Predicting the future: spatial facilitation further ahead of visual motion

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Tesis Doctoral

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Like beauty and colour, motion is in the eye of the beholder.
(Watson & Ahumada, 1985)

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Finally, I want to write down a beautiful poem that really transmits my feelings about life and maybe, about research in general as well.

Não sou nada.
Nunca serei nada.
Não posso querer ser nada.
À parte isso, tenho em mim todos os sonhos do mundo.

Álvaro de Campos (Fernando Pessoa's heteronym), poem "Tabacaria", 1933

Summary

There is strong evidence that motion elicits a fast spread of neural activity with a short neural latency mediated by horizontal connections. Facilitated motion signals modulate activity in adjacent neurons with receptive fields coaligned in the visual space. This modulation may lead to a facilitatory effect at those locations likely to be activated in the near future by the moving object. In this doctoral dissertation we aimed to obtain psychophysical evidence for perceptual facilitation in the area ahead of motion.

In the preliminary study (**Experiments 1 and 2**) it was observed that targets where more often detected and with lower reaction times if preceded by nearby predictable motion. We went further on the analysis of such facilitatory effects using a different type of paradigm aiming to test stimuli parameters known to modulate horizontal connections spread of information, i.e. contrast, orientation and distance. Additionally, we also tested the influence of the length and the number of motion trajectories. To this end we designed a series of experiments in which one target was displayed in the subsequent position after motion and the other target was displayed at a distant position, according to the constant stimuli method. We expected that by increasing contrast and trajectory length, temporal facilitation would be enhanced as well (i.e., target onset would be perceived earlier). On the contrary, by increasing the distance from motion trajectories and the subsequent target would diminish that effect. On the other hand, orientation of Gabor patches carrier orthogonal to the trajectory should facilitated targets detection in a lesser degree. Results of **Experiments 3 and 4** revealed that the target presented next to the leading edge of motion trajectories was perceived earlier and as brighter as compared to the target displayed in a distant location. In addition, such facilitatory effect increased with the number of motion trajectories. Results of **Experiment 5**

revealed significant facilitatory effects, indicating that facilitation was prompted as well for orthogonal Gabor patches. In **Experiment 6** we observed that all the distances between motion and target location were not sufficiently long to observe a suppression of such facilitatory effect, although a trend to it decreasing with distance was observed. Furthermore, results from **Experiments 7** showed that by increasing motion contrast such effect also incremented. However, contrarily to what was expected, the facilitatory effect did not vary across trajectory length conditions (**Experiment 8**). In **Experiment 9** we tested length trajectories under two levels of motion contrast, and we found again that facilitation depended on trajectory contrast whether it did not depend on trajectory length. To rule out the possibility that the presence of static Gabor could also facilitate targets onset detection, we tested the presence static Gabor patches next to the location of the subsequent target (**Experiment 10**). Results revealed that they did not yield a significant facilitatory effect indicating that the effect is specific to moving objects.

In conclusion, our data gives evidence that a target located next to the leading edge of a moving object is perceived earlier and as brighter than a target located in a distant position. Our results may be explained by facilitatory modulations across horizontal connections, which are thought to be responsible for a fast and enhanced spreading activity of adjacent neurons coaligned in visual space. Hence, our findings reveal a predictive anticipation for moving objects probably with heuristics strategies responsible to provide the best solution for a particular situation, as the scenario of an object that moved in two closed positions that was sufficient enough to boost a facilitatory effect.

Resumen

Varios estudios prueban que el movimiento induce una rápida propagación de la actividad neuronal y una corta latencia neuronal mediada por las conexiones horizontales. Las señales de facilitación del movimiento modulan la actividad de las neuronas adyacentes con campos receptivos alineados en el espacio visual. Esto podría implicar un efecto facilitador en las posiciones a ser activadas en un futuro próximo por el objeto en movimiento. En esta tesis doctoral nos planteamos obtener evidencia psicofísica sobre una facilitación perceptiva en la zona por delante del movimiento.

En el estudio preliminar (**Experimentos 1 y 2**) los *target* cercanos al movimiento fueron detectados un mayor número de veces y con menor tiempo de reacción cuando estaban precedidos por movimiento. Para profundizar en el conocimiento sobre el efecto de facilitación espacial, utilizamos un paradigma que permite evaluar las características de los estímulos que modulan el mecanismo de conexiones horizontales - el contraste, la orientación y la distancia. Además, estudiamos la influencia de la longitud y del número de trayectorias de movimiento. El movimiento se indujo con parches *Gabor* que se movían a lo largo de diferentes trayectorias lineales hacia uno de los dos *target* estáticos. Se manipuló el *onset* de los *target* de acuerdo con el método de los estímulos constantes. Los resultados de los **Experimentos 3 y 4** revelaron que los *target* presentados cerca de donde termina el movimiento se perciben antes en el tiempo y también como más brillantes en comparación con el *target* presentado en una ubicación más distante. Además, el efecto de facilitación aumentó con el número de objetos en movimiento. Para probar si el efecto dependía de la orientación de los parches *Gabor* llevamos a cabo el **Experimento 5**, en el que los *Gabor* se orientaban ortogonales respecto a la dirección de movimiento. Los resultados revelaron efectos facilitadores significativos. En el **Experimento 6**, se manipularon las distancias entre

