show, replicating previous results, that the task is a critical factor. The asynchrony appears when a judgment of correspondence is made between the attributes of color and motion, but not for temporal order judgments between color and motion changes. In *Chapter 4,* we find that the flash-lag effect also depends on task. We show that the spatial relationship between moving and flashed stimuli is correctly perceived when, instead of demanding a position judgments between them, they serve for perceiving a global shape. The dependence on task of both effects means that it is not possible to associate a single latency univocally for each visual attribute. Instead, different aspects of a visual attribute may be processed with different latencies which suggest the involvement of relatively higher visual areas. Therefore, neural latencies should not be understood as simply the transmission time of the neural signals in the early neural pathways.

CHAPTER 2: The flash-lag effect is reduced when the flash is perceived as a sensory consequence of our action[4]

Abstract

The flash-lag effect (FLE) is defined as an error in localization that consists of perceiving a flashed object to lag behind a moving one when both are presented in physical alignment. Previous studies have addressed the question if it is the predictability of the flash, or the moving object, that modulates the amount of the error. However, the case when the flash is self-generated, and hence can be internally predicted, has not yet been addressed. In Experiment 1, we compare four conditions: flash unpredictable, flash externally predicted by a beep, flash internally generated (and predicted) by pressing a key, and flash triggered by a key press but temporally unpredictable. The FLE was significantly reduced only when the flash was internally predictable. In Experiment 2, we rule out the possibility that the reduction of the FLE was due to the use of the key press as a temporal marker. We conclude that when the flash is perceived as a sensory consequence of our own action, its detection can be speeded up, thereby resulting in a reduction of the FLE. A third experiment supports this interpretation. The mechanism by virtue of which the detection is accelerated could be related to efferent signals from motor areas predicting the sensory consequences of our actions.

1. Introduction

In daily life, our visual system has to continuously update moving object positions to successfully interact with them. This is not a trivial task for the brain to perform. The diversity of localization errors when moving and static objects come into play illustrates how complex the processes underlying this task can be (see Whitney, 2002 for a complete review). A well known mislocalization visual phenomenon is the flash-lag effect (FLE). When an object is abruptly flashed in (retinal) alignment with a second moving object, the former is perceived to lag the moving object (see Nijhawan, 2002 for a review of different accounts). Although the FLE implies a mislocalization (spatial) error, a large contribution to the FLE might originate from an error in the temporal dimension. In other words, part of the mislocalization can be due to a temporal error (Brenner and Smeets, 2000 and Murakami, 2001; but see Kreegipuu & Allik, 2004, for a different interpretation). For example, according to the position sampling model (Brenner & Smeets, 2000) ascertaining the position of the moving object takes time and can only be made after the flash (as a time-

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marker) has been perceived. Therefore, one can match the respective positions of the flash and the moving object, but only at different times. Similarly, for the differential latencies explanation (Whitney & Murakami, 1998), the extra-time needed by the visual system to perceive the flash with respect to the moving object would also result in a temporal error. However, temporal and spatial factors may contribute to the FLE. A recent study by Vreven and Verghese (2005) shows that the spatial predictability of the flash can reduce the FLE, and that the magnitude of reduction can be even larger than that obtained with a temporal cue. On the other hand, there is evidence that points to an enhancement of the FLE when either the unpredictability of the flash (Baldo et al., 2002 and Eagleman and Sejnowski, 2000), or the moving object is increased (Kanai, Sheth, & Shimojo, 2004). Summing up, previous results show that helping subjects predict the flash, or the position of the moving object, by external means (e.g., external cues or other stimulus manipulations) has an effect on the magnitude of the FLE.

Previous studies, however, have not addressed whether the internal prediction of the flash has an effect on the FLE. In this study, we will focus on whether helping the observers anticipate in different ways when the flash will appear affects the magnitude of the FLE. In a first experiment, we show that external and internal prediction of the flash increase the sensitivity, but, only the latter reduces the FLE in a significant way. The results of Experiments 2 and 3 point to a possible mechanism that could account for this reduction of the FLE. To anticipate, we invoke mechanisms that, by predicting the flash as a sensory consequence of self-actions, affect the threshold for detecting incoming sensory events.

2. Experiment 1

In this experiment, we will measure the magnitude of the FLE for two different kinds of temporal predictions: an external auditory cue that predicts the flash and when flash is self-triggered.

2.1. Methods

2.1.1. Subjects

Four subjects with normal or corrected-to-normal vision participated in the experiment. All of them were naive with respect to the aims of the experiment except for the second author.

2.1.2. Stimuli

Stimuli (see Fig. 1) were displayed on a Philips 22 in monitor (Brilliance 202P4) at a refresh rate of 118 Hz and screen resolution of 1154 × 864 pixels.

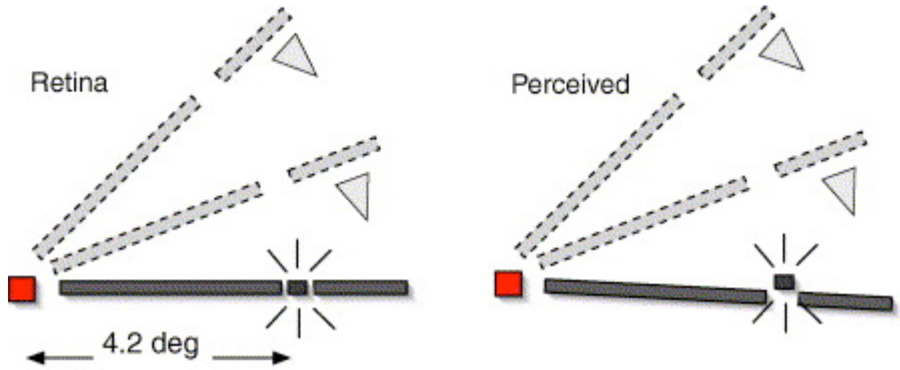

Fig. 1. Stimulus used in Experiments 1 and 2. The initial position of the moving bar was set at random before starting move. The red fixation point was placed at the center of the screen. See text for more details. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper).

A moving bar rotated clockwise or counter-clockwise, on a trial-to-trial basis, and was divided by a visual gap located at 4.2° from fixation. A flash was shown for one frame (8.33 ms) at some point along the imaginary circle centered at the fixation red point and passing through the middle of the visual gap of the moving line. Nine angular offsets of the flash with respect to the moving bar were used, and were independently chosen for each of six possible speeds to give a psychometric function. The bar could move at six different angular speeds: 38, 68, 99, 129, 160, and 190°/s that corresponded with the following nine tangential velocities of the tip of the rotating bar: 2.98, 5.34, 7.78, 10.13, 12.57, and 14.92°/s. The luminance of the flash and of the moving bar were subjectively equated by using Quest (Watson & Pelli, 1983).

2.1.3. Procedure

The experiment consisted of four conditions. In the control condition the flash was shown between 2.5 and 5.8 s after the bar started to move. The location of the flash relative to the bar and the speed of the bar were varied according to the procedure of the method of constant stimuli: the 54 stimuli (6 velocities * 9 offsets) were delivered in random order until all 54 had been presented. Then, the 54 stimuli were again randomized and all presented again, and so on. Observers had to report whether the flash was leading or trailing the moving bar by pressing one of two mouse buttons. The same response was recorded in all the conditions. In a second condition, the flash was self-triggered by the observers by pressing the spacebar. After the bar started move subjects could trigger the flash by pressing the spacebar at a time of their own choice. Subjects were told that the key press would not function if they pressed the button too early (less than 2 s after the bar started to move). This was so to allow for a duration of the motion trajectory comparable to that of the control condition. After the subjects pressed the spacebar, the flash appeared in one of the nine angular offsets relative to the rotating bar, therefore, the relative position of the flash with respect to the rotating bar was totally independent of the time of the key press. The different velocities and angular offsets were presented exactly as in the control condition. The same type of response as in the control condition was recorded with the mouse. The mouse click started the next trial. A third condition (variable interval) was identical to the self-triggered condition except for the fact that the time at which the flash appeared after the key press was randomly (uniform distribution) varied in the range [0.2–1.2] seconds. A fourth condition (auditory) was identical to the control condition except for the fact that the appearance of the flash (between 2.5 and 5.8 s after motion onset) was predicted by a sound that was played 300 ms earlier than the flash.

The four conditions were presented in different sessions (three sessions per condition), with a different order for the four subjects. Each subject was presented with a total of 2592 trials: (6 velocities * 9 offsets * 4 repetitions = 1 session) * 3 sessions * 4 conditions. The order of the conditions was randomized across subjects.

2.1.4. Data analysis

The percent of flash leading (ahead) responses was pooled over subjects and a cumulative gaussian was fitted by minimizing the mean square error. The mean of the gaussian gives us the point of subjective equality (PSE) and the deviation gives us the sensitivity. The PSE reflects the amount of FLE. The larger the PSE, the higher the FLE. To obtain the confidence intervals of these two parameters (mean and deviation) we used bootstrap (Efron & Tibshirani, 1993) as conducted by Kanai et al. (2004). This procedure was applied for two independent variables: the spatial offset and the temporal offset. When conclusions could not be drawn by merely looking at the overlap between two confidence intervals, parametric bootstrap and Monte Carlo simulations were used to compare two given psychometric curves by testing the null hypothesis that the observed difference between the two PSEs (or the two slopes) is not different than zero. To accomplish this, we used the same procedure as that implemented in pfcmp (Wichmann and Hill, 2001a and Wichmann and Hill, 2001b), but, we computed a bootstrap p value independently for each parameter, instead of a combined (PSE and slope) one as was carried out in pfcmp.

2.2. Results

2.2.1. Analysis as a function of spatial and temporal offsets

Fig. 2 shows the percentage of flash-ahead responses split by velocity as a function of the angular offset between the flash and the moving bar for the four different conditions. The pattern for the control condition is very similar to that reported by Murakami, 2001: not only the magnitude of the FLE increased with velocity (curves are shifted to the right), but also the deviation of the fitted gaussian (the curves are shallower). A similar pattern can be observed in the variable interval condition. In the remaining conditions, the FLE increases with velocity, but the deviation does not.

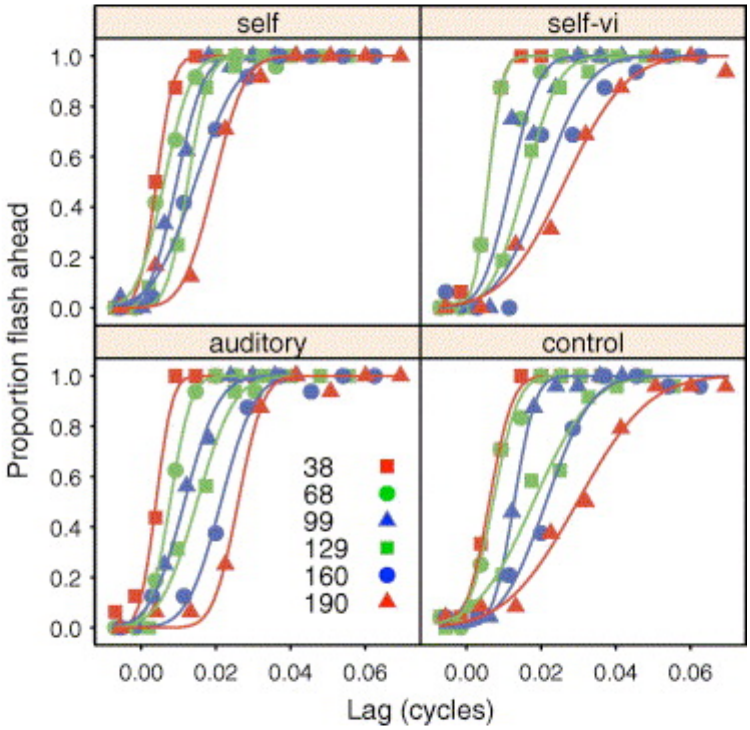

Fig. 2. Proportion of flash ahead responses as a function of the angular offset in cycles (1 cycle = 360°) between the flash and the moving bar. The different conditions are plotted in different panels. Data points are plotted separately for each velocity. The solid lines are the best fit of a cumulative gaussian.

Fig. 3 shows the same data but as a function of the temporal offset. As can be clearly seen, the data points for the different velocities are much less scattered than when they are plotted as a function of the angular offset. We fitted a different gaussian for each velocity but the confidence intervals for the mean and deviation of the curves overlapped completely. Therefore, two different angular offsets between the flash and the moving bar elicited the same percentage of ahead responses when both angular offsets correspond to the same temporal offset with respect to the moving bar. This set of patterns is consistent with an interpretation of the FLE as a temporal misjudgement rather than a spatial one. The magnitude of the FLE for the control condition (after averaging across velocities) is very similar (48 ms) to the one reported by Murakami (2001), who showed that the same kernel could be successfully fitted to the pattern of responses across different velocities.

2.2.2. Comparison of the different conditions

To compare the four different conditions, we pooled the data over velocities and fitted a single cumulative gaussian for each condition as a function of the temporal offset (Fig. 3). After running 2000 simulations of bootstrap, we obtained the confidence intervals for the two fitted parameters (PSE and deviation) in each condition. Fig. 4A shows the obtained PSE (mean of the fitted gaussians) for the four conditions.

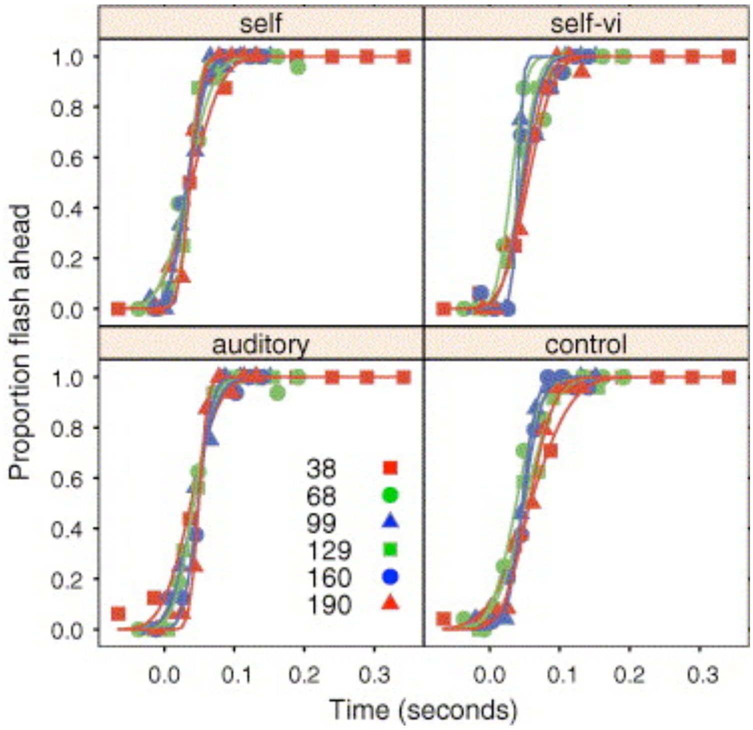

Fig. 3. The same data points as in Fig. 2, but now plotted as a function of the temporal offset between the moving bar and the flash.

With respect to the control condition, the magnitude of the FLE was significantly reduced only when the flash was self-triggered (48 vs. 34 ms, respectively). The obtained PSE (mean of the gaussians) for the other conditions were not significantly different from the control condition. The 95% confidence intervals clearly overlap. Although the PSE for the auditory (external prediction) and variable interval conditions were smaller than the control condition, these differences were not significant ($p = 0.098$ and 0.15, respectively).

Fig. 4B shows the deviation of the fitted gaussian for the four conditions. In the self-triggered condition not only the PSE, but also the variability decreased. This reduction was significant with respect to the control condition ($p < 0.001$) as it was when the flash was externally cued by the beep ($p = 0.004$). This means that while the external cue did not reduce the mean localization error (PSE is not different from the control condition), it helped observers improve their sensitivity in discriminating different temporal offsets between the flash and the moving bar (steeper curve when the beep was present). In the variable interval condition, the deviation was smaller than the control condition, although this difference was not significant ($p = 0.11$). Therefore, when the flash was not perceived as a sensory consequence of one's own action (variable interval condition), neither the magnitude of the FLE nor the deviation was reduced. This condition did not differ from the control condition.

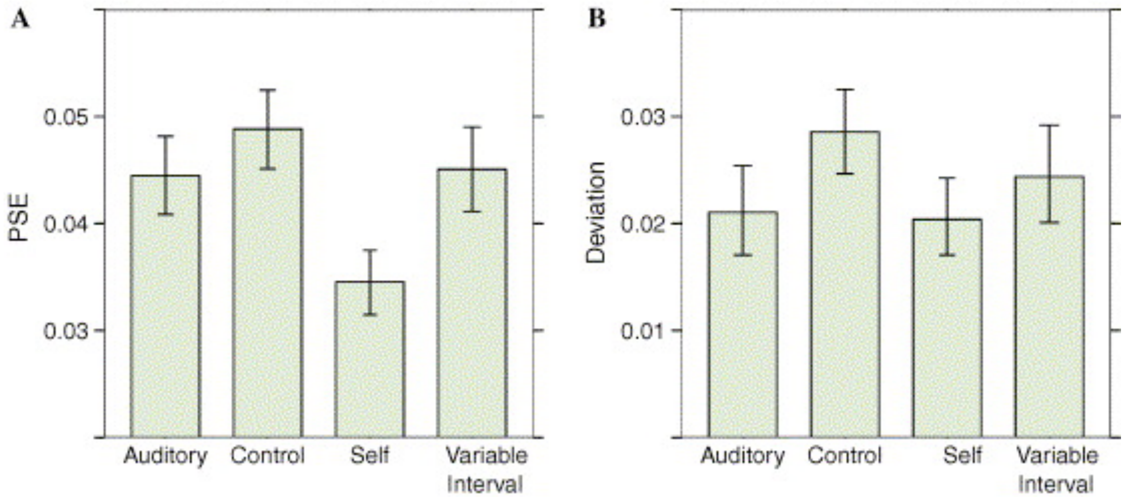

Fig. 4. (A) The obtained PSE (mean of the fitted cumulative gaussians) for each condition. To fit the curve, data points were averaged across velocities. (B) The deviation of the fitted cumulative gaussians for each condition. Error bars denote the 95% confidence interval in both panels.

2.3. Discussion

The results of our auditory condition show that by making the flash more (temporally) predictable, the variability of the responses was reduced. This finding is in agreement with previous work (Vroomen & de Gelder, 2004). However, the external auditory cue that we used failed to reduce the magnitude of the FLE. While some studies have found an effect of the predictability of the flash (e.g., Baldo et al., 2002, Eagleman and Sejnowski, 2000 and Vreven and Verghese, 2005), others have not (e.g., Khurana, Watanabe, & Nijhawan, 2000). Vreven and Verghese (2005) also used a sound that was played at the same time of the flash and found a reduction in the magnitude of the FLE. The same result was obtained by the previously cited study of Vroomen and de Gelder (2004). These authors found a reduction of the FLE when the sound was played 100 ms before the flash. The intervals between the sound and the flash used in these studies are much shorter than the interval we used here (300 ms). Therefore, the predictive power of our external cue could have been diminished due to the duration that we used between the sound (the cue) and the flash. The lack of prediction in our auditory condition is consistent with other studies on target localization during pursuit (e.g., Rotman, Brenner, & Smeets, 2002). Rotman et al. showed that the error in localizing a flash during pursuit was not reduced by auditory or visual external temporal cues. In their study, the interval between the sound and the flash was 500 ms, even longer that the interval we used. It seems, hence, that temporal proximity is an important factor for an external cue to reduce the localization error.