el movimiento y el *target* pero estas no fueron lo suficientemente largas para suprimir el efecto facilitador, a pesar de que se observó una tendencia a su disminución con el aumento de la distancia. Asimismo, los resultados del **Experimento 7** muestran que aumentar el contraste de movimiento provoca también un incremento en el efecto facilitador. Contrariamente a lo que se esperaba, el efecto facilitador no varió según la longitud de trayectoria (**Experimento 8**). En el **Experimento 9** probamos la longitud de trayectoria bajo dos niveles de contraste de movimiento, y encontramos una vez más que la facilitación dependió del nivel de contraste pero no dependió de la longitud de trayectoria. Para descartar la posibilidad de que la presencia de *Gabor* estáticos fuera la responsable del efecto de facilitación, se investigó también la presencia de uno, dos o tres *Gabor* estáticos junto a la ubicación del target (**Experimento 10**) observándose que la presencia de los *Gabor* estáticos no provoca un efecto facilitador significativo, lo que indica que el efecto es específico de objetos en movimiento.

En conclusión, nuestros resultados prueban que un *target* cercano al área donde termina el movimiento se percibe antes y como más brillante que un *target* situado en una posición lejana. Esto puede explicarse por las modulaciones facilitadoras a través de las conexiones horizontales, que se cree que son responsables de una difusión rápida de la actividad de las neuronas adyacentes y alineadas en el espacio visual. Por lo tanto, nuestros resultados revelan una codificación predictiva anticipatoria para objetos en movimiento, probablemente con estrategias heurísticas responsables de proporcionar la mejor solución para una situación particular, ya que el escenario de un objeto que se mueve en tan sólo dos posiciones fue capaz de provocar un efecto facilitador.

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Dedicated to my family,
Carlos, Ilda and Cat

who always unconditionally
believed in me and
supported me in all my choices

1. Introduction

Chapter 1

1. Introduction

Chapter summary

In this introduction we will present a brief overview of the current knowledge of motion processing based on psychophysical and neurophysiological studies. This introductory chapter is organized in three different sections. In the first section (Chapter 1.1), we introduce the relevance and the concept of visual motion and we describe how motion is processed along the visual hierarchy. With these concepts in mind in the next sections we intend to link the functional visual architecture to perception (Chapter 1.2). At first hand, we analyse how neural delays are inherent to visual processing and the problem these delays may represent to perceive motion adequately in time. Additionally, we explore what may do the visual system to cope with neural delays. To this end, we highlight the importance of the information that neurons receive from adjacent neurons introducing the concept of non-classic receptive fields. Furthermore, we will focus on the advantage of having a mechanism through horizontal connections that connect neurons across large distances within the same visual area. This mechanism may be the basis of a possible anticipation of future positions of moving objects. Thus, in the third section (Chapter 1.3), evidence is referred in favour of a predictive coding for motion as also in favour of anticipation of moving objects. In sum, motion signals modulate activity in adjacent neurons which may lead to a perceptual facilitatory effect at those locations likely to be activated in the near future by the moving object.

1.1. Visual motion

Visual motion is everywhere. When driving a car, for example, motion cues are all around and we have to be able to process motion information about pedestrians and other cars, integrating this information for the next driving steps. This is possible due to the specialized visual system we have, which performs numerous sensory processes allowing an adaptive interaction with our dynamic environment. In fact, impairment in motion processing may lead to dramatically difficult interactions as it is observed in Akinetopsia[1] patients. Zhil and cols (1983) found that the famous patient (named LM) could not perceive motion because she had part of the middle temporal area[2] (MT) damaged, which made her unable to perceive motion in a smooth manner. In addition, these people have difficulty to perform simple tasks as catching a ball or to perceive changes in facial expressions (Schenk, Ellison, Rice, & Milner, 2005; Shipp, de Jong, Zihl, Frackowiak, & Zeki, 1994). This syndrome shows clearly that motion perception is a key aspect of our everyday lives.

The ability to perceive motion allows an adequate interaction with the environment and it is an essential visual dimension for the visual system (Ehrenstein, 2003; Gibson, 1974; Nakayama, 1985). Indeed, a century ago motion perception was already hypothesized as a “primary sensation” or as a basic dimension of perception eliciting a perceptual sensation distinct from the other experiences [Exner, 1875; Wertheimer, 1912 as cited in Lu & Sperling, 1995]. The ability to detect motion is ubiquitous and may be one of the oldest and most basic of visual capacities as the ability to detect light and dark (Nakayama, 1985). Motion is a primary feature computed directly by the brain without the need to compute displacement. There are many examples that give empirical support for the fact that motion is perceived

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[1] This syndrome was first observed by Pötzl and Redlich in 1911 (as cited in Zeki, 1991). Nevertheless, it was not until some decades later that it was suggested by Zihl, von Cramon and Mai (1983) to be related with motion blindness and the lesion specific of the middle temporal area (MT). Fortunately, this syndrome is quite rare as it

[2] MT is an important area for motion processing, as we will see in the next section of the current Chapter.

directly, such as the Waterfall illusion[3] and the "apparent motion" effect, among others. Apparent motion is the perceptual phenomenon in which motion is perceived when actually there is no physical motion. In fact, Wertheimer used this phenomenon to argue that motion does not need to be computed from the comparison of objects in memory. He proposed instead that motion perception is a fundamental dimension and separated from form perception.

Motion, strictly as a physical phenomenon, is a spatiotemporal event defined as a change in spatial location over time. Moving objects are projected to the retina in the form of a spatiotemporal pattern of light intensity with two basic parameters: direction (angular direction: leftward, rightward, etc.) and speed[4] (change of location per unit of time: $\Delta x/\Delta t$). However, direction and speed are not explicitly encoded by the signal of individual photoreceptors. It is higher in the hierarchy of motion processing that neurons are tuned to speed and direction, becoming more prevalent in V1 and in MT areas (Borst & Euler, 2011; Chey, Grossberg, & Mingolla, 1998; Priebe, Lisberger, & Movshon, 2006). Thus, motion is a hierarchical processing that involves computation at multiple synaptic levels.

1.1.1. Hierarchy of motion processing

To consciously perceive an object in the world, the first necessary step is the transformation of the physical object into electrical signals by photoreceptors in the retina. Therefore, visual processing starts in the retina where photoreceptors transmit visual information (through bipolar and interneurons) to ganglion cells, by a spatially ordered set of activity. Earlier in the retina, visual information is carried by different pathways to the visual

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[3] Motion aftereffect was first mentioned by Aristotle (Aristotle, 1908; page G5r). He wrote that after looking to motion (e.g: river) "things at rest are then seeing moving" too. Moreover, a static object could be perceived as moving *contrary* to the direction of motion presented few milliseconds before.

[4] If we consider physics terminology, velocity refers to both speed and direction; however vision scientists typically use the term speed interchangeably with the term velocity.

cortex: magno and parvocellular pathways (see Figure 1). The former is responsible for finer spatial detail and colour processing and it is slower regarding the magnocellular pathway.

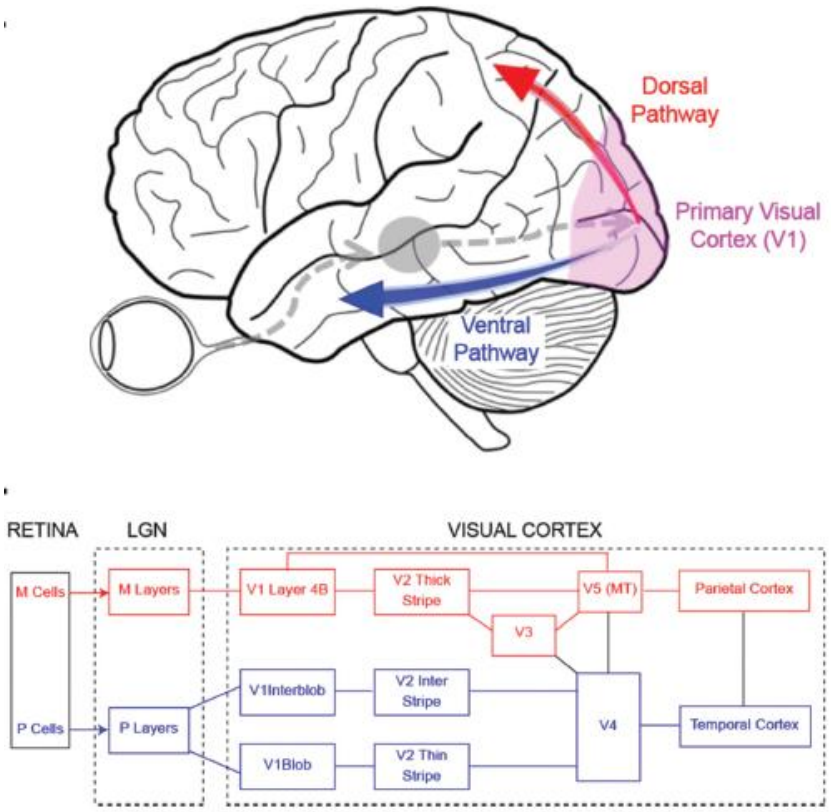

Figure 1. Visual processing pathways. The visual motion pathway equivalent to the magnocellular pathway is indicated in red and the parvocellular pathway in blue. Image retrieved from Kafalıgönül, Sİstemsel and Bakiş (2014).