The internal prediction clearly reduced the FLE. However, triggering the flash by itself does not significantly reduce the FLE (variable interval condition). Therefore, it is necessary that the duration between the key press and the flash is held constant.

Why is the FLE reduced in the self-triggered condition? One possibility is that the key press was used as a time-marker instead of the flash itself. This possibility can be easily accommodated by Brenner and Smeets account of flash-lag (Brenner & Smeets, 2000). Their explanation of the FLE is based on the time it takes for the system to ascertain the position of the moving object once the flash has been detected. This extra-time in sampling the moving object's position would be responsible for the FLE. Therefore, it is not unlikely that the key press acted as a time-marker just before the flash was presented. If this was so, subjects, even unintentionally, could start the sampling process not at the time the flash appeared but at the (earlier) time the key had been pressed. As a consequence, they would have sampled the position of the moving object earlier in time compared with the control condition. Why does this possibility not account for the lack of reduction of the FLE when an auditory cue is presented? We think that, while the subject begins sampling at the time of the key press (self-triggered) because the flash is immediately available, this sampling does not occur for the beep. The relatively long duration between the beep and the appearance of the flash could therefore have discouraged the use of the beep as a time-marker. The possibility that the key press served as a time-marker is explored in the second experiment.

3. Experiment 2: Inspecting the internal prediction mechanism

In this experiment, we aim at exploring whether the reduction of the FLE observed in Experiment 1 can be attributed to a sampling strategy triggered by the key press instead of the flash itself.

3.1. Methods

Three subjects participated in this experiment, the second author and two naive subjects. All of them had normal or corrected-to-normal vision. We used the same apparatus and stimuli as in Experiment 1.

3.1.1. Procedure

The procedure was almost identical to the self-triggered flash condition of Experiment 1, except for the time-lapses between the key press and the presentation of the flash. We used three possible intervals between the key press and the presentation of the flash: 0, 16, and 32 ms. These intervals were randomly interleaved in the session. Only one of the angular velocities of Experiment 1 (129°/s) and its corresponding nine different spatial offsets were used to obtain the psychometric curve. Within each session, subjects were presented with 270 trials and each subject took three sessions.

3.1.2. Hypothesis testing and data analysis

If subjects used the key press, and not the flash as a time-marker, we would expect different FLEs for the three used time-lapses between the key press and the flash. We relied on the sample position model (Brenner & Smeets, 2000) to derive the different predictions. As long as these predictions will be derived under the assumption that subjects used the key press as a time-marker, whatever result comes out of this will only concern the role of the key press action as a time-marker for doing the task and not the position sample model as an explanation of the FLE. In other words, we are not testing the position sample model itself but using it to test whether the key press is used as a time-marker to perform the task.

Let Tp and Tf, respectively, denote the registered time-markers of the key press and the flash. If the flash, and not the key press, triggers the sampling process, then the subject will have ascertained the position of the moving object at a time Tf + Δt, Δt being the time it takes for the sampling to be completed. Let us suppose, however, that an observer starts sampling the position of the moving object at the time of the key press Tp. The subject, then, would have ascertained the position of the moving object at time Tp + Δt. If the flash is progressively delayed in time with respect to the key press then the respective relative position judgements will result in smaller FLEs because the comparisons will be made with earlier sampled positions of the moving object with respect to the time of the flash. In sum, if the key press as a time-marker is used as a strategy, we would expect different FLEs for the three time intervals. To test this hypothesis, we fitted cumulative gaussian and ran bootstrap as in the previous experiment.

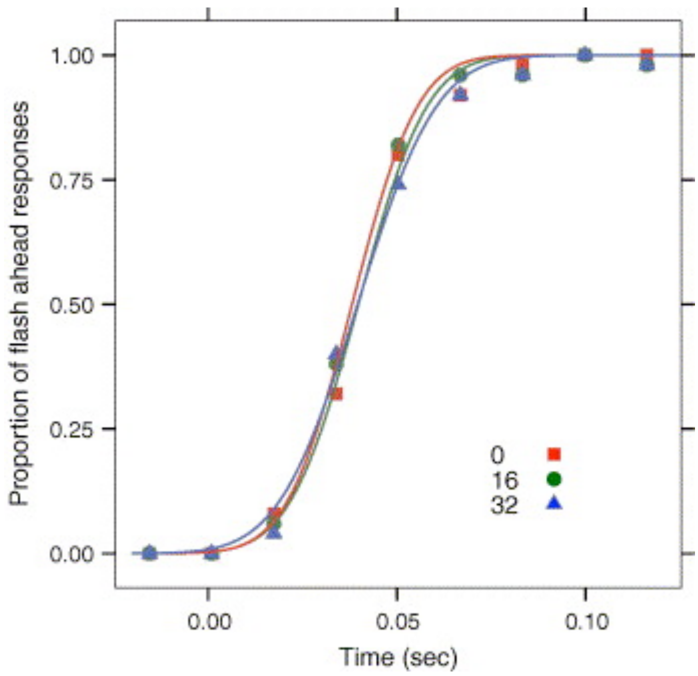

Fig. 5. Results of Experiment 2. Proportion of flash ahead responses as a function of the temporal offset between the moving bar and the flash. The data points are averaged across subjects. The solid lines denote the cumulative gaussian fits. The different symbols stand for the three different times lapses used in Experiment 2.

3.2. Results and discussion

Fig. 5 shows the proportion of flash-ahead responses as a function of the temporal offset between the flash and the moving object split by the elapsed time between the key press and the flash. We pooled the data over all the subjects as they showed the same pattern. As can be seen, the data pattern is very clear. There is no difference whatsoever among the three different conditions. The mean FLE is 39 ms (95%-CI: 0.035–0.043) which is not significantly different from the FLE found in the self-triggered condition of Experiment 1, and is significantly different from the FLE found in the control condition of the same experiment (the 95%-CI do not overlap). Upon questioning, none of the subjects were aware of the three different time-lapses, so they always perceived the flash lag as a sensory consequence of their own action.

On the basis of the results, we cannot conclude that the key press by itself was used as a temporal marker. Another mechanism has to be responsible for the reduction of the FLE when the flash is self-triggered at a constant time, or slightly after this time.

One alternative explanation that could be proposed to explain the reduction of the FLE when the flash is internally predicted, could be related to mechanisms that predict the sensory consequences of self-generated actions. Predicting the sensory events that are generated by our own actions is a very important capability to factor them out from the rest of the incoming sensory stream. Motor control theory suggests that the brain predicts the effect of motor commands via an efferent copy (Wolpert & Ghahramani, 2000). In addition, it has been shown that the perception of the sensory consequences of self-actions is temporally tuned (Bays, Wolpert, & Flanagan, 2005). Therefore, a comparative mechanism could have been involved in, for example, speeding up the detection of the flash when it was perceived as a sensory consequence of self-action (key press). This hypothesis would also be consistent with the finding that the perceived timing of self-generated events is moved forward in time (Haggard, Clark, & Kalogeras, 2002). If such a mechanism is responsible for the reduction of the FLE, we should be able to find the same result with longer delayed times between the key press and the flash. In other words, the narrow temporal continuities that we have used so far would not be necessary for the flash to be perceived as a consequence of the self-action. For example, Haggard et al. (2002) successfully used 250 ms between the action and the sensory consequences. In a final experiment, we test whether the causality effect is also developed when a longer delay is used.

4. Experiment 3

4.1. Methods

Three subjects, included the second author, took part in this experiment. All of them had normal or corrected-to-normal vision. We used the same apparatus as in Experiments 1 and 2. Except for small variations in the elapsed time between the key press and the flash, we used the same stimuli as in Experiment 2. The moving (129deg/s) bar appeared and a flash was self-triggered by the subjects. As before, different angular offsets were used to build the psychometric function. Within a single session, a high probable elapsed time (250 ms) between the key press and the presentation of the flash was used. There were 176 trials in each session. Eight out of these trials had a different time lapse (0 ms) between the key press and the flash presentation. The low probability trials (0 ms) were presented in random order interleaved with the high probable trials (250 ms) during the second half of the session. Subjects performed 10 sessions for a total of 1760 trials.

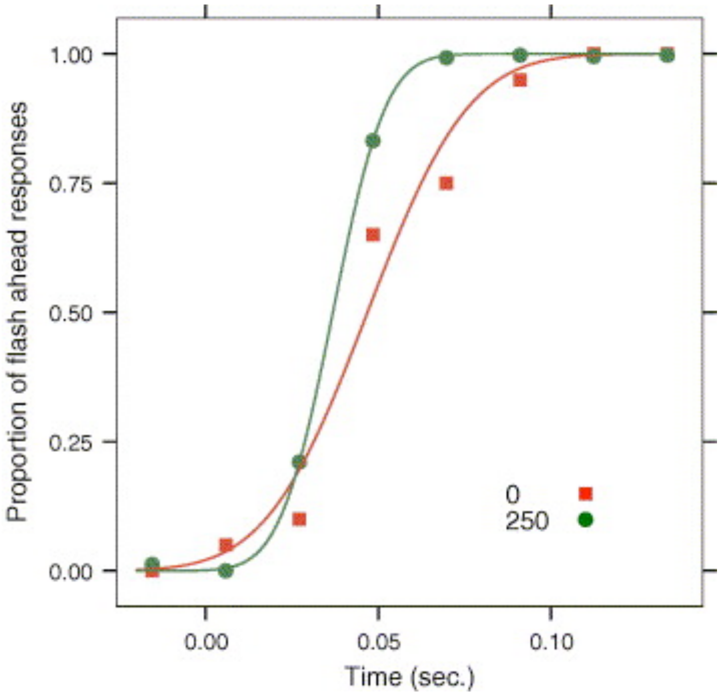

Fig. 6. Proportion of flash ahead responses as a function of the temporal offset between the moving bar and the flash. The data points are averaged across subjects. The solid lines denote the cumulative gaussian fits. Different symbols denote the different times lapses between the key press and the appearance of the flash. Solid circles denote the trials when the flash was shown 250 ms after the key press. This was the most frequent elapsed time. Solid squares denote those trials when the flash was presented unexpectedly early (0 ms).

4.2. Results and discussion

Fig. 6 shows the proportion of flash-ahead responses as a function of the temporal offset between the flash and the moving object split by the elapsed time between the key press and the flash. Again, there are no differences between subjects, therefore data was pooled. As can be seen, while the FLE is reduced for the 250 ms condition, it was not for the 0 ms (low probability) condition. The difference between PSEs was significant (bootstrap p value of 0.01). The estimated PSE for the 250 ms is 0.36 ms with a 95%-CI of [0.356–0.038]. This PSE is not significantly different (p value of 0.767) from the FLE obtained in the self-triggered condition of Experiment 1 (about 34 ms). The obtained PSE for the low probable elapsed time was 47 ms with a 95%-CI of

[40–54], making it virtually the same as the FLE obtained in the control condition of Experiment 1 (48 ms) (p value of 0.892). We can conclude that it is not the temporal proximity between the action and the flash that matters, but the development of a causal relationship between the action and the flash as a sensory consequence due to a perceived temporal contingency.

5. General discussion

We have shown for the first time that the perception of the FLE can be modulated by our own actions. The perception of the flash as a consequence of a self-action appears to be necessary to reduce FLE. After ruling out the possibility that the key press was used as a time-marker, we think that a mechanism similar to those involved in predicting the consequences of self-actions can explain the reduction of the FLE. Of greater interest would be to explore what sort of error is reduced by this internal prediction. It is known that temporal and spatial contributions may affect the FLE Murakami, 2001. For example, the significant FLE reported under flash terminated conditions in Kanai et al. (2004) may reflect spatial mechanisms that extrapolate the moving object (Nijhawan, 1994). Apart from these spatial mechanisms acting on the moving object, temporal contributions can also be of importance. Illustrating this is the fact that the magnitude of the FLE can also be modulated by manipulating the time it takes for the flash to reach awareness, or the time it takes to sample the position of the moving object in response to the flash Brenner and Smeets, 2000. An example of the former case is the effect on the FLE found in Purushothaman, Patel, Bedell, and Ögmen (1998). These authors showed that the manipulation of the luminance of the flash has an effect on the FLE. The difference between the control condition and the self-triggered condition could be mainly attributed to a reduction of the temporal error in the process of detecting the flash. In this respect, the effect found in the present study can be closely related to the modulation of the FLE when the luminance of the flash is manipulated.

Some theories have addressed how a sensory system gets information about the stimulus (e.g., Grice et al., 1979 and Link, 1992). Generally, these theories propose that sensory information accumulates in time until the difference between a signal and noise distribution reaches a certain threshold. An efferent copy of the key press broadcasted to sensory areas and predicting the sensory consequences could have modified (lowered) the threshold criteria. Therefore, the internal prediction could have shortened the time-course of the flash detectability. Although this explanation is similar, we claim that it cannot be considered a variant of the differential latencies explanation based on faster neural signals for moving objects when compared to static objects.

Finally, this interpretation is consistent with most accounts of the FLE. In Experiment 2, we relied on the sample position model of Brenner and Smeets, 2000 to test whether the key press was used as a time-marker giving place to a reduction of the FLE. Having ruled out this possibility, however, our findings do not necessarily undermine the explanatory power of this model, as the sample position model relies on ascertaining the position of a moving object. Our finding, we think, is better accounted for by a reduction of the detection time of the flash, leaving the contribution of the moving object to the FLE unaffected.

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We thank David Burr, Romi Nijhawan and an anonymous reviewer for their suggestions in a previous version of the manuscript and Scott Sinnett for improving the English style. This research was supported in part by Grant TINS2004-04363-C03-02 from the Ministerio de Educación y Ciencia of the Spanish government.

CHAPTER 3: Perceptual asynchrony between colour and motion with a single direction change[5]

Abstract

When a stimulus repeatedly and rapidly changes color (e.g., between red and green) and motion direction (e.g., upwards and downwards) with the same frequency, it was found that observers were most likely to pair colors and motion directions when the direction changes lead the color changes by approximately 80 ms. This is the color–motion asynchrony illusion. According to the differential processing time model, the illusion is explained because the neural activity leading to the perceptual experience of motion requires more time than that of color. Alternatively, the time marker model attributes the misbinding to a failure in matching different sorts of changes at rapid alternations. Here, running counter to the time marker model, we demonstrate that the illusion can arise with a single direction change. Using this simplified version of the illusion we also show that, although some form of visual masking takes place between colors, the measured asynchrony genuinely reflects processing time differences.

Introduction

What is the relationship between the timing of neural activity and the subjective time course of events represented by that activity? This question has recently been discussed in the context of the color–motion asynchrony illusion (Arnold, 2005; Arnold & Clifford, 2002; Arnold, Clifford, & Wenderoth, 2001; Bedell, Chung, Ogmen, & Patel, 2003; Johnston & Nishida, 2001; Moradi & Shimojo, 2004; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002). This striking illusion occurs when a stimulus repeatedly and rapidly changes color (e.g., between red and green) and motion direction (between two opposite directions) with the same frequency. In order to reliably bind one direction of motion with one color, direction changes must occur about 80 ms earlier than color changes (Moutoussis & Zeki, 1997).

According to the differential processing time explanation (Arnold & Clifford, 2002; Bedell et al., 2003; Moutoussis & Zeki, 1997), the illusion occurs because different attributes of a visual stimulus are processed in relatively separate cortical areas (Livingstone & Hubel, 1988). It is proposed that the subjective time course of changes in a visual attribute is related to the timing of neural activity of the areas that process this attribute. The illusion is thus explained because the neural activity leading to the perceptual experience of motion

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requires more time than that of color. Alternatively, it has been argued that the perceived time of occurrence may not correlate directly with neural processing time and would be, instead, the result of an interpretative process of the brain (Dennett & Kinsbourne, 1992; Eagleman & Sejnowski, 2000; Johnston & Nishida, 2001; Krekelberg, 2003; Walsh, 2002).

A hallmark of this illusion is that it seems to require a repetitive display in which the time interval between two successive changes is very short (~300 ms) (Arnold, 2005; Arnold & Clifford, 2002; Arnold et al., 2001; Bedell et al., 2003; Clifford, Spehar, & Pearson, 2004; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002). Nishida and Johnston (2002) specifically addressed this question. They asked observers to perform a synchronous judgment task; that is, they asked observers to make a yes–no judgment about whether or not the two attribute oscillations were perfectly in phase while varying the relative phase between color and motion changes. They found the color–motion asynchrony illusion when the time between two successive changes was 250 ms, which replicated previous results. However, they showed by increasing the time between two successive changes that the perceived asynchrony decreased until it disappeared when the time interval was 2000 ms. Furthermore, the order of a single change in motion direction and a single change in color was reliably perceived (Bedell et al., 2003; Nishida & Johnston, 2002). These findings posed a challenge to simple versions of the differential processing time explanation that predict a motion delay regardless of the frequency of changes. Nishida and Johnston proposed the time marker explanation as an alternative (Nishida & Johnston, 2002). This explanation for the illusion claims that the misbinding is due to a failure in matching the neural representations (time markers) of the different sort of changes. They argue that at the high temporal frequencies that characterize the illusion, the second-order changes in position (motion changes) are difficult to detect. Consequently, the first-order changes in color are matched with the first-order changes in position (motion direction) resulting in perceived asynchronies.

However, a recent version of the differential processing time explanation (Bedell et al., 2003) suggests that the critical factor for the appearance of the illusion is the type of judgment that observers perform rather than the mismatching between time markers at high frequencies. The model proposes that judgments of correspondence between attributes (e.g., which direction is the red stimulus moving) imply the use of sustained information for which the differences in processing time between color and motion are significant, whereas temporal order judgments (e.g., did the color change occur after or before the direction change) involve transient information for which the differences in processing time are not significant. Accordingly, the illusion will appear only when a correspondence task will be performed, but not for a temporal order judgment task.

However, as previously mentioned, Nishida and Johnston (2002) required observers to perform a synchronous judgment task. This task is more similar to a temporal order judgment task than to a correspondence task. Therefore, the differential processing time model of Bedell et al. (2003) would not predict an asynchrony. Nishida and Johnston, however, did observe the typical asynchrony for high frequencies. How can this apparent contradictory result be explained? Bedell et al. proposed that observers may have changed the task depending on the temporal frequency. That is, although observers were asked to perform a synchronous judgment task, they may have instead performed a correspondence task for high frequencies.