The magnocellular pathway is the primary responsible for motion processing. This pathway starts with cells in the retina projecting into two magnocellular layers of the Lateral Geniculate Nucleus of the thalamus (LGN) sensitive to low spatial contrast and high temporal frequencies. In the primary visual cortex (V1) ~25% of the cells are selective for motion (speed or direction) and are highly concentrated in layer 4B which receives inputs from M cells and projects this information to middle temporal area (MT) (Priebe et al., 2006). Additionally, there is another pathway that bypasses LGN by going from the retina to the superior colliculus: the retino-tectal pathway. This pathway is important in processing spatial localization of objects and particularly, in visuo-motor behaviour as reflex adjustment of head and eyes (Waleszczyk, Wang, Benedek, Burke, & Dreher, 2004).

As mentioned previously, after NGL information is projected to V1. This area, V1, present a series of important organization properties as retinotopic visual field representation and cortical magnification (Daniel & Whitteridge, 1961; Horton & Hoyt, 1991; Hubel & Wiesel, 1968), see Figure 2. The former property refers to the orderly representation of the visual field, in such a way that neighbouring regions of the image are represented by neighbouring regions of the visual area. Additionally, information from the right half of the visual field is represented in the left half of the brain, and vice versa. However, this representation is distorted by the cortical magnification factor. Cortical magnification refers to the fact that there are a great number of neurons devoted to processing input from the fovea regarding neurons devoted to the periphery, in such a way that 1% of our visual field occupies approximately 50% of the V1 cortical area. Other areas in the visual cortex present as well these organization properties, however, research is needed to ascertain these properties (eg. Wandell, Brewer, & Dougherty, 2005).

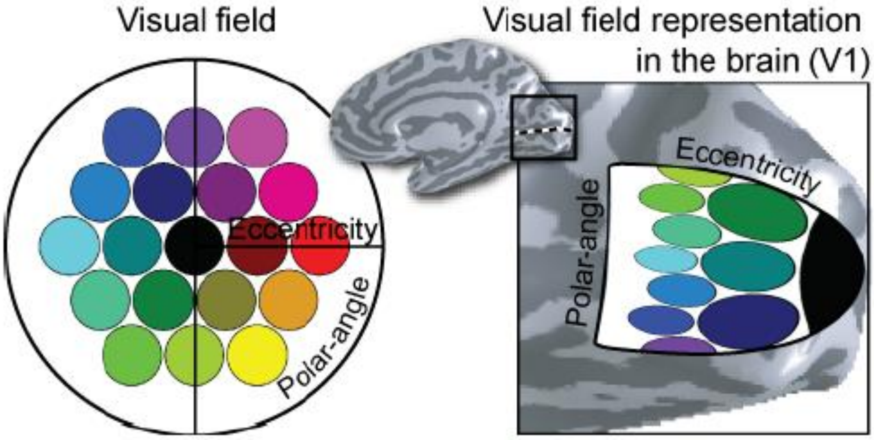

Figure 2. Visual field representation and cortical magnification in the primary visual cortex. Primary visual cortex (V1) is retinotopically organized and the representation of the central part of the visual field is enlarged, a phenomenon named cortical magnification. Image from retrieved from Dumoulin (2015).

V1 neurons motion tuning properties are coarse and limited with small receptive fields[5] (RFs). Additionally, some V1 neurons are tuned for the orientation and spatial frequencies of small and fixed elements of the retinal image over short distances, probably for an accurate spatial encoding. Neurons in this area are responsible to detect edges, to distinguish small changes in visual orientations, spatial frequencies and colours. Moreover, neurons with similar tuning properties are clustered together as cortical columns and are strongly interconnected through horizontal or lateral connections from pyramidal neurons stretching over 4 mm on the cortical surface (Lamme, Supèr, & Spekreijse, 1998). As we will see later in this chapter (Chapter 1.2.3), these connections spread important information about the surrounding (context) of neurons' RFs through a facilitatory travelling wave. Neurons in V1 provide information for neurons in highest levels and are considered as the basic units for motion processing (Livingstone & Hubel, 1988). Although it seems that V1 neurons are not responsible for complex tasks, they provide the code to build complex tasks performed by neurons that held more complex processing.