In the present study, we show that, in opposition to the time marker explanation, a single change in motion direction demonstrates the perceived asynchrony that characterizes the illusion. Using this simplified display we show that, although it does not contribute to the measured asynchrony, some form of visual masking takes place between colors. Furthermore, we also show that motion signals briefly displayed after a direction reversal are not perceived, revealing what we think is the origin of the illusion.

General method

The stimuli were displayed on a 21-in. CRT monitor (Sony Trinitron GM 520) at a refresh rate of 100 Hz viewed binocularly from a distance of 50 cm in a dimly lit room. It consisted of 200 dots (size: 0.11° × 0.11°) randomly distributed in a circular aperture with a diameter of 8° of visual angle on a dark background. All dots moved coherently at 6°/s. The dots could be red (luminance: 17 Cd/m2; chromaticity: 0.62, 0.34) or green (luminance: 17 Cd/m2; chromaticity: 0.28, 0.61). Three observers participated in the experiment, the first author and two observers who were naïve as to the purposes of the study. Observers reported normal, or corrected to normal, visual acuity and color vision. Observers were instructed to maintain fixation on a cross, presented at the center of the aperture. A demonstration of the stimuli can be found at http://www.ub.edu/pbasic/visualperception/joan/en/demos.html.

Experiment 1

According to the time marker explanation (Nishida & Johnston, 2002), the use of a repetitive display is a necessary condition for the illusion to appear. However, according to the differential processing time explanation suggested by Bedell et al. (2003), the critical factor is the type of task: performing a correspondence task would lead to perceptual asynchrony whereas temporal order judgments would not. Bedell et al., however, used a repetitive display and so it is not entirely clear whether the correspondence task requires repetitive changes. Here, we test both explanations by performing two types of tasks (a correspondence task and a temporal order judgment task) using a variation of the typical cycle displays (Arnold, 2005; Arnold & Clifford, 2002; Arnold et al., 2001; Bedell et al., 2003; Clifford et al., 2004; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002) in which only a single change in motion direction was presented.

Methods

Correspondence task

We studied the perceptual binding of color around a single direction change when observers performed a correspondence task. Three experimental conditions were randomized within each session:

* 180° direction change: The stimulus (diagrammatic representation of the temporal relationship between color and motion changes in Figure 1A) consisted of 200 random dots that were displayed for 300 ms moving either upward or downward (at random in each trial). After this interval, the dots abruptly reversed direction maintaining it up to the end of the trial. The color of the dots was red during an interval of 300 ms close to the direction change. Before this red interval the dots were green, and after that the dots were green again for 300 ms, after which the dots disappeared. Consequently, the display consisted of one direction change and two color changes. The relative timing between the red interval and the direction change was varied from trial to trial (see below).

* 90° direction change: The stimulus (diagrammatic representation in Figure 1B) was the same as described above except that the direction change was 90° either to the right or to the left (at random in each trial).

* Without last color interval: The stimulus (diagrammatic representation in Figure 1D) was the same of the 180° direction change condition except that the dots disappeared after the red interval. That is, the last green interval was not displayed.

Observers performed a motion correspondence task; that is, they made judgments about the predominant direction of motion (the first or the second direction of motion) when the dots were red (two forced-choice judgment). The relative timing between the direction change and the red interval varied from trial to trial. We assigned a relative timing of zero in the situation where the red interval was centered on the direction change. Hence, the dots were red during 150 ms before and 150 ms after the direction change. We denoted positive values of the relative timing for those values in which the direction change occurred before the point of time that corresponded to the center of the red interval and negative values for those in which the direction change occurred after that point. Eight relative timings ranging from −100 to 250 ms in increments of 50 ms were used.

Each observer performed two different sessions: one in which the target color was red (as described above) and another in which the colors were reversed and the target color was green. The order was counterbalanced across subjects. For the sake of clarity, hereafter we will refer to red as the target color. During a session, each relative timing was sampled 20 times according to the method of constant stimuli.

Temporal order judgment task

The stimuli were identical to the 180° condition. The only difference was the task performed by the observers. In this case, whether the direction change occurred before or after the first color change was to be reported (diagrammatic representation in Figure 1C). For this task, we assigned a relative timing of zero to the situation in which the color and the motion change were physically synchronous. Positive and negative values corresponded to the situations in which the color change followed or preceded, respectively, the direction change. Eight relative timings ranged from −150 to 200 ms in steps of 50 ms were used. The sessions were administered exactly as in the correspondence task, as were the relative timing values. Subjects performed the task in different orders.

Data analysis

For the correspondence task, the set of data of each participant provided a distribution of the proportion of trials in which the second direction was paired with red color as a function of the relative timing between the direction change and the center of the red interval. For the temporal order judgment task, the distribution denotes the proportion of trials in which the first color change is reported as occurring after the direction change. We fitted cumulative Gaussian to derive the point of subjective equality (the mean of the distribution), which served as a measure of the perceptual asynchrony. If the pairing was veridical, the distribution would be centered on 0. Positive values would correspond to apparent motion delays (motion–color asynchrony illusion) and negative values to apparent color delays. In order to obtain the 95% confidence intervals of the parameters of the cumulative Gaussian functions, we used the parametric bootstrap method (Efron & Tibshirani, 1993) as conducted by Kanai, Sheth, and Shimojo (2004). When conclusions could not be drawn by merely looking at the overlap between two confidence intervals, parametric bootstrap and Monte Carlo simulations were used to compare two given psychometric curves by testing the null hypothesis that the observed difference between points of subjective equality PSEs (or the two slopes) is not different than zero. To accomplish this, we used the same procedure as that implemented in PFCMP (Wichmann & Hill, 2001a, 2001b); however, we computed a bootstrap p value independently for each parameter (López-Moliner & Linares, 2006) instead of a combined (PSE and slope) one as was carried out in PFCMP.

Results and discussion

Figure 1 (solid circles) shows the proportion of trials in which the second direction of motion was reported for red dots (correspondence task) as a function of the relative timing between the 180° direction change and the center of the red interval (individual results). If the pairing was veridical, the distribution of results would be centered on a relative timing of 0. However, the distribution is centered around 73 ms (mean across observers) reflecting the typical delay in the perception of motion. Actually, when the red interval was physically centered on the direction change (relative timing of zero), observers bound the second direction of motion with red in only 5% of the trials.

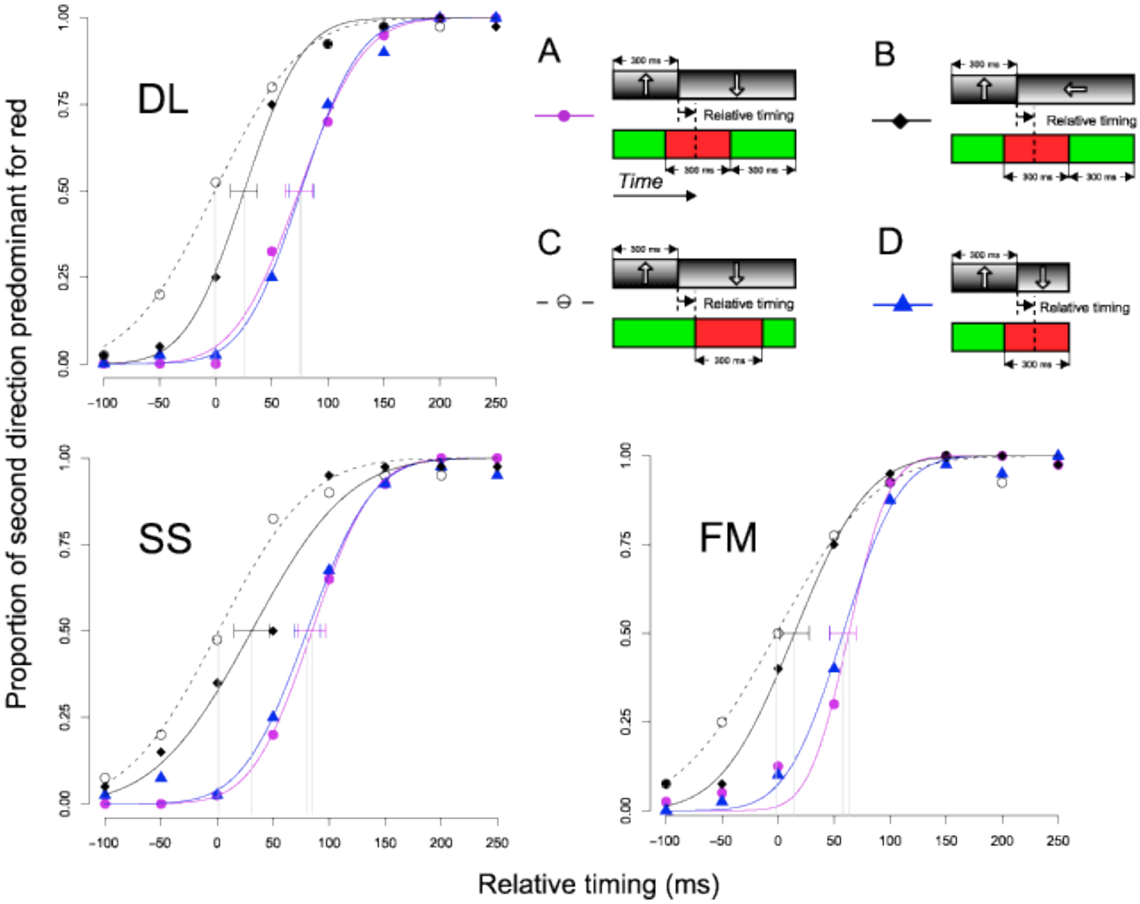

Figure 1. Diagrammatic representation of the temporal relationship between color and motion for each condition and results in form of individual psychometric functions in Experiment 1. (A) A single change in motion direction was sufficient to obtain the asynchrony between color and motion. The distribution of solid circles shows the proportions of trials in which the second direction of motion was reported for red dots as a function of the relative timing between the direction change and the center of the red interval. (B) A direction change of 90° strongly reduced the asynchrony (distribution of diamonds). (C) When a temporal order judgment was made between the direction change and the first change in color no asynchrony appeared (unfilled circles). (D) Removing the last green interval in the first condition resulted in the same asynchrony. The horizontal segments around the PSE correspond to 95% confidence intervals of the mean of the cumulative Gaussian function obtained with bootstrap method.

One important property of the illusion is that it depends on the angle between the two directions of motion (Arnold & Clifford, 2002; Bedell et al., 2003; Clifford et al., 2004), with a direction change of 180° producing the maximum asynchrony. Thus, if the angle decreases, so must the illusory effect. Precisely, this result is the main current evidence contrary to the time marker model because a direction change is a second-order change independently of the specific directions of motion. In order to make sure that the measured shift reflected a perceived asynchrony not confounded with response biases in favor of the first direction, we also measured the magnitude of the illusion for an angle of 90° between directions (distribution of solid diamonds in Figure 1). As expected, the asynchrony decreased significantly ($p < .001$). The average value of the asynchrony for this case was 26 ms.

We have thus shown that when a correspondence task is performed, against the time marker explanation, a single direction reversal suffices to obtain a similar asynchrony between color and motion as those reported elsewhere using repetitive displays (Arnold, 2005; Arnold & Clifford, 2002; Arnold et al. 2001; Bedell et al., 2003; Clifford et al., 2004; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002).

For the temporal order judgment task, in agreement with previously reported results (Bedell et al., 2003; Nishida and Johnston, 2002), we found that observers judged the temporal order very accurately (distribution of unfilled circles in Figure 1, notice that in this case the relative timing is between the direction change and the first color change and the ordinate represents "direction change occurring first"). This shows that the critical factor is the task; hence, the obtained patterns were not an artifact of the new stimulus we have used.

Repetitive stimulation has been considered a necessary condition for the color–motion asynchrony illusion to occur (see for example the review of visual illusions of Eagleman, 2001). Explaining this has proven to be a major obstacle to the differential processing time explanation because there is no reason why the latency for perceiving a change of motion direction, for example, should depend on whether this change appears in isolation or is embedded in other direction changes. Here, however, we solve this problem by showing that a single direction change is sufficient for motion to be systematically bound to a color that appears later in time.

According to the time marker explanation, the illusion arises because direction changes are difficult to detect when displayed at high frequencies. In the present investigation, although only used a single directional change, an attempt was made to maintain the similarity with previous studies reporting the illusion. Accordingly, we showed the first direction of motion for a very short time (300 ms). It could be argued that our results can still be accommodated by the time marker explanation considering that when motion is displayed for such a short interval of time, the detection of the direction change is impaired as in the case of several direction changes displayed at high frequencies. However, our finding showing accurate temporal order judgments demonstrates that the direction change could be correctly detected. Furthermore, it could also be suggested that the detection of the direction change is only impaired when a correspondence task is performed. But in this case, as the task involves the use of sustained information, it is not clear how the time marker explanation, which is formulated for temporal order judgments between events, can be applied.

Therefore, our results run counter to the time marker explanation (Nishida & Johnston, 2002) and are consistent with the differential processing time explanation of Bedell et al. (2003) for which the critical factor to obtain a perceptual asynchrony consists in performing a correspondence task between attributes. Interestingly, a similar dependence on task was found using the attributes of color and orientation (Clifford, Arnold, & Pearson, 2003). However, the question still remains as to why Nishida and Johnston (2002) find the illusion for rapid alternations even when they asked observers to perform a synchrony task (that is similar to a temporal order judgment task). We think, as Bedell et al. proposed, that for rapid alternations subjects might perform a correspondence task instead of a synchrony task. As subjects were explicitly asked to make synchrony judgments, we suggest that this hypothetical switch they made to a correspondence task might be due to the impossibility of performing a synchrony task under conditions of rapid alternations. We think that this may somehow be related to attentional limitations.

In order to maintain consistency with typical repetitive displays, we presented 300 ms of green color following the color target interval (red). However, according to the differential processing time explanation the asynchrony should occur regardless of the presence of this last color interval. To further ensure that the asynchrony that we measured is not caused by an influence of the last green interval over the red interval following the direction change, we eliminated the last green interval (Figure 1D). Indeed, the distribution corresponding to this manipulation (solid triangles in Figure 1) completely overlaps with the one having green as the last color. Hence, consistent with the differential processing time explanation, the perceived asynchrony does not depend on the presence of the last color interval.

However, upon questioning the observers, all of them reported experiencing a different percept when the last green interval was not present (compare the two demos shown in the Web page): they observed the red color moving in the two directions of motion more frequently. In contrast, they saw red moving in the second direction of motion much less often when the last green color interval was present. As observers were required to bind red to the predominant direction, this misperception of red color in the second direction would not affect the measured asynchrony. So as to explore this possible influence of the last green interval in the perceived color after the direction change, we carried out Experiment 2.

Experiment 2

In Experiment 1 we showed that, inconsistent with the time marker explanation, the perceptual asynchrony between color and motion can be observed when a correspondence task is performed on a single direction change. We also showed that the interval of color that followed the color on which the task was performed did not contribute to the measured asynchrony. However, informal reports of observers suggested that the color of the stimulus presented after the color target had an effect on the visibility of the color target. In Experiment 2, we explored this issue using a similar stimulus, but changing the task: observers were asked to report the number of directions they saw for the target color when the last color interval was present or absent. We hypothesize that if the last green color interval makes the perception of the red color difficult after the direction change, then the red color moving in two directions would be reported less frequently with respect to the situation where the last green color interval was absent.

Methods

The stimuli were very similar to that of Experiment 1 except that red is always presented 150 ms before the direction change and the amount of red after the direction change was varied on a trial-to-trial basis (see Figure 2). In this experiment, observers had to report whether they saw one or two directions of motion for red while varying the presence (Figures 2B and 2D) or absence (Figures 2A and 2C) of the last green color interval. We used two angles for the direction change: 180° (Figures 2A and 2B) and 90° (Figures 2C and 2D). Within one session, each relative timing value was sampled on 20 occasions according to the method of constant stimuli. Each observer performed two sessions with the color target being different in each one.

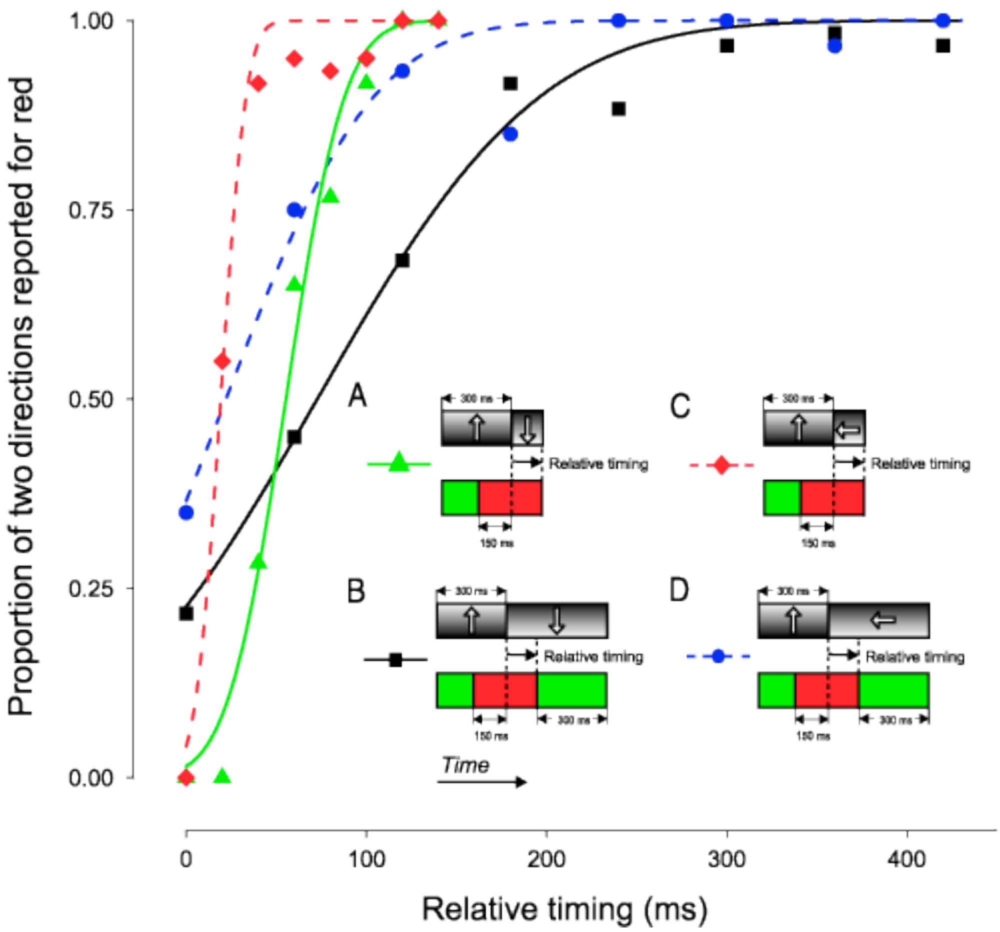

Figure 2. Diagrammatic representation of the temporal relationship between color and motion for each condition and data pooled over all participants in Experiment 2. Observers had to decide whether red color was perceived in one or two directions of motion while the relative timing between the direction change and the offset of red color was manipulated. (A) Direction change of 180° without last green interval. (B) Direction change of 180° with last green interval. (C) Direction change of 90° without last green interval. (D) Direction change of 90° without last green interval.

Results and discussion

Figure 2 shows the proportion of two directions reported for red while varying the amount of red presented in the second direction (data pooled over all participants). The mean of the distribution indicates how long red must be shown along the second direction for observers to report two directions for red color in 50% of trials.

When the last green color interval was absent we found a mean of 55 ms for the 180° direction change (distribution of triangles in Figure 2) and a mean of 19 ms for the 90° direction change (distribution of diamonds in Figure 2). These results show that when the dots move along the second direction for very short times, this direction of motion is not perceived. Interestingly, the mean is significantly reduced for the direction change of 90° with respect to the 180° condition ($p < .001$) and in a magnitude very similar to that reported in Experiment 1. This suggests that the perceptual delay in motion perception, as measured in Experiment 1, reflects that motion signal needs integration time to reach awareness (Burr & Santoro, 2001) and that this time depends on the former direction of motion. As the maximum asynchrony is obtained when reversing the direction, we think, as stated elsewhere (Arnold & Clifford, 2002; Bedell et al., 2003; Clifford et al., 2004), that mechanisms of opponency in MT underlie this perceptual asynchrony (Snowden, Treue, Erickson, & Andersen, 1991).

When the last green interval was present, the red dots had to be shown moving along the second direction for a slightly longer time (mean of 73 ms) to be equally perceived moving in one or two directions in comparison to when green was absent ($p < .001$ for the 180° condition distribution of squares in Figure 2). For the 90° condition (distribution of circles in Figure 2), this difference was not significant. In agreement with an effect of the last green interval, one would expect larger differences in the PSE (e.g., curve shifted further to the right when the green is present). We think that the lack of such an effect might have been caused by a response bias that shifts the curve to the left. The fact that subjects responded in several trials “two directions” for the relative timing of 0 for which red only is presented in one direction may reflect this bias. In any case, it is clear that the last green interval has an effect on the visibility of the red interval, which is shown by the significant variation of the slopes for the two angle conditions. The standard deviation increased from 25 to 97 ms for the 180° condition and from 11 to 64 ms for the 90° condition presumably reflecting a higher difficulty of the task.

Our findings share similarities with previous results published by Moradi and Shimojo (2004). They also reported a misbinding of color and motion within a single event. In one condition of their Experiment 5, observers were asked to report the color of a briefly moving surface that became perceptually segregated. During motion, the dots inside this surface were gray and the color switched back to green when they stopped. Subjects reported the color following motion offset more often than gray, which was the actual color during motion. Moradi and Shimojo regarded this result as the onset of a new surface triggering the analysis of the properties (including color) of the surface. They suggested that these properties are computed during a temporal window of 50–150 ms following the onset of the surface. Remarkably, the gray color was not perceived even when presented for 120 ms. As the temporal window of analysis lasts for 150 ms at the most, this implies that the color is not treated uniformly during the time window of analysis (Arnold, 2005) but it is temporally weighted distinctly favoring color information available later in time.

We think that another, and maybe simpler, explanation of the effect of the last color interval could be backward masking (Bachman, 1994). According to it, the last green color interval would mask red color in the last part of the red color interval. This account does not require any direction change to work. Thus, regardless of the direction change, a fixed quantity of red color would be masked. Although, it may seem contradictory, we think this is consistent with the fact that the difference ($p < .001$) between the two direction changes (90° and 180°) has the same trend as when the last color interval is absent: the last green color interval could mask a physically longer interval of red presented after a direction change of 180° simply because the first part of motion is not perceived in this case (last interval absent condition).

In summary, taking into account the results of Experiments 1 and 2, we believe that in a typical cycle display with several alternations, the perceived asynchrony genuinely reflects differential processing latencies between color and motion: perceptual experience of motion is delayed when motion in the opposite direction is previously displayed. However, we show that some form of visual masking also contributes to the percept making the perception of color after direction changes more difficult and facilitating the pairing of colors with directions presented before direction changes.

Conclusions

The color–motion asynchrony illusion has been used to study the temporal perception of events and the binding of visual attributes. The asynchrony is typically measured using repetitive displays in which the relative phase between motion direction changes and color changes is varied using the entire range of the cycle. One advantage of such displays is that any response bias should be eliminated. Here, we did not follow this tradition because we were interested in the binding between motion and color when only a single change was displayed. Although this might have created some response bias, it cannot account for the whole perceptual asynchrony we found as shown by the dependency on the angle.

In Experiment 1, using a single direction change display, we showed that the perceived asynchrony cannot be explained according to the time marker explanation. However, the results were perfectly compatible with the differential processing time explanation for which the differences in processing time between attributes result in perceptual differences. Importantly, the asynchrony arose when a correspondence task was made, but not for temporal order judgments. This means that the perceptual delay of motion is not a fixed quantity but depends on the mechanisms engaged in the task. Normally, the delay in motion perception is associated with mechanisms of opponency of MT.

The results of Experiment 2 without a last color interval following the color target support this view: motion needs integration time below a threshold to be perceived, and this integration time depends on the direction of motion before the change being maximum when the directions are totally opposed.

Although in Experiment 1, we showed, using a typical task of pairing, that the color interval that follows the color target interval has no effect on the measured asynchrony, the results of Experiment 2 with a color interval following the color target showed that this last color interval had a perceptual effect of masking.

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CHAPTER 4: Absence of flash-lag when judging global shape from local positions[6]

Abstract

When a flash is presented aligned with a moving stimulus, the former is perceived to lag behind the latter (the flash-lag effect). We study whether this mislocalization occurs when a positional judgment is not required, but a veridical spatial relationship between moving and flashed stimuli is needed to perceive a global shape. To do this, we used Glass patterns that are formed by pairs of correlated dots. One dot of each pair was presented moving and, at a given moment, the other dot of each pair was flashed in order to build the Glass pattern. If a flash-lag effect occurs between each pair of dots, we expect the best perception of the global shape to occur when the flashed dots are presented before the moving dots arrive at the position that physically builds the Glass pattern. Contrary to this, we found that the best detection of Glass patterns occurred for the situation of physical alignment. This result is not consistent with a low level contribution to the flash-lag effect.

1. Introduction

In view of the biological relevance of detecting moving objects, neural mechanisms have been postulated so as to reduce (Whitney, Murakami, & Cavanagh, 2000; Whitney & Murakami, 1998) or correct (Nijhawan, 1994) the inevitable neural delays associated with their visual processing. The flash-lag effect, in which a briefly flashed object presented aligned with a moving one in the retina is perceived to lag behind it, has been suggested as the most convincing evidence for the existence of such mechanisms (Whitney, Murakami, & Cavanagh, 2000; Whitney & Murakami, 1998; Nijhawan, 1994), although other alternative explanations have been proposed (rev. Nijhawan, 2002; Krekelberg & Lappe, 2001).

It is still an open question where in the visual pathway the mislocalization takes place, but some neurophysiological studies suggest a low-level contribution of these special mechanisms for the processing of moving stimuli that could occur as early as in the retina (Berry, Brivanlou, Jordan & Meister, 1999) or LGN (Orban, Hoffmann, & Duysens, 1985).

If there is a contribution of early visual areas to the spatial mislocalization between moving and flashed stimuli, then this mislocalization can be expected to occur at a spatially local level and independently of the task. Here, we test this prediction by performing a form detection task in which a precise spatial

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local relationship between moving and flashed information is needed to perceive a global shape.

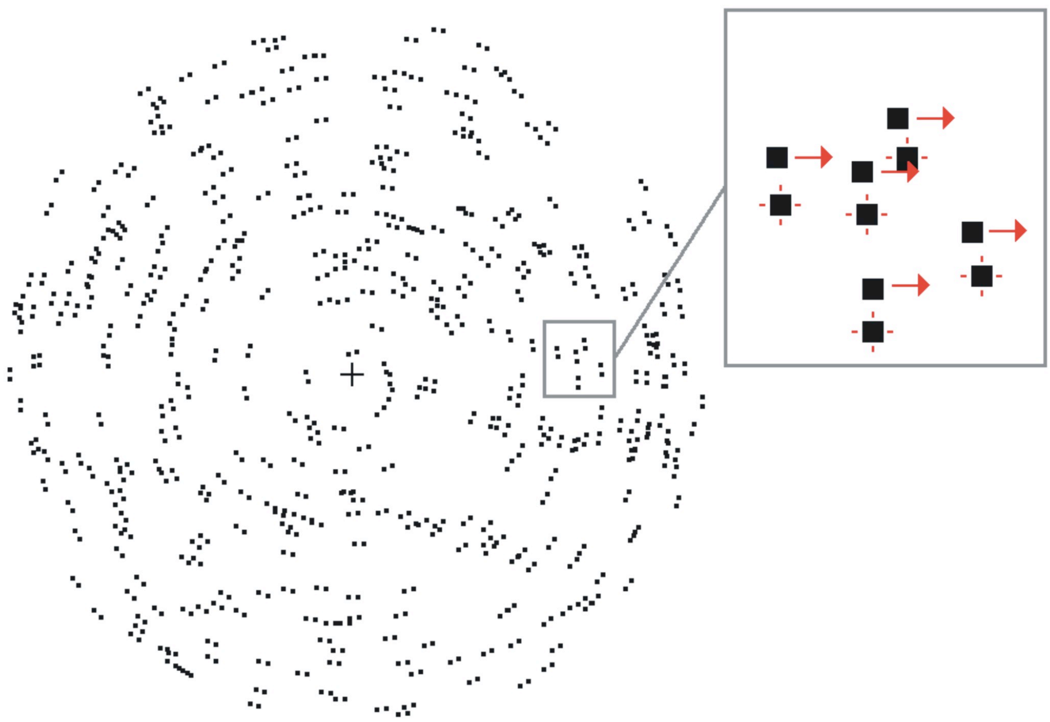

Fig 1. Representation of the stimulus in the moving dots condition for a relative timing of zero. In the real experiment the contrast was reversed (white dots on black background).

Specifically, we used a concentric Glass pattern (Glass, 1969). Concentric Glass patterns consist of a large number of pairs of dots. The first dot of each pair is positioned randomly within the stimulus area. The position of the second dot is determined by rotating the radial vector corresponding to the first dot by a fixed amount. The pattern creates the visual impression of a rotary visual structure (see Figure 1). In our experiment one dot of each pair was flashed while the other was presented in motion (all the moving dots had the same direction). The best global form is physically obtained when the flashed dots of each pair are physically aligned (see inset of figure 1). However, if there is a flash-lag effect for each pair then the best global form should occur when the flashed dots are presented before the moving dots arrive at the position of physical alignment. As in the flash-lag, this would be so because a perceived (not physical) alignment would allow one to recover the global shape. By varying the timing at which the flashed dots were presented we explored when the best performance was achieved in a global form detection task.

2. Method

Stimuli were displayed on a 19” CRT monitor (Philips Brilliance 109P4) at a refresh rate of 100 Hz and viewed binocularly from a distance of 50 cm in a dimly lit room. The dots (size: 0.16 deg x 0.16 deg) were shown within a circular aperture with a diameter of 23 deg of visual angle on a dark background. Three observers participated in the experiment, the first author (DL) and two observers who were naïve with respect to the purposes of the study (ML, SS). Observers reported normal, or corrected to normal, visual acuity and color vision. Observers were instructed to maintain fixation on a cross presented at the center of the aperture. Observers were tested in two sessions for each of the conditions that will next be explained.

2.1. Moving dots condition

Each trial consisted of two successive intervals temporally separated by one second. The concentric Glass pattern was presented at random in either the first or the second interval. After each trial, the observer had to indicate which interval contained the concentric Glass pattern.

The interval that contained the concentric Glass pattern consisted of 400 dots (luminance 23 cd/m^2) moving at 6 deg/s. All the dots moved in the same direction. The direction was chosen at random from all possible directions in the plane and so was the initial location of each dot within the circular aperture. When a moving dot reached the limit of the invisible aperture, then it appeared on the opposite site of the aperture. After 500 ms, another 400 dots (flashed dots, luminance 93 cd/m^2) were displayed for 10 ms to build the concentric Glass pattern (see Figure 1). The moving dots kept moving for 500 ms after the flashed dots were presented and then disappeared. So each interval lasted for one second and the concentric Glass pattern was available just for one frame (10 ms). The luminance was measured with steady presentation of the dots. The luminance of the flashed dots was greater in order to equate the perceived luminance.

The concentric Glass pattern was built by presenting a flashed dot at a distance of 0.32 deg from each moving dot (distance between the centers) in a direction perpendicular to the radial vector corresponding to the moving dot. The interval that did not contain the concentric Glass pattern was identical except that the direction between each moving dot and its associated flashed dot was chosen at random.

We have just described the situation of physical alignment: the flashed dots were displayed at the time relative to the position of the moving dots that allowed to built the concentric Glass pattern. We refer to this situation as the one corresponding to a relative timing of zero. But in each trial we varied this relative timing in a way that sometimes the flashed dots were presented before the moving dots arrive at the position of physical alignment (positive relative timings) and sometimes the flashed dots were presented after (negative relative timings). We used 10 relative timings ranged from -100 ms to 120 ms. Each relative timing was sampled 20 times within a single session according to the method of constant stimuli.

2.2. Static dots condition

This condition was identical to the moving dots condition, except for the fact that the dots that we previously referred to as moving dots here remained still for one second. The relative positions between the fixed dot and the corresponding flashed dot matched those that we used in the moving dots condition. As before the flashed dots were presented for 10 ms. This condition was used to examine how much the shift of half of the dots blurred the Glass pattern in absence of motion. For the sake of clarity, we keep using the term “relative timing” although here it has only a spatial meaning. We used the same 10 relative timings as before and were sampled 20 times.

2.3. One-dot position judgment condition

Each trial consisted of a single dot moving at a 6 deg/s in a random direction for one second. The initial position was chosen randomly within the area of the circular aperture. When a moving dot reached the limit of the aperture, it was replaced as in the moving dots condition. After 500 ms, another dot was flashed during 10 ms at a distance of 0.32 deg perpendicularly to the direction of the motion of the moving dot. This situation corresponded to a relative timing of zero, but in addition to this value we used other values depending on whether the flashed dot was presented before (positive values) or after (negative values). In each trial, subjects had to judge the position of the moving object (behind or ahead) with respect to the flashed dot along the direction of the moving dot. In order for the psychometric functions to be saturated, we used different relative timings depending on the observer ranging from -150 ms to 300 ms. Each relative timing was sampled 20 times.

2.4. Set-of-dots position judgment condition

This condition was similar to the one-dot position judgment condition. In this case, however, participants had to compare the spatial localization of two overlapped populations of dots: a moving population and a flashed population. The moving population consisted of 15 dots moving laterally (all in the same direction) at a 6 deg/s. The direction (leftwards or rightwards) was constant within one session but changed between sessions. These dots were initially located randomly within a squared aperture (side of 3.95 deg). The density of the dots was the same as in the moving dots condition. The center of the aperture was located at a random position within a circular aperture of 12 deg of diameter relative to the fixation point. The dots moved for 500 ms, and then another 15 dots were flashed for 10 ms. The relative location between the dots of each pair was the same as in the one-dot position judgment condition. Participants were asked to report whether the flashed population appeared ahead or behind the moving population.

2.5. Data analysis

The following model was fitted to the data points for the moving and the static dots conditions: p(correct) = (pmax - 0.5) * exp(-(x-μ)^2/σ) + 0.5 where pmax stands for the maximum number of correct responses, μ and σ are the mean and deviation of the Gaussian respectively.

For the position judgment task, the set of data from each participant provided a distribution of the proportion of trials in which the moving dot is perceived behind the flashed dot as a function of the relative timing. We fitted a cumulative Gaussian to obtain the point of subjective equality (the mean of the distribution), which served as a measure of the flash-lag effect.

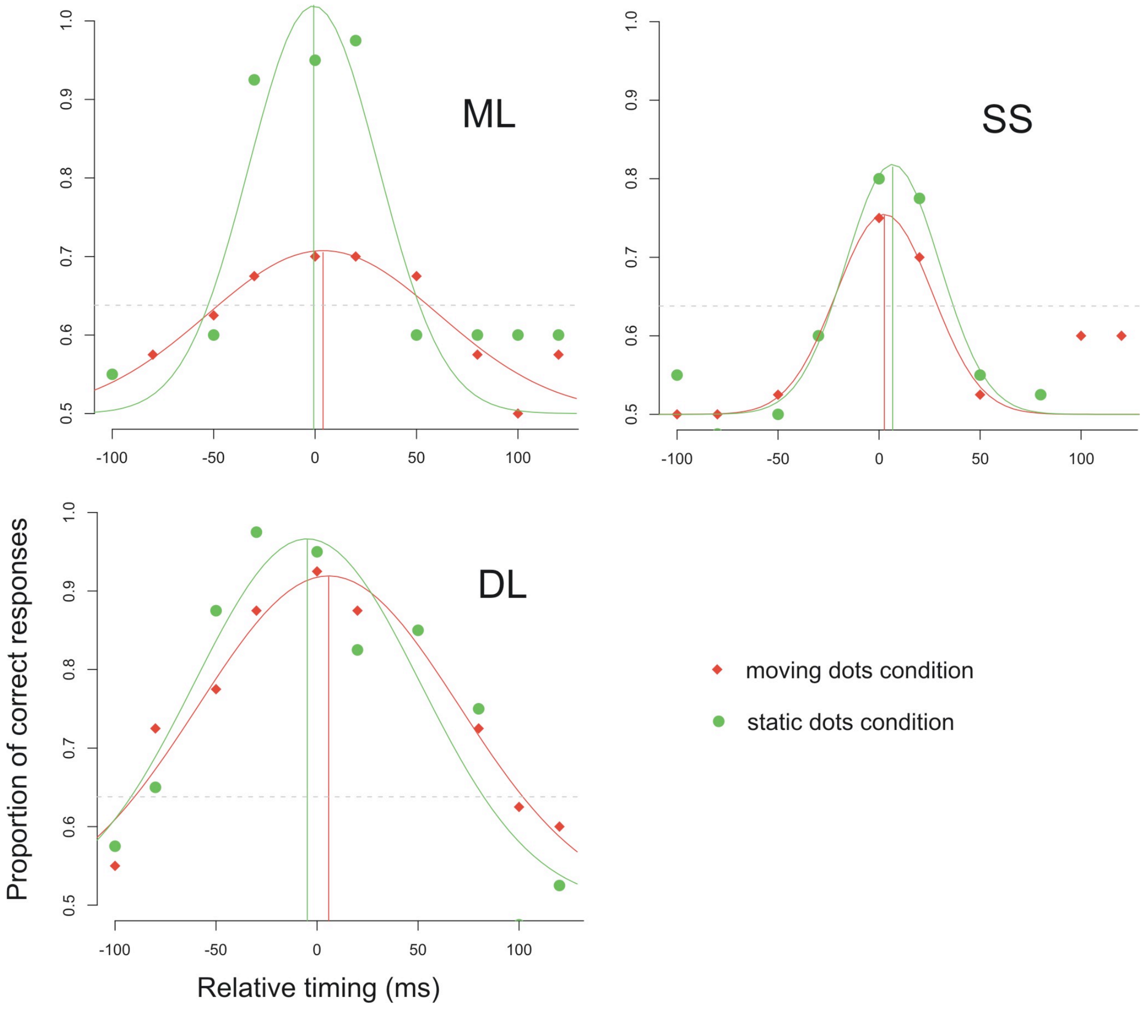

Fig 2. Proportion of correct responses as a function of the relative timing for each observer. The distribution of solid circles corresponds to the static dots condition and the solid diamonds to the moving dots condition. The solid line denotes the best fit of a Gaussian curve scaled between 0.5 and 1. The horizontal dotted lines denote the upper limit of the chance performance interval according to a binomial distribution.