MT is considered the main area for motion processing and it is a central component of the dorsal processing stream. MT receives the majority of information from V1 through direct projections, but it also receives some via indirect inputs from V2 and V3. Neurons in V1, V2 and V3 exhibit preference for motion direction (Wang, Merriam, Freeman, & Heeger, 2014) and are selective to the location of the moving object within its trajectory. That is, neurons show higher activity for objects at the trailing edge of motion (motion onset) compared to the leading edge (motion offset) (Schellekens, van Wezel, Petridou, Ramsey, & Raemaekers, 2014). The areas V1, V2 and V3 also exhibit a preference for coherently moving stimuli as compared to MT (Wang et al., 2014). An important property of the area V3A is that it is able to detect whether objects move inward or outward as observed in studies using functional

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[5] The receptive field (RF) of a visual neuron is classically defined as the area of the visual field where a visual stimulus elicits a change in its firing activity, corresponding to a Gaussian function in which the response peak is located at the centre of its RF.

magnetic resonance imaging (fMRI). Specifically, higher activity in V3A was found when motion was displayed toward a given voxels' region of interest (ROI), which shows an inward bias. This area, together with MT, also exhibits patterns of neural activity according to the actual position of an object showing an anticipation of (future) position coding (Maus, Fischer, & Whitney, 2013). That is, the position is in accordance with the actual position of the object, but due to neural delays we should not expect an accurate representation in space and time (we will address this specifically in Chapter 1.2.1). Importantly, crucial investigation on motion processing has been conducted intending to understand the role of the interactions between areas V1, V2, V3 and MT (eg: Medathati, Chessa, Masson, Solari, & Kornprobst, 2015).

Similar to V1's orientation preference, MT is also organized in a columnar fashion and contains neurons with larger and oval receptive fields tuned to the direction and speed of motion. However, direction of motion tuning of MT neurons is not sharp so information about the direction of motion may be carried in a distributed population code. MT neurons have a strong myelination responding rapidly to a moving stimulus ensuring that action potentials travel at high speed along the axons. Accordingly, neural latency for a moving object is increased when disrupting MT activity (by pulses of transcranial magnetic stimulation), which reveals a possible role of MT in neural latencies (Maus, Ward, Nijhawan, & Whitney, 2013).

After the MT stage there are other areas that process motion as, for example, the dorsal part of the medial superior temporal region (MSTd). In this area neurons have larger RFs compared to V1 and MT and are sensitive to optic flow patterns as rotation, expansion and contraction (Price & Born, 2010).

In sum, it is very plausible the existence of a hierarchy of motion processing with extensive ascending (lower to higher cortical areas) feedforward, descending (higher to lower cortical areas) feedback connections between areas at different levels of the visual system whose neurons are selective to distinct aspects of the retinal image motion. Importantly, horizontal (parallel) connections add more information to neurons as it link neurons across large distances within each area.

Nevertheless, how perception emerges from the functional architecture of the visual system is a fascinating question that is still unsolved.

1.2. Linking functional architecture of the visual system to perception

Summary

The current Chapter 1.2 is organized in three sections. In the first one we discuss an important factor that may constrain perception: the inherent timing consumption underlying neural processing of visual information. In this regard, we will address the problem of neural delays and the consequences it imposes, specifically on motion perception (Chapter 1.2.1). Then, we intend to present neurophysiological evidence for the most probable mechanism responsible to cope with neural delays in order to accurately perceive in time positions of moving objects. On one hand, we will remark the importance of contextual information outside the classical receptive field of neurons that may facilitate as well their responses, and how this could be related with an anticipation of subsequent stimulus presentation (Chapter 1.2.2). On the other hand, the probable mechanism in which contextual information travels along cortical areas linking neurons spatially distributed will be detailed (Chapter 1.2.3). Such mechanism may account for psychophysical data on anticipation of moving objects.

1.2.1. Neural delays

As mentioned previously in Chapter 1.1.1, the coding of visual motion information starts in the retina going further in the visual hierarchy. However, neural processing takes time (see Figure 3a) and nervous fibers transport information at a slow speed (1-100 meters per second). So, when a stimulus is detected in the visual RF by the retina a series of mechanisms start in order to process that object; i.e. photoreceptors send information to ganglion cells (represented with the letter A in Figure 3b) that transmit that information to cortical neurons (A’ in Figure 3b). After the delay of the transmission, the peak of the cortical activation will register the position of the object. Consequently, when we perceive the position of the object some milliseconds had already passed due to nervous fibers transportation of visual processing. Therefore, at that time the object has already moved to its new position in the physical world and, for that reason, will be mislocalized in its neural representation, i.e. cortical position will not be in accordance with the actual position in the world at that time.

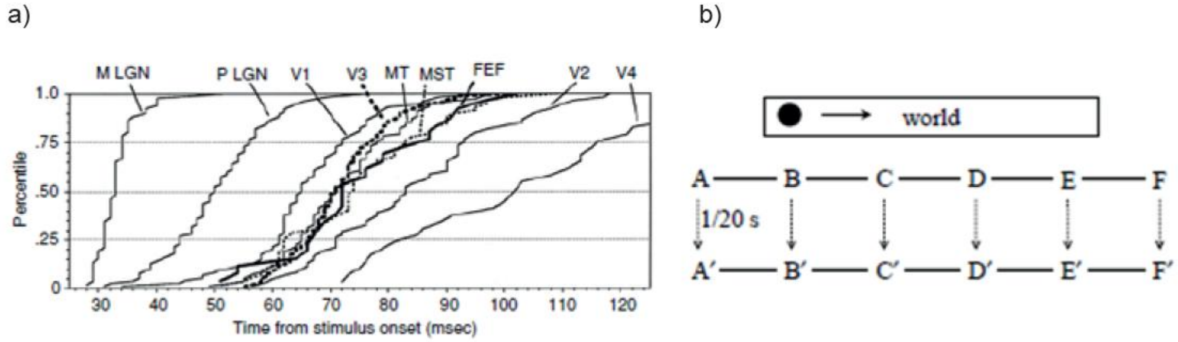


Figure 3. (a) Percentage of active cells and their neural latencies as a function of the stimulus onset. It can be observed that M LGN cells have a short delay which is in accordance with the fact that they are responsible to transmit information of moving objects along the magnocellular pathway. Data from the macaque visual system retrieved from Schmolesky et al. (1998). **(b)** Representation of the transmission of visual information through neurons. An object moves in the visual field stimulating photoreceptors which transmit information to ganglion cells (A-F) and from ganglion cells to cortical cells (A’-F’). Lines between cells indicate (lateral) horizontal connections between them. Image retrieved from Nijhawan and Wu (2009).

Thus, neural delays represent a limitation for the interaction with moving objects where an accurate timing is crucial (Nijhawan, 2002). Returning to the example giving at the beginning of this Chapter; when driving a car, we need to adequately predict future locations of other cars and pedestrians. Therefore, the visual brain should have a strategy to cope with these inherent neural processing delays. Additionally, it is very likely that some compensation for neural delays should occur at each processing level of the visual system enhancing neural speed for an adaptive behaviour (Jancke, Chavane, & Grinvald, 2010; Jancke & Erlhagen, 2010b; Nijhawan, Watanabe, Khurana, & Shimojo, 2004; Paradis, Morel, Seriès, & Lorenceau, 2012; Sato, Nauhaus, & Carandini, 2012).

The possibility that the visual system compensates for these delays has been explored in several studies mainly on the context of the Flash Lag Effect (Jancke, Erlhagen, Schöner, & Dinse, 2004; Maiche, Budelli, & Gómez-Sena, 2007; Nijhawan, 1994; Oğmen, Patel, Bedell,

& Camuz, 2004; Paradis et al., 2012; Purushothaman, Patel, Bedell, & Ogmen, 1998; Subramaniyan et al., 2015; Yilmaz, Tripathy, Patel, & Ogmen, 2007). This effect refers to the fact that a moving object is perceived ahead of a static object when both are presented at the same time and spatially aligned (Figure 4a). There are several explanations but the most accepted one, the *differential latency* hypothesis, states that moving objects prompt faster processing times than static ones (Purushothaman et al., 1998; Whitney, Murakami, & Cavanagh, 2000; Whitney & Murakami, 1998). The moving object is processed with shorter neural latency mainly due to its past trajectory (its localization over time); such that an object that moves activates several neurons along its trajectory. These neurons transmit the information to adjacent neurons with RF along the predicted trajectory of the object through a travelling wave. Contrarily, a flash does not have a past trajectory, so there is no information spreading to adjacent neurons about its future appearance. Possibly, for this reason, population of neurons have lower response amplitudes for static objects regarding moving ones in cat area 17 (see Figure 4b).