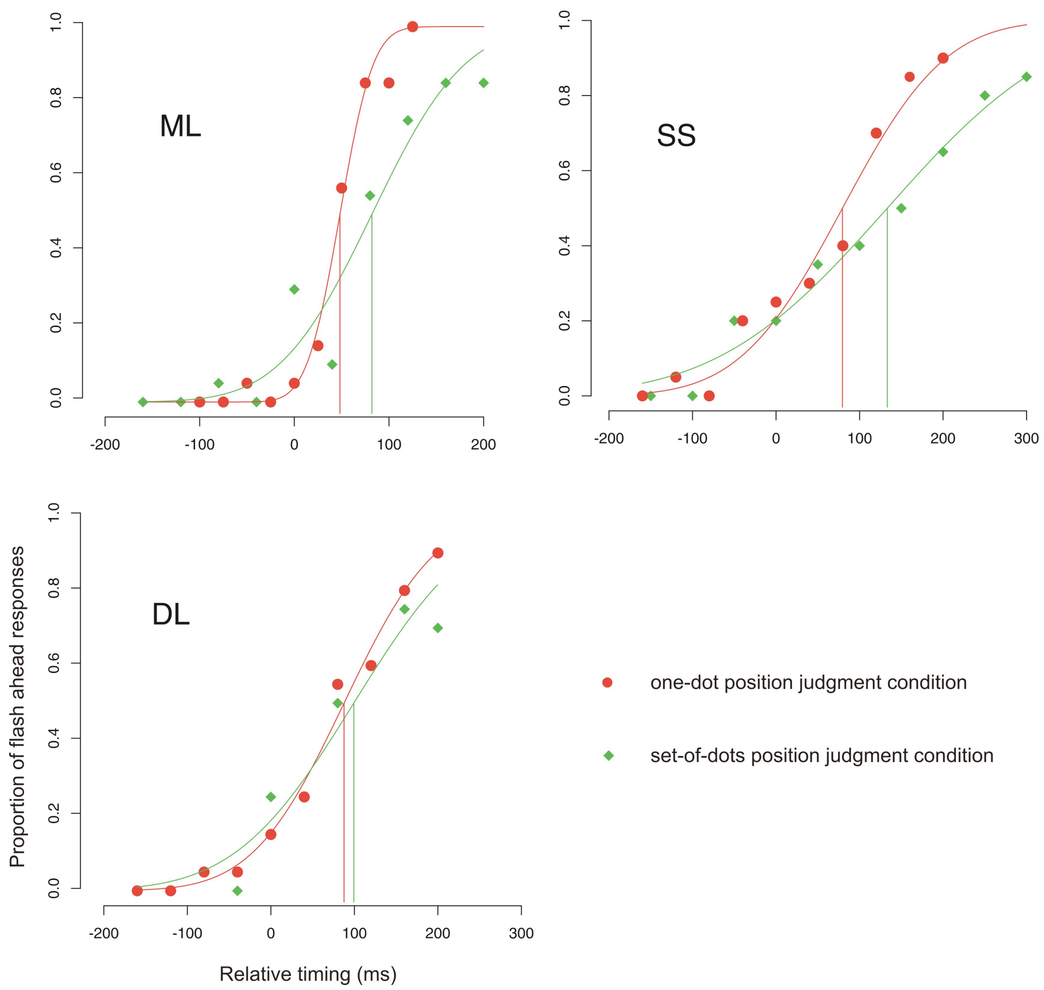

Fig 3. Proportion of flash ahead responses as a function of the relative timing for each observer. The distribution of solid circles corresponds to the one-dot position judgment condition and the solid diamonds to the set-of-dots position judgment condition. The solid lines denote the best cumulative Gaussian curve.

2. Results

Figure 2 shows the percent of correct detection as a function of the relative timing for the moving dots condition and the static dots condition (individual results).

If a flash-lag effect occurs between each pair of dots, then we expect the mean of the Gaussian for the moving dots condition to be shifted to the right relative to the static dots condition and this shift be significantly different from zero. By eye analysis one can easily see that the means are very close to the zero timing. We ran a parametric bootstrap (Efron & Tibshirani, 1993) as conducted in Kanai et al. (2004) and López-Moliner & Linares (2006) for each participant and obtained the 95% confidence intervals (CI) for the means of the two conditions. For all participants the CI intervals completely overlapped and always contained the zero.

For both conditions, the detection performance was over chance not only for the zero relative timing, but also for relative timings near zero. This means that for small shifts of half of the dots the Glass pattern was still available for detection. Larger shifts would be necessary for the Glass pattern to get blurred. Chung, Kharn and Oh (2004) actually showed that the effect of shifting a small distance half of the dots in a circular Glass pattern results in a shift of the focus of the Glass pattern in a direction orthogonal to that in which the dots were shifted. A small shift of focus could be observed in our stimuli for small relative timings, for which the global form can yet be often recovered. However, our naive subjects became aware of this shift only when they were explicitly told to look at it in a set of post-experiment trials.

The results of the position judgment tasks are summarized in Figure 3. For the position judgment task of a single moving dot and its flashed partner, we found a mean flash-lag effect of 72 ms (Observer ML: mean of 49 ms and deviation of 30 ms; observer SS: mean of 80 ms and deviation of 97 ms; observer DL: mean of 88 ms and deviation of 86 ms). A significant flash-lag effect was also found for the position judgment task between the two populations of dots. The mean flash-lag effect was of 125 ms (Observer ML: mean of 82 ms and deviation of 80 ms; observer SS: mean of 133 ms and deviation of 160 ms; observer DL: mean of 100 ms and deviation of 112 ms).

4. Discussion

Our results demonstrate that mislocalizations between moving and flashed stimuli do not always happen. Specifically, we show that the local spatial relationships between moving and flashed dots are preserved when they are used to detect a global shape. This result is not consistent with a low level contribution to the flash-lag effect which would predict a mislocalization in all situations, and suggests the involvement of higher visual areas.

When the task, however, required reporting local relative positions between a single moving dot and its flashed "partner" a typical flash-lag was found. In order to explore the position judgment task in a situation more similar to that corresponding to the moving dots condition, the task was also performed using sets of dots. In this case, a significant flash-lag effect was also found. Therefore, it seems that a necessary condition for the flash-lag to appear is the performance of a position judgment task.

Glass patterns (Glass, 1969) have been extensively used to explore local and global stages of the visual form pathway (Wilson & Wilkinson 1998), as the visual system must identify local orientation cues and combine them to extract the global structure. It has been suggested that area V4 could be involved in the global stage of processing (Wilson & Wilkinson 1998) given that neurons in macaque V4 have been reported to be selective for complex shapes similar to Glass patterns, including radial, concentric and hyperbolic gratings (Gallant, Braun & Van Essen, 1993). Our finding suggests that the spatial relationship between moving and flashed information is maintained at this level. This however cannot be conclusive, as it has been shown that the distortions in the retinotopic map of V4 do not always correspond to perceptual mislocalizations (Sundberg, Fallah, & Reynolds, 2006).

The flash-lag illusion is a robust effect and, to our knowledge, only one study has found a lack of mislocalization between flashes and moving objects (Kanai & Verstraten, 2006). Kanai and Verstraten found that when a ring was flashed surrounding a moving disk, the percept corresponding to the disk split in two: one disc was perceived ahead of the flashed ring which reproduced the flash-lag effect, but the other appeared just centered inside the flashed ring showing no relative spatial mislocalization. They also found that when the disc did not fill in completely the ring, only the percept corresponding to the mislocalized ring occurred. Therefore, they attributed the perception of the veridical localization to a filling-in process. In our case, as there is a spatial separation, though small, between moving and flashed dots we think that filling-in might not be the cause. Anyway, these two sets of results (Kanai and Verstraten and ours) show that sometimes the spatial relationship between moving and flashed stimuli are preserved running counter to a low-level explanation of the flash-lag effect.

Acknowledgments

We thank Eli Brenner, Ryota Kanai, and two anonymous reviewers for their comments and suggestions. This research was supported in part by Grant TINS2004-04363-C03-02 from the Ministerio de Educacion y Ciencia of the Spanish government.

CHAPTER 5: Motion signal and the perceived positions of moving objects[7]

Abstract

When a flash is presented in spatial alignment with a moving stimulus, the flash appears to lag behind (the flash-lag effect). The motion of the object can influence the position of the flash, but there may also be a reciprocal effect of the flash on the moving object. Here, we demonstrate that this is the case. First, we show that the position of a moving object that suddenly materialises in the visual field appears progressively further forward in its trajectory until the shift reaches a steady state after one second. Second, this shift is mediated by the integration of motion signals. Third, the proximity of a flash disrupts this process of integration.

1. Introduction

Localisation of objects in visual space is one of the primary functions of the visual system. Spatial localisation depends not only on position in retinotopic maps, but also on other influences (Schlag & Schlag-Rey, 2002) like the motion signal (Whitney, 2002). For example, it has been shown that the perceived location of a stationary envelope filled with a moving pattern is biased in the direction of motion (Ramachandran & Anstis, 1990; De Valois & De Valois, 1991). Moreover, if after prolonged viewing, the pattern stops, then not only is the stationary pattern perceived as moving in the opposite direction – the motion aftereffect (MAE), but the perceived position of the envelope is also shifted in the direction of the MAE (Nishida & Johnston, 1999; Snowden, 1998), indicating position shifts can arise from internally generated motion. Interestingly, it has been shown (Nishida & Johnston, 1999) that the shift induced by MAE gradually increases over the first one or two seconds post adaptation suggesting that the representation of position is influenced by a dynamic system that integrates motion information over time.

The flash-lag effect (Nijhawan, 1994) has also been used extensively to study the perceived location of moving objects. When a flash is presented in spatial alignment with a moving stimulus, the flash appears to lag behind. The cause of the illusion is still a matter of debate (Krekelberg & Lappe, 2001; Nijhawan, 2002; Whitney, 2002). While some investigators support the view that the flash-

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lag mislocalisation is caused by purely temporal mechanisms (Baldo & Klein, 1995; Brenner & Smeets, 2000; Krekelberg & Lappe, 2000; Purushothaman, Patel, Bedell, & Ögmen, 1998; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000), others propose spatial mechanisms that directly influence the coded location of the moving object shifting its apparent position in the direction of motion (Nijhawan, 1994; Snowden, 1998). If this is the case, given that it has been shown that the motion signal is integrated over time (Nishida & Johnston, 1999), one might also expect the magnitude of the flash-lag effect to evolve over time. Specifically, one would predict that the flash-lag effect magnitude should increase as the duration of the pre-flash trajectory increases.

Previous empirical work on the flash-lag effect, however, does not support this prediction. Several studies have compared the magnitude of the flash-lag effect when the presentation of the flash coincides with the onset of the moving object against conditions in which the flash is presented during continuous object motion. While some studies found that the magnitude of the effect for continuous object motion and flash initiated motion are the same (Baldo & Klein, 1995; Eagleman & Sejnowski, 2000; Nijhawan, Watanabe, Khurana, & Shimojo, 2004), others found a larger effect for the flash at onset presentation (Müsseler, Stork, & Kerzel, 2002; Ögmen, Patel, Bedell, & Camuz, 2004; Chappell, Hine, Acworth, & Hardwick, 2006).

We believe that the apparently incongruous results, with respect to the temporal dependence of spatial position shifts, between the MAE and flash-lag experiments may be explained if, in the flash-lag effect, the sudden appearance of a near flash influences the perception of the moving object. Here we show that when a flash is presented near the moving object, the flash-lag effect does not depend greatly on the duration of the pre-flash trajectory. However, when the flash is presented sufficiently far away from the moving object, the flash-lag effect increases with the duration of the pre-flash trajectory, until it reaches an asymptotic level. We also show that the interaction of the flash with the perceived position of the moving object can occur when the flash is task-irrelevant. Finally, using the MAE we confirm that the progressive shift that we observed involves the integration of motion signals.

2. General methods

The stimuli were displayed on a 21” CRT monitor (Sony Trinitron GM 520) at a refresh rate of 100 Hz and were viewed binocularly from a distance of 50 cm in a dimly lit room. Observers reported normal, or corrected to normal, visual acuity. They were instructed to maintain fixation on a dot presented at the center of the display.

We presented observers with a pair of dots, diametrically opposed to each other, rotating about the fixation point. We measured the perceived position of the pair at several intervals from their motion onset (flash presentation time) in the visual field by flashing another pair of diametrically opposed dots and asking observers for relative position judgments (Figure 1).

Both, the moving and the flashed dots subtended 0.8 deg of visual angle. They were displayed on a dark background. The moving dots (luminance = 23 cd/m^2, angular speed= 60 deg· s^{-1}) were presented at an eccentricity of 7.5 deg of visual angle. The direction of rotation varied at random in each trial between clock-wise and anti-clock-wise. The flashed dots (luminance = 93 cd/m^2) were displayed for 10 ms. The fixation dot was the same size as the flashed dots (luminance = 23 cd/m^2).

Participants judged whether the flashed dots were displayed behind or ahead of the moving dots. We expressed the spatial misalignment as an orientation difference between the imaginary lines that pass through the moving dots and the flashed dots (Figure 1A). Their relative position (orientation) was varied according to the method of constant stimuli. Nine relative orientations ranging from -3.6 deg to 25.2 deg in increments of 3.6 deg were used to derive a psychometric function. Positive values corresponded to the flashed dots presented ahead with respect to the moving dots. Each psychometric function provided distributions of the proportion of trials in which the moving dots were seen behind the flashed dots as a function of their relative orientation. We fitted cumulative-Gaussians to derive the points of subjective equality (the means of the distributions), which served as measures of the flash-lag effect. Measurements were made for several flash presentation times in each of the three reported experiments

We used the parametric bootstrap method (Efron & Tibshirani, 1993) to obtain the 95% confidence intervals for the parameters of the cumulative-Gaussian functions. When conclusions could not be drawn by merely looking at the overlap between two confidence intervals, parametric bootstrap and Monte Carlo simulations were used to compare two given psychometric curves by testing the null hypothesis that the observed difference between points of subjective equality is not different from zero. To accomplish this, we used procedure implemented in pfcmp (Wichmann & Hill, 2001a, 2001b).

3. Experiment 1

In the first experiment we investigated the dependency of the flash-lag effect on the timing of the motion trajectory. As we suspected that the proximity of the flash might also affect the perceived position of the moving object, we also varied the distance between the flash dots and the moving dots.

3.1. Methods

Three observers participated in the experiment, the first author and two psychophysically trained observers who were naïve as to the purposes of the study. We measured the flash-lag effect at various time points (flash presentation time: 200, 400, 800 and 1600 ms) as a function of the distance between the flash and the moving object (1, 2.5 and 5 deg). Each observer conducted 5 sessions. The experimental conditions were randomised within each session. For each flash presentation time, each relative distance was sampled 20 times. So, each orientation error was calculated using 60 measures.

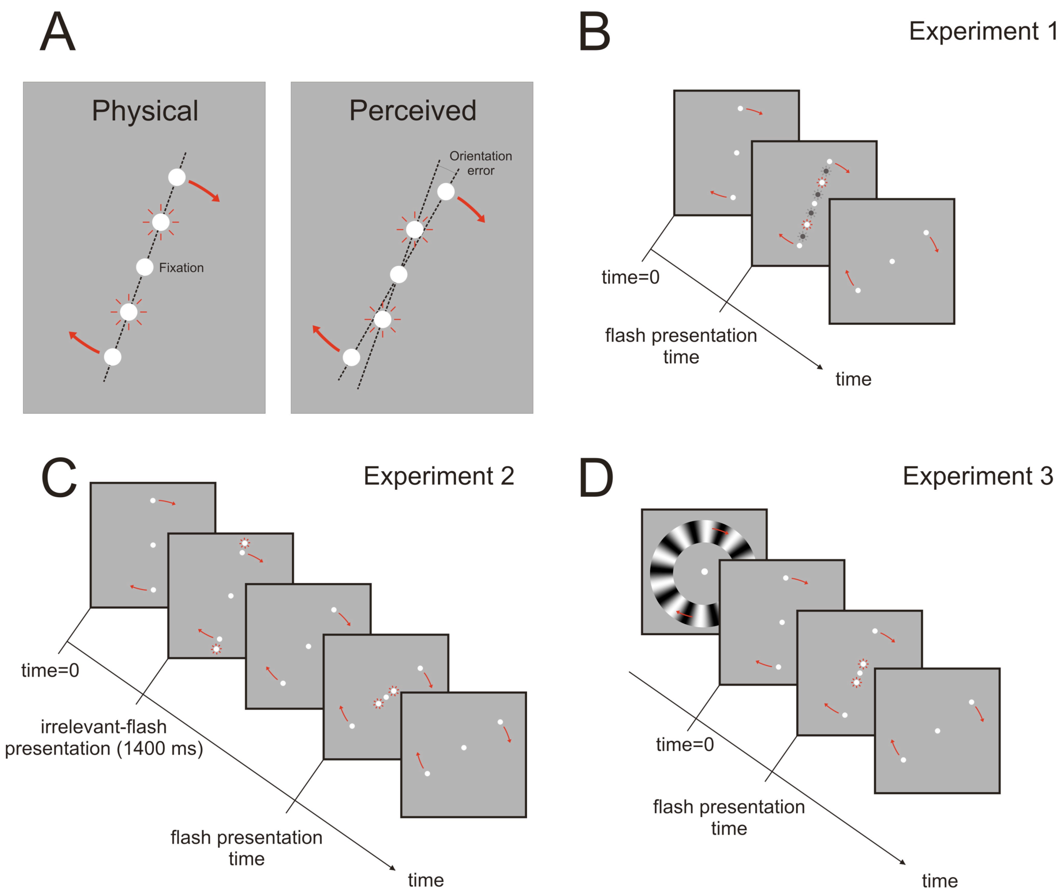

Figure 1. (A) Illustration of the flash-lag effect. (B) Experiment 1. Three different positions for the flashed dots were tested. (C) Experiment 2. In addition to the flashed dots used to measure the flash-lag effect another two flashed dots completely irrelevant for the task were displayed. (D) Experiment 3. Before each trial, a sinusoidal grating was displayed to produce adaptation.

3.2. Results

Figure 2A shows the orientation error as a function of the flash presentation time and the relative distance between the flashed and moving dots. The flash-lag effect was greater when the flash was presented 800 ms as compared to 200 ms after the onset of motion ($p<0.05$) for each of the three relative distances. The difference between these two flash presentation times, however, was larger for the 5 deg separation (orientation error difference: 4.00 deg) than for the 2.5 deg separation (orientation error difference: 1.47 deg) or for the 1 deg separation (orientation error difference: 1.23 deg).

For the three relative distances, the flash-lag effect was very similar for the 800 ms and 1600 ms latencies, although for the 1 deg separation condition the difference reached significance ($p=0.036$).

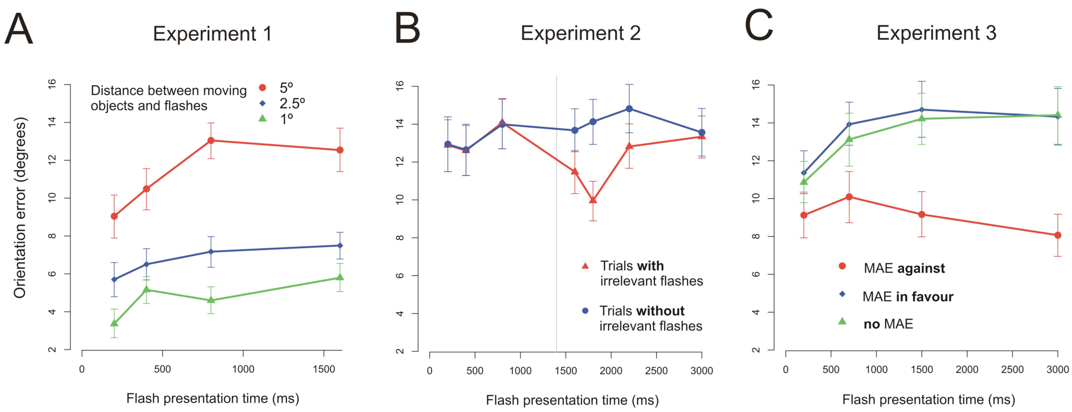

Figure 2. (A) Results of Experiment 1. (B) Results of Experiment 2. The vertical gray line represents the presentation time for irrelevant flashes (1400 ms). (C) Results of Experiment 3. The error bars represent a 95% confidence interval estimated by using bootstrap.

3.3. Discussion

The results (Figure 2A) show the typical flash-lag effect: the moving dots appear ahead of the flashed dots when they are physically aligned (Figure 1A). We also found that the magnitude of the lag decreased as the eccentricity of the flashed dots increased (red, green and blue lines in Figure 1A). Baldo and Klein (1995) used a similar display, but they presented the flashes more peripherally than the moving objects. They showed that the flash-lag effect increased as the eccentricity of the flashes increased. Therefore, our findings complement theirs showing that not only the absolute eccentricity of flashes matters, but also the relative distance between the flashes and the moving objects.

Interestingly, we found that the lag gradually increased with the duration of the pre-flash trajectory until it reached an asymptotic level (Figure 2A), indicating some temporal recruitment of the apparent shift in spatial position (Nishida & Johnston, 1999).

The effect of the pre-flash trajectory is substantially reduced for flashes presented near moving objects (green and blue lines in Figure 2A) suggesting an interaction between flashes and moving objects. Since in flash-lag studies, flashes are typically presented relatively close to moving objects, this result is consistent with studies showing no differences between the flash-onset and the continuous flash-lag effect (Baldo & Klein, 1995; Eagleman & Sejnowski, 2000; Nijhawan et al., 2004).

As mentioned in the Introduction, others studies, however, have found significant differences between the flash-onset and the continuous flash-lag effect (Müsseler et al., 2002; Ögmen et al., 2004; Chappell et al., 2006). It is possible that in these studies the hypothetical interaction between the flash and the moving object is not sufficient strong to make these conditions indistinguishable. Here, we tried to manipulate the influence of flashes by varying their distance to moving objects, but other parameters might matter. In the study of Ögmen et al. (2004), for example, the distance between the moving object and the flashes is very small, nevertheless the size of the flash is much smaller than the size of the moving object which could diminish the hypothetical interaction.

Importantly however, we show that the flash-lag effect increases with the pre-flash trajectory. We did not measure the flash-lag effect at flash-onset, but extrapolating our results, one would predict a smaller flash-lag effect for the flash-onset condition with respect to the continuous motion condition. As the empirical evidence is contrary to this prediction (Müsseler et al., 2002; Ögmen et al., 2004; Chappell et al., 2006), we think that there may be another influence in the flash-onset condition in addition to some common mechanism (Müsseler et al., 2002). Chappell et al. (2006), for example, speculate that this additional component involves the allocation of attentional resources to a new object appearing in the visual field (Yantis, 1996). Indeed, the flash-lag effect at flash-onset is similar to the Frohlich effect (Frohlich, 1923) which is considered to involve attentional mechanisms (Kirschfeld & Kammer, 1999).

4. Experiment 2

It has been shown that a moving object can influence the perceived position of a flash (Durant & Johnston, 2004; Whitney & Cavanagh, 2000), but the results of Experiment 1 suggest that there is also a reciprocal effect of the flash on the moving object.

In order to determine whether the flash has some direct effect, on the Experiment 2 we explored whether this effect could be also caused by task-irrelevant flashes. In each trial two types of flashes were presented: task-irrelevant flashes were displayed near to the moving objects after 1400 ms from the onset of motion and, in order to measure the flash-lag effect in different instants of time, task-relevant flashes were displayed far away from the moving objects.

4.1. Methods

Ten naïve observers participated in the experiment. None of them had experience of psychophysical experiments. We measured the flash-lag effect using the most remote flashes of Experiment 1 at different points in time (flash presentation time: 200, 400, 800, 1600, 1800, 2200 ms and 3000 ms). In half of the trials, after 1400 ms from the onset of motion we presented a pair of flashed dots (irrelevant flashes) close to the moving dots instructing the observers to ignore them. The eccentricity of the irrelevant flashed dots was 8.5 deg. Each observer performed 4 sessions. The experimental conditions were randomized within each session. Each flash presentation time was sampled 16 times (8 times with irrelevant flashes and 8 times without). So, each orientation error was calculated using 80 measures.

4.2. Results

Figure 2B shows the orientation error as a function of the flash presentation time. The red line corresponds to the condition in which the task-irrelevant flashes were displayed and the blue line to the condition in which they were not displayed. Before the presentation of task-irrelevant flashes (flash presentation times: 200, 400 and 800 ms) the confidence intervals for these two conditions completely overlap. However, at 200, 400, and 800 ms after the presentation of the task-irrelevant flashes (flash presentation times: 1600, 1800 and 2200 ms) the flash-lag effect was significantly smaller ($p<0.05$) in the presence of irrelevant flashes. No differences were found when the flash-lag was measured 1600 ms after the occurrence of the task-irrelevant flashes (flash presentation time: 3000ms).

As before 1400 ms (flash presentation times: 200, 400 and 800 ms) the task irrelevant flashes had no effect, we included the data of the conditions in an analysis of the change in the flash-lag effect over time. The flash-lag effect measured at 200 ms and 400 ms after motion onset did not differ significantly but the effect at 400 ms was smaller than at 800 ms ($p<0.05$). This increase in the flash-lag effect for the longer presentation time, is however smaller than that found in Experiment 1.

After 1400 ms (flash presentation times: 1600, 1800, 2200 and 3000 ms), when the task-irrelevant flashes were not presented, there were no significant differences flash-lag effect between the various presentation times. When the task-irrelevant flashes were presented, however, some differences appeared: the flash-lag effect at 1800 ms was not significantly different from that at 1600 ms, but it was smaller than for the 2200 and 3000 ms conditions.

4.3. Discussion

The flash-lag effect measured before 1400 ms was not influenced by the occurrence of the irrelevant flashes (Figure 2B). This was expected since trials with irrelevant flashes and without irrelevant flashes are identical in this time interval. Crucially, the occurrence of the irrelevant flashes affected the measured lag for more than one second after (Figure 2B), showing a clear effect of flashes on the perceived positions of moving objects that seems to consist of re-starting the process of spatial repositioning.

Except the postdiction account (Eagleman & Sejnowski 2000) for which the flash resets motion signal, the other explanations assume no interaction between the moving object and the flash (Krekelberg & Lappe, 2001; Nijhawan, 2002; Whitney, 2002). The flash, therefore, is considered for the most of accounts as just spatiotemporal marker that indicate when position judgments should be made. Here, against this view we show that a flash (even when task-irrelevant) presented near a moving object perturbs its perceived position. This is consistent with a very recent investigation (Chappell et al., 2006) showing that both onset and reversal trajectories of a moving object are affected by the presentation of an adjacent task-irrelevant flash. They proposed attention “capture” as an explanation, but this cannot explain our results because it would be expected to enhance the lag. In addition, we show that the effect of irrelevant flashes lasted for more than one second after.

Against expectation, we found that the initial progressive shift (flash presentation times: 200, 400 and 800 ms) was less pronounced than in Experiment 1. We think this result could be explained as an effect of flash predictability on the flash-lag effect (Namba & Baldo, 2004). In Experiment 2, we measured the flash-lag effect in more points in time than in Experiment 1. Thus, flashes appearing immediately after the onset of moving objects are less probable which could have caused more “surprise” in observers which would increase the flash-lag effect (Namba & Baldo, 2004).

5. Experiment 3

In the previous experiments we show that the flash-lag effect evolves over time. We suggest that this time dependence is caused by the motion signal of the moving object itself. In Experiment 3, to confirm that the progressive shift we observed is caused by the integration of motion signals from the moving object, we added an extra motion signal in the form of a MAE. To generate a MAE, before each experimental trial we presented a rotating ring that covered the area in which the moving dots subsequently appeared.

5.1. Methods

Two psychophysically trained observers who were naïve as to the purposes of the study participated in the experiment. We measured the flash-lag effect at different instants in time (flash presentation time: 200, 700, 1500 and 3000 ms) using the most remote flashes of Experiment 1. Observers conducted two types of sessions: with and without adaptation. Before each trial of the adaptation sessions a ring (smallest radius=4.5 deg, biggest radius=9.5 deg) carrying a sinusoidal grating was displayed for 10 seconds (60 s for the first trial of each session) at an angular speed of 60 $deg \cdot s^{-1}$. The direction was maintained in each session. After adaptation, the direction of motion of the moving dots was chosen at random between clock-wise and counter-clock-wise. Each observer completed 15 sessions with adaptation and 5 without adaptation. Each orientation error was calculated using 30 measures.

5.2. Results and discussion

The results (Figure 2C) showed that a MAE signal in the direction of the moving dots had no effect. However, a MAE whose direction was against the dot motion globally reduced the flash-lag effect and prevented the moving object from progressively shifting forward confirming that motion signals mediate the flash-lag effect. This result would not be predicted on the basis of a purely temporal mechanism, such as differential latency (Krekelberg & Lappe, 2001; Nijhawan, 2002; Whitney, 2002).

It has been shown that the flash-lag effect vanishes when the moving object disappears just when the flash is presented (Eagleman & Sejnowski, 2000). The lack of overshoot in this situation is not consistent with the proposal that spatial mechanisms extrapolate the position of moving objects (Eagleman & Sejnowski, 2000). It has been also shown, however, that there is a small overshoot of the final position of the moving object when the moving object is blurred (Fu, Shen, & Dan, 2001) or presented at large eccentricities (Kanai, Sheth, & Shimojo, 2004) which is consistent with spatial extrapolation. Since we presented the moving objects in the periphery, it is possible the effects reported here are specific to the visual periphery. Further research may answer this question.

Since we were able to demonstrate with this experiment that the progressive shift involves motion signals, the results of Experiment 2 imply that a sudden transient like a flash disturbs motion integration. So flashes, not only capture attention (Chappell et al., 2006), but also influences how motion is used to code spatial location.

6. Conclusions

Here, we demonstrate that spatial mechanisms that integrate motion signals contribute to the flash-lag mislocalization. Temporal explanations are not sufficient. Importantly, these spatial mechanisms might go unnoticed if flashes are presented near moving objects indicating that flashes cannot be considered as innocuous spatio-temporal markers.

CHAPTER 6: Conclusions

1. The flash-lag effect 'in action'.

In *Chapter 2*, we demonstrated that when subjects perceive the flash as a sensory consequence of their own action (a key press) the flash-lag effect was reduced. This finding could be accommodated by the processing time explanation considering that the time for the flash to reach awareness is shorter when is internally predicted. The experiments discussed in *Chapter 2* were not planned to test the alternatives to the processing time explanation. So, any explanation could be at the core of the flash-lag effect. Nevertheless our results suggest that it must include that the flash-lag effect can be modulated by varying the latency to perceive the flash.

For the position sampling explanation, the flash-lag effect is caused because the visual system takes time to obtain the position of the moving object in response to the flash (Brenner & Smeets, 2000). We hypothesized that, according to this explanation, observers could have decided to sample the position of the moving object using the time marker that the event corresponding to their own action provided. Furthermore, they could have decided to sample the position of the moving object in some instant of time previous to the key press, as intention should precede action (Eagleman, 2004). To ensure that observers were using the flash as a time marker, we conducted a control experiment in which the occurrence of the flash was disentangled from the action by introducing small delays between them. We found that the flash-lag effect did not depend on the delay which is not consistent with events associated to action controlling the sampling.

We also showed that, when the appearance of the flash was predicted by a sound presented 300 ms before the flash, the flash-lag effect was not reduced. This finding suggests that the effect of reduction is not due to an increase of the global attentional resources based on predictability (Namba & Baldo, 2004). In other study however, it was found that a sound presented in close temporal proximity to the flash significantly modulates the flash-lag effect (Vroomen & Gelder, 2004). In this study, the sound and the flash were temporally separated no more than 100 ms. As it has been shown that the temporal proximity between visual and auditory stimuli could trigger crossmodal interaction effects that shift the perceived time of occurrence (Lewald, Ehrenstein, & Guski, 2001; Morein-Zamir, Soto-Faraco, & Kingstone, 2003), we think that this result is not incompatible with our finding.

In the last experiment of *Chapter 2*, we showed that it was not the temporal coincidence between the flash and the key press action which reduces the flash-lag effect. We used two types of trials. In the high-probability trials, the flash was presented 250 ms after the key press. In the low-probability trials, the flash was presented simultaneously with the key press. We found that the flash-lag effect was reduced for the high-probability trials. But, for the low-probability trials, despite the temporal coincidence between the flash and the key press, the flash-lag effect was not diminished. Interestingly, in a very recent study it has been shown that when participants are adapted to an artificial delay between a key press and the appearance of a flash, then flashes occurring at unexpectedly short delays after the key press are perceived as occurring before the key press (Stetson, Cui, Read Montague, & Eagleman, 2006). This finding suggests that in our low-probability trials, observers may have experienced some time reversals between the flash and their action. In this case, as we did not find a reduction of the flash-lag effect, our findings suggest that the temporal shift in the perception of the flash is not absolute, but relative to the point in time corresponding to the perception of the key press (Haggard, Clark, & Kalogeras, 2002). It might be interesting in future research to explore more systematically this temporal reversal by using a flash-lag effect paradigm. By using this approach, hypothetical response bias associated to direct comparison might be minimized (Arnold, Johnston, & Nishida, 2004; Fujisaki, Shimojo, Kashino, & Nishida, 2004).

The most of investigations used the flash-lag effect to study the position computation process involved in the perception of moving objects. It has been also suggested, however, that the flash-lag effect could be a useful tool to study the time course of some other perceptual phenomena (Watanabe, Nijhawan, Khurana, & Shimojo, 2001). Watanabe and cols., for example, used the flash-lag effect to study the perceptual organization of objects (Watanabe, Nijhawan, Khurana, & Shimojo, 2001; Watanabe, 2004). We think that, in some sense, our study could be also understood in this way. We measured the influence of an action on the time to perceive a new visual object using a “clock” being this “clock” the moving object. We think that this interpretation is plausible because we compared the flash-lag effect in situations that are visually identical, but one must be cautious when generalizing this interpretation. Let us consider, for example, the flash-lag experiments involving changes in luminance of the flash. It could be proposed that by means of the flash-lag effect the effect of luminance on the latency to perceive an object could be measured. But, this interpretation supposes an independency between the moving object and the flash that the experiments reported in *Chapter 5* discount. We showed that the flash actually interacts with the moving object, being the distance between the flash and the moving object an important factor. Other parameters, however, might also be involved in this interaction. It is not unreasonable that, for example, the interaction would be enhanced by increasing the luminance of the flash.

2. Motion processing and the colour-motion asynchrony illusion.

In *Chapter 3,* we showed that the colour-motion asynchrony illusion could be obtained by using a single direction change and without presenting a colour interval following the colour interval target of the task. We think that these findings are compatible with the processing time explanation and challenge the two alternative explanations proposed. Hence, our results support that the colour-motion asynchrony illusion reflects processing time differences between the brain areas involved in the perception of colour and motion (Zeki & Bartels, 1998; Zeki, 2003; Bartels & Zeki, 2006). However, we also found visual masking effects between colours which hinder an explanation of visual awareness based only in when a stimulus reaches a “perceptual end-point”.

2.1 The time marker theory

According to the time marker account, the colour-motion asynchrony illusion results from inappropriate matching of time markers assigned to first-order change of colour and position. A temporal marker should reference the time a specific event occurs rather than the time the processing of the event completes in the brain.

Replicating previous results (Arnold & Clifford, 2002; Bedell, Chung, Ogmen, & Patel, 2003; Clifford, Spehar, & Pearson, 2004), in *Chapter 3*, we showed that the colour-motion asynchrony was significantly weakened when the angle of direction change was reduced from 180 deg. This finding is not predicted by the time marker theory since a direction change is a second order change regardless of the angle. In our study, like in the others studies using random-dot stimuli, the effect of angle was especially large. Amano, Johnston and Nishida (submitted manuscript), indeed, suggest that the use of random dots may introduce an artefact component. They proposed that observers might use the motion streaks generated by motion blur (Burr, 1980; Burr & Ross, 2002) to make colour-orientation synchrony judgments -for which the asynchrony is smaller (Moutoussis & Zeki, 1997b)- rather than colour-motion synchrony judgments. Consistently with this interpretation, they have shown that the effect of angle is strongly reduced by using plaids free from the motion streak artefact. They have also shown, however, that a significant reduction remains which lead them to introduce an additional assumption in their time marker theory: time markers associated to first-order changes in position can be affected by the time course of the recruitment of neural responses to the direction of motion following a direction change. So, in this way the time marker theory explicitly specifies that the assignment of a time marker depends on the formation of low-level stimulus features.