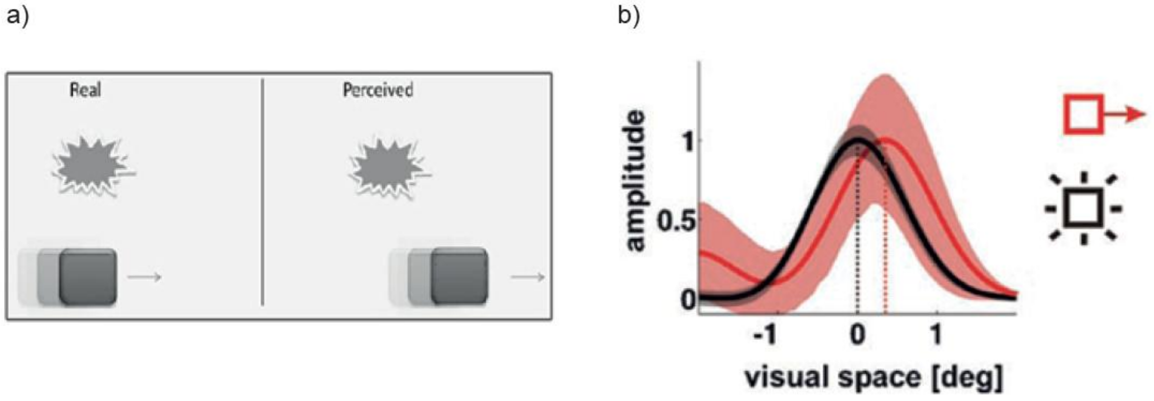


Figure 4. (a) The Flash Lag Effect. A moving object and a static object are presented at the same vertical location and at the same time, however, the moving object is perceived ahead of the static target which may be the result of differential neural delays. **(b)** Amplitudes for population activity in cat visual area 17 for static (black) and moving stimulus (red) by applying the Optimal Linear Estimator approach (OLE) in combination with a bootstrap analysis. It represents the activity 50-60 ms after the presentation of the flash. Shaded areas show 99% confident intervals. The moving object is significantly ahead regarding the amplitude peak for the static object. Data retrieved from Jancke et al. (2010).

1.2.2. Non-classic receptive field

Traditionally, the classic receptive field (RF) have been thought to be local and independent, but recent psychophysics and physiological research support evidence that integration and processing of visual information are build in a rich network and that a single neuron can summate information over a larger area than previously thought. That is, neurons receive modulatory activation by neurons located in adjacent areas, allowing the integration of contextual information about their surroundings. The surrounding of the receptive field (the silent" periphery or "non-classic receptive field" - nCRF) influences neurons responses yielding to a series of effects as orientation tuning and preference (Chavane et al., 2011; Kapadia, Ito, Gilbert, & Westheimer, 1995; Kapadia, Westheimer, & Gilbert, 1999; Seriès, Georges, Lorenceau, & Frégnac, 2002). Thus, neurons are not isolated in integrating just the information from their RF but also integrating incoming information from adjacent neurons, which allows them to create an interpretation of the surrounding neural dynamics in space and time.

Hence, a stimulus processed by a specific neuron's RF evokes as well the cortical activity of thousands of interconnected neurons. Single neurons fire when a stimulus is presented at their RF, however, if a stimulus is located outside their RF they may receive sub-threshold activation as well that besides the fact that do not elicit a firing threshold, they would be preactivated by the input they receive by the long-range horizontal connections (see Figure 5). This subthreshold activation is characterized by modulation of neurons membrane potential, with depolarizing responses, and thus, it is thought to be facilitatory (Sato et al., 2012). The strength of the postsynaptic response evoked by the sub-threshold activation decreases almost linearly as a function of distance between the stimulus and the RF (Bringuier, Chavane, Glaeser, & Frégnac, 1999; Jancke et al., 2010; Sato et al., 2012). Importantly, V1 responses to a stimulus in the RF are modulated by a prior stimulation in its surroundings at least 80 milliseconds before (Palmer, Marre, Berry, & Bialek, 2015; Seriès et al., 2002).