Very recently, it has been replied us (personal communication with Shin’ya Nishida) that our finding showing apparent asynchrony occurring even for single changes does not contradict the time marker account. He argues that the apparent delay for the binding task we found can be reconciled with the time marker theory by assuming that the required task alters the selection of time marker. Let us consider, for example, the situation in which the direction change occurs just in the middle of the colour target period. According to the revised time marker explanation, the time markers assigned to first order changes have different time courses depending on the attributes. While the time marker assigned to a brief colour period would be close to the onset (~50ms), the time marker assigned to a brief motion period would close to the center (~150 ms). The misbinding that we reported in this situation, therefore, would arise because of the tendency of the visual system to take erroneous matching of first-order changes. We propose that following this reasoning by increasing the length of the first motion interval the time marker corresponding to the motion period and the time marker corresponding to the color period will be progressively separated which should cause the asynchrony to disappear. Future experiments might test this prediction.

2.2 The postdiction explanation

In *Chapter 3*, we showed that, consistently with the misbinding reported by Moradi and Shimojo (2004), the colour interval that follows the colour target interval influences the perception of the colour target. As we said, we think that this finding could be consistent with postdiction or backward masking accounts. Whatever the explanation, it has been proposed that both (Eagleman & Sejnowski, 2000a, 2000b; Enns & Di Lollo, 2000) reflect the feed-back architecture of the brain (Lamme, Supèr, & Spekreijse, 1998; Lamme, Zipser, & Spekreijse, 2002; Supèr, Spekreijse, & Lamme, 2001). We think, therefore, that a model only based in feed-forward processing hardly could account for all the binding effects between colour and motion. Despite this effect of masking, when we measured the perceptual asynchrony using the standard procedure (Experiment 1), we found that the presence or absence of the interval following the target interval did not influence the measured asynchrony suggesting that the postdiction account cannot explain the asynchrony. In the following paragraphs, we will discuss in more detail this point.

Moradi and Shimojo (2004) suggested a postdictive account of the colour-motion asynchrony illusion in a study about the relationship between surface segregation and perceptual binding. The proposal was based on the results of their Experiment 5. In this experiment, they presented observers a square region composed by static dots. At a given moment, a subset of dots in a small square region moved briefly producing the impression of a segregated surface. Dots were gray during motion and the colour changed when they stopped. When observers were asked about the colour of the dots during motion, they reported the colour that followed the motion more often than gray that actually was the true colour. Moradi and Shimojo explained this result proposing that the appearance of a new surface or the direction reversal of a persistent surface triggers the analysis of the properties (including colour) of the surface. They suggested that these properties are computed during a temporal window of 50-150 ms following the onset/reversal of the surface. The model is postdictive because they proposed that the consequences of the analysis are experienced as having occurred at the time corresponding to the onset/reversal. Remarkably, the gray colour was not perceived even when was presented for 120 ms. As the temporal window of analysis lasts for 150 ms at the most, this implies that, as it has been pointed out before (Arnold, 2005), the colour is not treated uniformly during the time window of analysis and the colour appearing in the later period of analysis is favoured instead.

In the colour-motion asynchrony illusion, Moradi and Shimojo proposed that direction changes would reset the integration of colours and then, the new colours would be calculated by using the colour signal in a temporal window following direction changes, but perceived as having occurred at the point in time at which the direction changes commenced. In a typical experiment to measure the perceptual asynchrony each colour is presented in two directions of motion (apart from the situation of physical synchrony in which each colour is presented in one direction). So, each colour interval can be thought of as being composed by two subintervals: the first subinterval corresponding to the direction of motion presented before a direction change and the second subinterval corresponding to the direction of motion presented after a direction change. Consider, for example, the situation in which red colour must be paired with its predominant motion direction. Following the Moradi and Shimojo proposal, the second red subinterval could not be perceived as red, as the gray colour was not perceived as gray in their Experiment 5. Instead, it would be perceived as green because is followed by green colour (the first green subinterval associated to the next direction change). But, if the second red subinterval is perceived as green, then observes would always pair red colour with the direction of motion presented before the direction change which could cause the illusion.

We think, however, that taking into account the typical timings used to measure the asynchrony between colour and motion, the misbinding that Moradi and Shimojo reported can hardly cause the colour-motion asynchrony illusion. In a typical display of the illusion each colour is displayed for 300 ms. Therefore, following with the example above, if the red colour interval is just centred around a direction change each red subinterval would last for 150 ms. But, according to the Moradi and Shimojo proposal, the temporal window of integration lasted for 150 ms at the most. This means that for the misbinding in the second red subinterval to occur it should last less than 150 ms. Hence, the first red subinterval would last for more than 150 ms. In this case, observers would always pair red with the direction of motion displayed before the direction change, but crucially this pairing is consistent with the physical situation. So, the temporal integration window proposed by Moradi and Shimojo cannot explain the asynchrony. Only by considering an unlikely extended duration (more than 150 ms) of this temporal window would be possible for the misbinding to contribute to the perceived asynchrony. Anyway, to ensure that postdiction cannot explain the perceptual asynchrony, in Experiment 1 we explored the effect of eliminating the colour interval following the colour target. Against the postdiction explanation, we found that the perceived asynchrony did not depend on the presence of it.

2.3 Motion is different

In Experiment 2 of *Chapter 3*, we showed that after a direction reversal, observers did not perceive a motion signal briefly presented. This finding supports the view that opponent motion inhibition delays the time at which the new motion signal becomes detectable. To further explore this interpretation, we have recently conducted preliminary experiments using our single-change display and the motion aftereffect. Supposing that the delay in the perception of the second direction is due to suppression of the mechanisms tuned to this direction during the presentation of the first direction, we hypothesized that reducing the suppression by means of motion adaptation we could reduce the asynchrony. Our preliminary results confirm this hypothesis. We have repeated the main condition of Experiment 1 of *Chapter 3,* but presenting motion for 5 seconds before each trial. We found that motion adaptation displayed in the same direction of the first interval of motion (the expected aftereffect would have the same direction of the second motion period) reduced the asynchrony and in the opposite direction increased it.

It has been pointed out (Moradi & Shimojo, 2004) that the colour-motion asynchrony illusion and the flash-lag effect cannot be reconciled with the processing time explanation: while in the colour-motion asynchrony illusion motion seems to be the slow attribute, in the flash-lag effect is considered to be the faster attribute. We think that this is an oversimplification and that it does not make sense to associate processing speeds to visual attributes univocally. The findings reported in the previous paragraph together with the dependence on angle effect suggest that, for example, in the colour-motion asynchrony illusion the illusory effect is due to the specific characteristics of motion processing in a reversal point. The dependence on task is also consistent with the conception that processing latencies are not uniquely for each attribute. Furthermore, some authors (Clifford, Arnold, & Pearson, 2003) suggest that the effect of task in illusory perceptual asynchronies could be related to use of neural representations based upon different aspects of the neural activity (Shadlen & Movshon, 1999; Singer & Gray, 1995). Finally, it is worth mentioning that the salience of the stimulus could also affect the processing latencies (Adams & Mamassian, 2004). This factor may explain why some authors (Aymoz & Viviani, 2004; Viviani & Aymoz, 2001) against the most of the investigations (including ours) found apparent asynchronies between colour and motion in temporal order judgments.

3. Neural site of the flash-lag effect.

In *Chapter 4*, we showed that the spatial relationship between flashed and moving information could be perceived accurately when it is used to judging a global shape, but is misperceived as usual for positions judgments. This result is not compatible with a low level explanation of the flash-lag effect which would predict mislocalization independently of the task.

A strong dependence on task was also found by using the simultaneous tilt-contrast illusion (Arnold, Durant, & Johnston, 2003). This illusion describes the shift in the perceived orientation of one stimulus when is surrounded by another oriented stimulus. The strength of the illusion depends on the relative orientation between the inner and the outer stimuli. In the study conducted by Arnold and cols. the inner stimulus was flashed and the outer stimulus was moving. It was found that the larger illusion occurred when the inner stimulus was flashed 20 ms before the moving stimulus arrived at the position that when the outer stimulus was presented statically maximized the illusion. The authors proposed that such a small advantage was insufficient to account for the flash-lag effect. Indeed, they found a flash-lag effect of 75 ms using similar conditions. Their findings, therefore, are not consistent with a low level explanation accounting for the whole effect, but a low level contribution cannot yet be discarded. Importantly, however, we did not find a simple reduction of the flash-lag effect for the form discrimination task; we completely eliminated it. As discussed in *Chapter 4*, Kanai and Verstraten (2006) using a completely different stimulus configuration also showed absence of flash-lag. The lack of flash-lag effect strongly suggests that it is not caused by early visual areas.

It has been reported, however, that predictive responses to moving stimuli can occur as early as in the retina (Berry, Brivanlou, Jordan, & Meister, 1999). Berry and cols. showed that a moving bar elicits a moving wave of spiking activity in the retinal ganglion cells of rabbits and salamanders that is shifted towards the leading edge. In another study it was reported a small advantage of approximately 15 ms in the processing of moving respect to flashed stimuli in the cat LGN (Orban, Hoffmann, & Duysens, 1985). One possibility to reconcile the absence of flash-lag effect with these neurophysiologic reports is consider that there are fundamental differences in the processing of moving objects in humans and other species. Considering the results of *Chapter 5*, we speculate about another possibility. The neurophysiologic studies, contrary to flash-lag experiments, explore neural activity to moving objects and flashes individually. So, in these studies flashes and moving objects are not subject to mutual interaction. If this interaction would occur at an early level, then it might hide the mechanisms that the visual system uses to process moving objects in these stages.

Finally, to say that the recent study showing a neural correlate of the flash-lag effect in extrastriate visual area V4 (Sundberg, Fallah, & Reynolds, 2006), like the study of Berry and cols., also points towards some form of motion extrapolation. Sundberg and cols. showed that the lag in the direction of motion was apparent in the first 33 ms of neuronal responses evoked by the flash. This result is especially problematic for the explanations including some form of temporal integration because the length of the temporal windows typically proposed are much longer that these 33 ms.

4. Spatial mechanisms and visual transients

By using motion aftereffects we showed in *Chapter 5* that spatial mechanisms influence the flash-lag effect. We also reported a progressive shift forward in the position of the moving object that disappears when a motion aftereffect was present in the opposite direction. The influence of aftereffects suggests the implication of direction selective mechanisms. These results, therefore, support that the motion signal of the moving object itself contributes to the flash-lag effect. So, temporal explanations are not sufficient to explain it (Whitney, 2002). Spatial mechanisms, as those described in the introduction section of *Chapter 5*, might be involved in the flash-lag mislocalization. It has been suggested (McGraw, Walsh, & Barrett, 2004; Nishida & Johnston, 1999; Whitney & Cavanagh, 2000b) that such mechanisms could be implemented at neural level by back-projections from area V5/MT to V1 which have been proposed to support visual awareness of motion (Pascual-Leone & Walsh, 2001; Silvanto, Cowey, Lavie, & Walsh, 2005; Silvanto, Lavie, & Walsh, 2005). It must be noted that the implication of spatial mechanisms suggest that the standard flash-lag effect for spatial position and the flash-lag effect generalizations (Alais & Burr, 2003; Sheth, Nijhawan, & Shimojo, 2000), although can share mechanisms, are not exactly the same phenomenon.

To study the perceived position of a moving object, it is a common practice in the laboratories to introduce a transient spatial marker (flash) in the visual field and to require a comparison between it and the moving object. Although such a sudden appearance, however, is very rare in natural environments, it is usually assumed implicitly that this irruption does not affect the perceived position of the moving object. In *Chapter 5*, we demonstrated that a flash does actually interact with the perceived position of a moving object. We think that this is one of the main findings of this thesis. Indeed, as discussed along this Chapter, this result modulates part of the conclusions that we can extract from our own experiments. We consider that future research on spatial localization, not only during fixation, but also during eye movements should also keep in mind that the introduction of flashes in the visual field so as to measure the position of moving objects might not be appropriate to tap the mechanisms that the visual system uses to perceive the location of moving objects.

5. Final conclusions

While the existence of neural delays in the visual system is undeniable, their consequences at perceptual level are a matter of debate. In this doctoral thesis, following the tradition of the last years, we addressed this question by studying two perceptual phenomena: the colour-motion asynchrony illusion and the flash-lag effect.

Our results concerning the colour-motion asynchrony illusion strongly support that the asynchrony reflects processing time differences between colour and motion. Nevertheless, in addition to the asynchrony, we also found masking effects which suggests the involvement of feedback mechanisms.

We claim that the differences in processing time are due to the form in which motion is processed around a direction reversal. We think, therefore, that processing delays are variable and it makes no sense to associate a single latency for each attribute. Supporting this view, we found that the perceptual asynchrony was influenced by the task.

For the flash-lag effect, our results are less determinant so as to discuss about the involvement of processing times. Taking into account our findings we can make the following claims. First, the flash and the moving object are not independently processed as assumed by the processing time explanation. Second, the processing time explanation, if matters, it should be combined with spatial mechanisms. Third, and finally, the differences in processing time cannot be due to mere transmission delays in the early areas of the visual pathway.

CHAPTER 7: Spanish version

1. Introducción

En el sistema visual de los primates pueden pasar alrededor de unos 50-100 ms desde que la luz incide en la retina hasta que las neuronas corticales responden. Por lo tanto, inevitablemente la percepción de eventos ocurre después de su ocurrencia física. Esto podría dar lugar a una mala interacción del individuo con su entorno. A continuación explicaré dos problemas no triviales asociados a la existencia de retrasos neuronales.

El primer problema involucra la percepción de objetos en movimiento. Considerando, por ejemplo, un retraso neuronal de 100 ms y un objeto que se mueve a 5 km por hora, deberíamos percibir el objeto más de 10 cm por detrás de la posición que realmente ocupa. Esto podría suponer un problema a la hora de interaccionar con objetos en movimiento. Sin embargo, en la naturaleza se observan acciones de interacción que requieren precisión de milisegundos. ¿Cómo es posible? El punto de vista dominante es que el éxito en las acciones de interacción es debido a compensaciones de alto nivel en la respuesta motora. Sin embargo, algunos investigadores consideran que los retrasos neuronales pueden ser compensados también a nivel sensorial. Este problema ha sido debatido extensamente utilizando el efecto *flash-lag*: cuando un flash se presenta físicamente alineado con un objeto que se mueve, el flash se percibe retrasado respecto al objeto en movimiento.

El segundo problema surge considerando la naturaleza modular del cerebro. Es sabido que diferentes atributos son procesados en relativamente diferentes áreas corticales. Los tiempos de procesamiento en cada una de estas áreas no tienen porque ser los mismos. Asumiendo que la experiencia consciente de un atributo esta relacionada con la actividad neuronal del área que procesa este atributo, esto podría conducir a una experiencia visual no unificada. ¿Compensa el cerebro estas diferencias en tiempo de procesamiento para que el precepto sea unificado y refleje la sincronía de los eventos reales? Esta pregunta se ha estudiado utilizando la ilusión de asincronía entre color y movimiento, entre otras. En esta ilusión, un estímulo cambia de color y de dirección de movimiento. Para que los cambios se perciban ocurriendo al mismo tiempo los cambios de dirección tienen que ocurrir antes que los cambios de color.

Para algunos investigadores el efecto *flash-lag* y la ilusión de asincronía entre color y movimiento son la evidencia psicofísica más fuerte a favor de la existencia de retrasos neuronales en las vías visuales. Sin embargo, otros investigadores piensan que estas ilusiones no están reflejando los retrasos neuronales. Los experimentos de esta tesis están enmarcados dentro de este debate. Específicamente, abordamos las siguientes cuestiones. Primero, ¿son estas ilusiones compatibles con una explicación basada en diferencias en tiempo de procesamiento? Segundo, ¿cómo tiene que interpretarse la explicación basada en tiempos de procesamiento para poder ser compatible con estas ilusiones? Estos dos objetivos principales se elaboran a continuación.

La compatibilidad de las ilusiones con una explicación basada en tiempos de procesamiento sugiere que el tiempo de procesamiento en el cerebro tiene consecuencias directas a nivel perceptivo. En el caso del efecto *flash-lag*, quizás la evidencia más importante que favorece una explicación basada en tiempos de procesamiento es la variación del efecto con la luminancia. Se ha demostrado que el efecto disminuye cuándo la luminancia del flash aumenta. De acuerdo con una explicación basada en tiempos de procesamiento, esto ocurre porque al aumentar la luminancia del flash se esta disminuyendo la latencia para que sea percibido. Por otro lado, se ha sugerido que el tiempo que se tarda en percibir un evento visual es más corto cuando éste es la consecuencia de una acción propia. Esto nos sugirió que si en el efecto *flash-lag* el flash es percibido como consecuencia de una acción, entonces la percepción se vería acelerada resultando en una disminución del efecto. Demostramos que esto es efectivamente así (apartado 2). Este hallazgo sugiere que el tiempo que se necesita para percibir un evento, no sólo depende de sus propiedades visuales, sino también de la dinámica interna del cerebro asociada a la respuesta motora.

En el caso de la ilusión de asincronía entre color y movimiento se han propuesto dos explicaciones alternativas: la teoría de las marcas temporales y la explicación *postdictiva.* En los experimentos que describimos en el apartado 3 abordamos la plausibilidad de estas tres explicaciones. Demostramos que un único cambio de dirección es suficiente para que se produzca la ilusión de asincronía. Mientras que este resultado es perfectamente compatible con la explicación de los diferentes tiempos de procesamiento, es incompatible con la teoría de las marcas temporales. Con esta versión simplificada de la ilusión estudiamos los efectos que tenia el color que se presentaba justo después del color objetivo de la tarea. Vimos que, contrariamente, a la explicación *postdictiva* la asincronía no dependía del color que se presentaba después del color objetivo. Este resultado, sin embargo, también es compatible con la explicación basada en tiempos de procesamiento.

Sin embargo, además del efecto de asincronía entre los atributos de color y movimiento, también encontramos un efecto de enmascaramiento entre colores. Aunque, este enmascaramiento no contribuyó a las medidas de las asincronía, si que cambiaba el precepto. Este efecto es compatible con la explicación postdictiva, así como con las teorías que propones un enmascaramiento hacia atrás, pero no es compatible con una teoría basada en tiempos de procesamiento. Por lo tanto, el precepto global no puede ser explicado atendiendo solo a las diferencias en tiempo de procesamiento.

En el apartado 5, describimos como además encontramos que en el caso del efecto *flash-lag,* también una explicación basada únicamente en tiempos de procesamiento no puede explicar completamente el efecto. Por un lado, mostramos que, mecanismos de tipo espacial que actúan integrando señales de movimiento contribuyen al efecto. Por otro lado, también demostramos que el flash interacciona con la posición percibida del objeto en movimiento. Este resultado, no sólo va en contra de la explicación basada en diferentes tiempos de procesamiento, sino también en contra de la mayor parte de las teorías propuestas para explicar el efecto.

En el apartado 3, demostramos que la asincronía medida en la ilusión de asincronía entre color y movimiento es sólo compatible con la explicación basada en los tiempos de procesamiento. Sin embargo, replicando resultados de otros autores, demostramos que la tarea que se realiza es un factor crítico. Mientras que la asincronía aparece cuando se realizan juicios de correspondencia entre los atributos, cuando se realizan juicios de orden temporal entre cambios de color y cambios de movimiento desaparece. En el apartado 4, describimos que también encontramos un efecto de tarea para el efecto *flash-lag.* Mostramos como cuando la relación espacial entre estímulos que se mueven y estímulos presentados brevemente se mantiene cuando se utiliza para percibir una formar global. La dependencia con la tarea de ambos efectos sugiere que no es posible asociar unívocamente una latencia a cada atributo visual. En su lugar, diferentes aspectos de cada atributo deben ser procesados con diferentes latencias lo que sugiere que la implicación de áreas corticales de alto nivel. Por lo tanto, las latencias neuronales no deben ser entendidas como simplemente el tiempo de transmisión de las señales neuronales en las etapas iniciales del procesamiento visual.

2. El efecto *flash-lag* se reduce cuando el flash se percibe como una consecuencia sensorial de nuestra propia acción.

La localización de objetos en movimiento es una de las tareas básicas que el sistema visual tiene que resolver para que podamos interactuar correctamente con el entorno. Una gran cantidad de estudios psicofísicos muestran que en determinadas condiciones el sistema visual comete errores de localización. El efecto *flash-lag* es uno de estos errores. El efecto hace referencia a la deslocalización perceptiva entre dos objetos que están alineados en la retina cuando uno se presenta muy brevemente (flash) y el otro está en movimiento.

Aunque el efecto *flash-lag* es un error de tipo espacial, cómo uno de los objetos está en movimiento, puede ser que parte del error sea temporal. Al menos dos tipos de hipotéticos errores temporales se han propuesto para explicar el efecto. Según el primero el efecto *flash-lag* sería debido a una diferencia en los tiempos de procesamiento del objeto en movimiento y el flash. El objeto en movimiento se procesaría más rápido que el flash y eso daría lugar al error espacial que se observa. De acuerdo con el segundo tipo de error temporal el efecto *flash-lag* sería debido a que la posición del objeto en movimiento debe ser muestreada en respuesta al flash y este proceso tardaría un tiempo.

Por otro lado, hay una serie de estudios en que se muestra que la predictibilidad del flash o del objeto en movimiento tiene consecuencias en la magnitud del efecto. Esta influencia podría estar relacionada con la aceleración de la percepción debida a la focalización atencional que algunos autores proponen. En estos estudios se consigue variar la predictibilidad del flash mediante la introducción de pistas espaciales que señalan donde va a aparecer el flash o de pistas temporales que señalan cuando va a aparecer. Nosotros ampliamos estos estudiando explorando cuál es el efecto de predecir el flash cuando es generado por una acción propia.

En el Experimento 1, demostramos que cuando los participantes percibieron el flash como una consecuencia de su propia acción (pulsación de tecla) el efecto *flash-lag* se vio reducido. Este hallazgo puede explicarse según una explicación basada en tiempos de procesamiento considerando que el tiempo para que el flash llegue a la conciencia visual se acorta cuando se puede predecir internamente.

De acuerdo con una explicación basada en el muestreo de la posición, el efecto *flash-lag* es debido al tiempo que tarda el sistema visual para obtener una posición del objeto en movimiento. De acuerdo con esta explicación, los observadores podrían haber decidido muestrear la posición del objeto en movimiento usando la marca temporal que el evento asociado a su propia acción proporciona. Para asegurarnos de que los participantes estaban usando el flash como marca temporal y no la pulsación de tecla, realizamos un experimento control (Experimento 2) en el que la ocurrencia del flash estaba descorrelacionada con la ocurrencia de la acción introduciendo pequeños retrasos entre ellas. Encontramos que el efecto *flash-lag* no dependía del retraso lo cual es consistente con el hecho de que los participantes estaban realmente usando el flash como marca temporal.

También encontramos que cuando la aparición del flash iba precedida por un sonido que se presentaba 300 ms antes que el flash, el efecto *flash-lag* no se redujo. Este hallazgo sugiere que el efecto de reducción no es debido a un incremento global de los recursos atencionales basados en la predictibilidad.

En el experimento 3 mostramos que no es la coincidencia temporal entre el flash y la pulsación de tecla lo que reduce el efecto *flash-lag* sino el establecimiento de causalidad entre ellos. En este experimento utilizamos dos tipos de ensayos. En los ensayos de probabilidad alta, el flash se presentaba 250 ms después de la presión de tecla. En los ensayos de probabilidad baja, el flash se presentaba simultáneamente con la presión de tecla. Encontramos que el efecto *flash-lag* se redujo sólo para los ensayos de probabilidad alta. En los ensayos de baja probabilidad, a pesar de la coincidencia temporal del flash y la pulsación de tecla, el efecto no se redujo.

3. Asincronía perceptual entre color y movimiento con un único cambio de dirección.

¿Cuál es la relación entre el tiempo de la actividad neuronal y el tiempo subjetivo que representa esta actividad? Esta cuestión ha sido abordada recientemente utilizando la ilusión de asincronía entre color y movimiento. Esta ilusión ocurre cuando un estímulo cambia rápida y repetidamente de color (entre rojo y verde por ejemplo) y dirección de movimiento (entre dos direcciones opuestas). Para que el color y la dirección de movimiento se apareen correctamente, los cambios de dirección tienen que ocurrir 80 ms antes que los cambios de color.

De acuerdo con una explicación basada en tiempos de procesamiento, la ilusión ocurre porque diferentes atributos del estímulo se procesan en diferentes áreas corticales. Se propone que el tiempo subjetivo de los cambios de un atributo esta relacionado con el tiempo de la actividad neuronal en las áreas que procesan este atributo. De acuerdo con esta explicación la ilusión ocurre porque la actividad neuronal vinculada a la percepción de movimiento requiere más tiempo que la requerida para el color. De manera alternativa, se ha sugerido que el tiempo percibido no tiene porque correlacionar directamente con la actividad neuronal, sino que en su lugar, se debe a un proceso de interpretación del cerebro.

Una característica de la ilusión es que parece requerir un estímulo repetitivo. La asincronía se va reduciendo a medida que el intervalo de tiempo entre dos cambios sucesivos aumenta llegando incluso a desaparecer. Además los juicios de orden temporal entre un único cambio de dirección y un cambio de color se realizan correctamente. Basándose en estos resultados Nishida y Johnston formulan la teoría de las marcas temporales. Según esta explicación la ilusión se debe a un fallo en la correspondencia entre las representaciones neuronales (marcas temporales) correspondientes a los dos tipos de cambios. De acuerdo con la teoría de las marcas temporales, a las altas frecuencias que caracterizan la ilusión, los cambios de segundo orden (cambios de dirección) son difíciles de detectar por lo que el sistema visual establece correspondencias entre cambios de primer orden (dirección y cambios de color) y de ahí las asincronías percibidas.

Sin embargo, de acuerdo con una versión más reciente de la explicación basada en tiempos de procesamiento el factor crítico para la aparición de la ilusión es el tipo de tarea que se ejecuta. El modelo propone que los juicios de correspondencia entre atributos implican el uso de información sostenida para la cual las diferencias de procesamiento entre color y movimiento son significativas, mientras que los juicios de orden temporal involucran información transitoria para la cuál las diferencias no son significativas. De acuerdo con este modelo, la ilusión por lo tanto sólo aparecería para los juicios de correspondencia.

En nuestro estudio mostramos que en contra de la teoría de las marcas temporales, una asincronía entre color y movimiento cómo la que encuentran todos los estudios utilizando cambios repetitivos se puede obtener cuando una tarea de correspondencia se realiza alrededor de un cambio de dirección de 180 grados. Este resultado resuelve uno de los problemas asociados a la explicación de las latencias neuronales porque de acuerdo con esta explicación el tiempo que se tarda en percibir un cambio no podía depender de los cambios entres los que lo acompañaran.

También encontramos, replicando previos resultados, que cuando el cambio de dirección es de 90 grados la asincronía se reduce fuertemente. Este resultado también es contrario a la teoría de las marcas temporales porque un cambio de dirección se supone que es un cambio de segundo orden independientemente del ángulo que lo defina. Replicando también los estudios previos encontramos que los juicios de orden temporal se realizan adecuadamente.

Utilizar nuestro estímulo reducido a un único cambio nos permite testear otra explicación que se ha sugerido: la explicación postdictiva. En contra de esta explicación encontramos que el intervalo de color que sucede al intervalo objetivo de la tarea de correspondencia no tiene ningún efecto en la asincronía percibida. Sin embargo, en un experimento complementario analizamos el papel que juega el color que sucede al intervalo objetivo y vemos que tiene un efecto de enmascaramiento. Este resultado implica que una explicación únicamente basada en tiempos de procesamiento no puede explicar todos los efectos de apareamiento entre color y movimiento.

4. Ausencia de efecto flash-lag cuando se juzga una forma global a partir de posiciones locales.

Dada la relevancia biológica que tiene el detectar objetos en movimiento, se han postulado mecanismos que corrigen o reducen las latencias neuronales asociadas al procesamiento visual. El efecto *flash-lag* se ha considerado como una prueba convincente de la existencia de estos mecanismos, aunque otras explicaciones alternativas han sido propuestas.

Es una cuestión no resuelta en que lugar del procesamiento visual ocurre el efecto, pero algunos estudios neurofisiológicos sugieren una contribución de bajo nivel que puede ocurrir tan tempranamente como en la retina o en el núcleo geniculado lateral. Si hubiera una contribución de estas áreas visuales de bajo nivel a la deslocalización, entonces sería esperable que el efecto ocurriera localmente e independientemente de la tarea. Nosotros exploramos esta predicción usando una tarea de detección de formas en la cuál se necesitaba una relación precisa entre información presentada brevemente e información en movimiento para percibir una forma global.

Específicamente, utilizamos estructuras de Glass concéntricas. Esta estructuras consisten en una gran cantidad de parejas de puntos. Cada punto se coloca aleatoriamente sobre el área estimulas. La posición del segundo punto se determina rotando una cantidad fija el vector radial correspondiente al primer punto. La estructura crea la impresión visual de una estructura rotacional. En nuestro experimento un punto de cada par se presentaba en forma de flash mientras que el otro se presentaba en movimiento. La forma global mejor se obtiene físicamente cuando los puntos de casa par están alineados. Sin embargo, si hubiera un efecto *flash-lag* para cada par entonces la mejor percepción global ocurriría cuando los puntos presentados en forma de flash aparecieran antes de que los puntos en movimiento llegaran a la posición de alineamiento. En el experimento variamos el tiempo relativo entre la presentación de los flashes y esta posición de alineamiento y encontramos que la mejor ejecución se dio para la situación de alineamiento físico. Este resultado por lo tanto es contrario a una explicación del efecto *flash-lag* basada en mecanismos de bajo nivel.

Sin embargo, cuando la tarea consistió en localizar las posiciones relativas entre una única pareja de puntos se obtuvo un efecto *flash-lag* similar a los típicos que se suelen encontrar. Este resultado sugiere que una condición necesaria para obtener el efecto es la ejecución de una tarea de juicio de posición relativa.

Las estructuras de Glass se ha utilizado extensamente para explorar las etapas locales y globales de procesamiento visual. Se ha sugerido que el area V4 podría estar involucrada en el procesamiento relativo a la etapa global puesto que se ha demostrado que neuronas del área V4 en macacos son selectivas a formas complejas similares a las estructuras de Glass. Por lo tanto, la ausencia de flash-lag local que encontramos parece sugerir que la relación espacial se mantiene a este nivel.

5. Señales de movimiento y percepción de objetos que se mueven.

¿Dónde percibimos un objeto cuando se mueve? Esta pregunta se ha debatido extensamente utilizando el efecto *flash-lag*: cuando un flash se presenta espacialmente alineado con un objeto que se mueve, el flash se percibe por detrás. Se ha observado que el movimiento del objeto puede influir en el flash pero podría ser que hubiera un efecto recíproco del flash sobre el objeto en movimiento. En este estudio demostramos que este es el caso. Primero, mostramos que la posición de un objeto en movimiento que aparece de repente en el campo visual se percibe progresivamente más hacia delante. Segundo, demostramos que este desplazamiento esta mediado por integración de señales de movimiento. Tercero, mostramos que la proximidad del flash interrumpe el proceso de integración.

La localización de objetos en el espacio visual es una de las funciones principales del sistema visual. Una gran cantidad de ilusiones muestran que esta habilidad no sólo es función del mapa retinotópico, sino también de otros factores como la señal de movimiento. Por ejemplo, se ha demostrado que la posición percibida de una contorno estático cuando dentro está incluido una estructura en movimiento se percibe sesgada en dirección del movimiento. Además, si después de un tiempo prolongado la estructura se para, entonces no solo la estructura estacionaria se percibe moviendo en la dirección opuesta (postefecto de movimiento), sino que también la posición percibida del contorno también se percibe sesgada en la dirección del postefecto, lo cuál indica que las posiciones percibidas dependen de movimiento internamente generado.

De manera interesante, se ha mostrado también que el desplazamiento en la posición inducido por el postefecto incrementa gradualmente en los primeros segundos lo que sugiere que la representación de la posición involucra un sistema dinámico que integra movimiento en el tiempo. Este desplazamiento espacial dependiente en el tiempo, sin embargo, no ha sido documentado en los estudios del efecto *flash-lag.* En su lugar se han encontrado o bien que la magnitud del efecto es independientemente de la trayectoria o bien que el efecto flash-lag es mayor cuando el objeto en movimiento aparece a la vez que el flash. Nosotros pensamos que estos resultados incongruentes podrían ser explicados considerando que en el efecto *flash-lag* la irrupción inesperada del flash influía la percepción del objeto en movimiento.

Para estudiar esta cuestión, en el Experimento 1 medimos el flash-lag in diferentes instantes temporales en función de la distancia entre el flash y el objeto en movimiento. Exactamente, lo que hicimos fue presentar a los observadores una pareja de puntos, diametralmente opuestos entre ellos, rotando alrededor del punto de fijación. Medimos la posición percibida de esta pareja de puntos en diferentes intervalos desde su aparición en el campo visual presentando otra pareja de puntos brevemente (flashes) y preguntado a los observadores acerca de su posición relativa. Los flashes fueron presentado en tres distancias relativas. Los resultados mostraron el típico efecto *flash-lag:* los puntos en movimiento aparecen por delante de los flashes cuando están físicamente alineados. Replicando resultados previos también mostramos que la magnitud del desplazamiento se incrementa cuando la distancia entre los flashes y los puntos en movimiento se incrementa. De manera interesante, encontramos que cuando los flashes se presentaban lejos de los puntos en movimiento, entonces el desplazamiento espacial gradualmente se incrementó con la duración de la trayectoria pre-flash hasta alcanzar un nivel asintótico lo cuál indica que alguna forma de integración temporal media la posición percibida de los objetos en movimiento. Tal y como preveíamos, cuando los flashes se presentaron cerca de los objetos interaccionaron con ellos ocultando el efecto de la trayectoria previa, lo que explicaría la falta de diferencia entre el flash-lag estándar y el flash-lag cuando el objeto en movimiento se presenta a la vez que el flash, lo que a su vez ha sido considerado por varios autores como una evidencia empírica en contra de la hipótesis de extrapolación de movimiento.

Para explorar más aún la interacción entre objetos en movimiento y flashes, en el Experimento 2, estudiamos la influencia del flashes que fueran irrelevantes para la tarea. Después de 1400 ms desde el comienzo del movimiento presentamos una pareja de flashes cerca de los objetos en movimiento indicando a los observadores explícitamente que los obviaran. Medimos la posición percibida de los puntos en movimiento utilizando los flashes más remotos del Experimento 1. Tal y como es de esperar, los desplazamientos relativos medidos antes de los 1400 ms no fueron influidos por la ocurrencia de los flashes irrelevantes. Sin embargo, la ocurrencia de los flashes irrelevantes si que afecto la medida del desplazamiento relativo posterior indicando un efecto claro de los flashes irrelevantes en la posición percibida de objetos en movimiento. Por lo tanto, contrariamente a la mayoría de las explicaciones propuestas para explicar el efecto *flash-lag,* los flashes no pueden ser considerados como simples marcas espacio-temporales que indican cuando el juicio de posición se tiene que hacer.

En el Experimento 3, para confirmar que el desplazamiento progresivo que observamos estaba causado por la señal de movimiento del propio objeto, añadimos señal de movimiento extra en forma de postefecto. Para generar el postefecto, antes de cada ensayo presentamos una corona circular en rotación que cubría la zona espacial donde posteriormente iban a ser presentados los objetos en movimiento. Los resultados mostraron que el postefecto en la dirección de los objetos en movimiento no tuvo efecto. Sin embargo, el postefecto presentado en dirección contraria eliminó el efecto progresivo de desplazamiento tenia la dirección contraria a la de los objetos en movimiento. Este resultado no puede predecirse según mecanismos puramente temporales.

Resumiendo, en este trabajo se demuestra que mecanismos de tipo espacial que integran señal de movimiento contribuyen al efecto *flash-lag.* Por lo tantos, los mecanismos temporales por si solos no son suficientes. De manera relevante, estos mecanismos de tipo espacial pueden pasar desapercibidos si la medidas se efectúan utilizando flashes muy próximos a los objetos en movimiento indicando que los flashes no pueden ser considerados como marcas espacio-temporales inócuas.

6. Conclusiones

Mientras que la existencia de retrasos neuronales en el sistema visual es innegable, sus consecuencias a nivel perceptivo son un tema de debate. En esta tesis, siguiendo la tradición de estos últimos años, hemos abordado esta cuestión utilizando dos ilusiones preceptúales: la ilusión de asincronía entre color y movimiento y el efecto *flash-lag.*

En lo que respecta a la ilusión de color y movimiento, nuestros resultados apoyan fuertemente que ésta es debida a diferencias de tiempo de procesamiento entre atributos. Sin embardo, además de la asincronía, también hemos encontrado efectos de enmascaramiento, lo que sugiere la contribución de mecanismos de retroalimentación desde áreas de alto nivel hacia áreas sensoriales.

En cuanto al efecto *flash-lag* nuestros resultados son menos restrictivos a la hora de validar la explicación basada en diferentes tiempos de procesamiento. Aunque las latencias neuronales pueden estar implicadas en el efecto, nuestros resultados indican que no son el único mecanismo que esta actuando y que además no sus diferencias no pueden estar originadas en las primeras etapas del procesamiento visual.

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