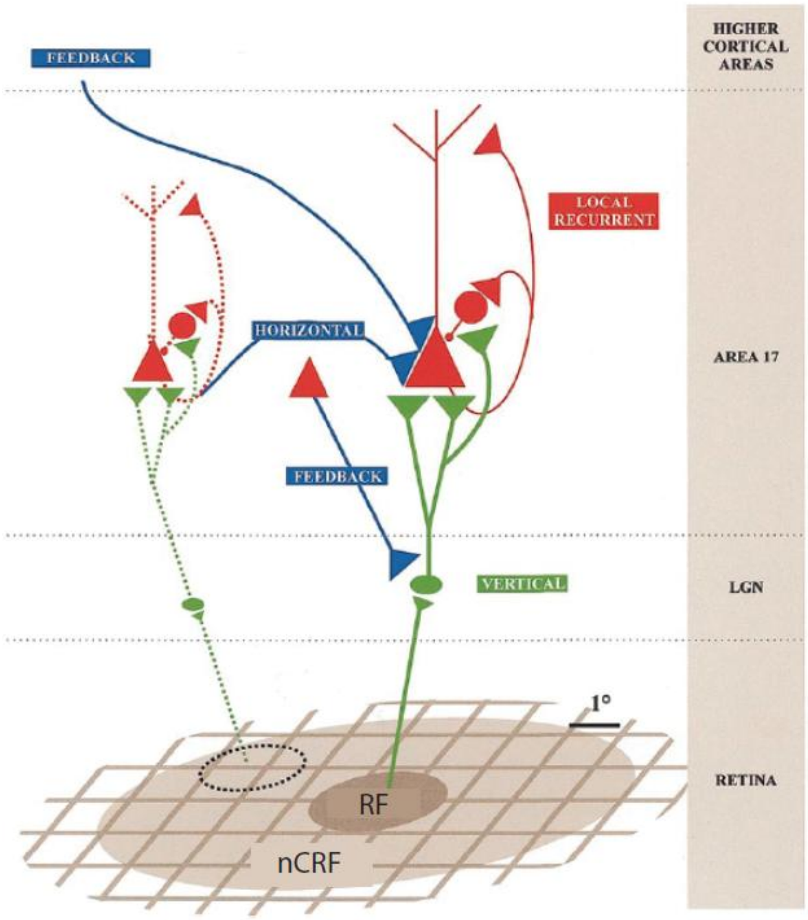


Figure 5. Representation of neurons receptive field (RF) and non-classic receptive field (nCRF). Horizontal connections provide input about adjacent areas in the retina (in blue colour). Thalamic feedforward input is represented in green colour and local intracortical circuits in red. Image adapted from Chavane et al. (2000).

1.2.3. Long range horizontal connections and travelling waves

In the last 50 years, the predominant view assumes that neurons are sharply tuned and organized in vertical columns signalling different attributes from their neighbouring neurons along the horizontal dimension (Hubel & Wiesel, 1968; Sato et al., 2012). However, it would be more efficient if neurons with similar parameters were adjacent because this would reduce the cost of wiring and enhance neural speed information (Chklovskii, Schikorski, & Stevens, 2002; Kaplan, Lansner, Masson, & Perrinet, 2013). Therefore, it is remarkably important the role of connectivity pattern between neurons that would be a solution to this problem. In fact, V1 and MT neurons receive connections from neighbouring neurons located in the same cortical area, but also in parallel by feedforward or feedback connections from lower and higher cortical areas, respectively. Thus, input of several retinotopic origins converges onto these neurons.

One likely candidate to integrate information over large regions of space is the dense network of long range horizontal connections. Horizontal axons connect neurons separated by distances of several millimetres and spatially distributed with similar orientation preference, as observed in cats, tree shrews and monkeys (Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Georges, Seriès, Frégnac, & Lorenceau, 2002; Jancke et al., 2010). Horizontal connections modulate neurons responses strength in V1 that has been reported to be correlated with several visual functions as visual segmentation, orientation-specific centre-surround interactions, perceptual grouping of line segments, perceptual pop-out, perceived brightness, figure ground segregation, contour integration and orientation tuning (Angelucci & Bressloff, 2006; Chavane et al., 2011; Kapadia et al., 1995, 1999; Kastner, Nothdurft, & Pigarev, 1997; Knierim & van Essen, 1992; A F Lamme, 1995; Rossi, Rittenhouse, & Paradiso, 1996; Seriès et al., 2002).

Neural facilitation is also observed when a target is surrounded by coaligned static Gabor patches (Cass & Spehar, 2005; Georges et al., 2002; Kapadia et al., 1999; Paradis et al., 2012). Collinear facilitation refers to the fact that detection threshold is lower for a Gabor if flanked by coaligned Gabor patches. The hypothesis is that a neuron with coaligned non-overlapping RF may depolarize its neighbours through long-range horizontal connections (Paradis et al., 2012; Seriès et al., 2002). In agreement, neurons in V1 that are selective to the same orientation are often linked through long-range horizontal connections (Sincich & Blasdel, 2001; Ts’o, Gilbert, & Wiesel, 1986). This supports the idea that (lateral) horizontal connections may be the mechanism that connects columns of similar orientation and thus, are responsible for collinear facilitation (Cass & Spehar, 2005; Georges et al., 2002). Moreover, the modulatory influence of neighbouring neurons may lead to shortened response latencies when neuron's RF is activated by a stimulus.

Neural facilitation is also affected by contrast: neural latency increases as the stimulus contrast decreases (Paradis et al., 2012; Purushothaman et al., 1998; Yilmaz et al., 2007). It is suggested that long-range horizontal connections contribute to propagate facilitatory modulations as a function of stimulus contrast (Paradis et al., 2012). The neural processing speed is dependent on the contrast of the stimulus, being that low contrast stimuli elicit higher neural latency. In similar manner, increasing distance between stimulus location and the RF of V1 neurons decreases neurons' responses strength and increases their responses delay for a subsequent stimulus (Bringuier et al., 1999; Chavane et al., 2000).

Hence, stimulation of RF cells in V1 depends strongly on the (facilitatory or inhibitory) modulations by orientation, contrast and distance from stimuli located outside their RF (Georges et al., 2002; Kapadia et al., 1995; Paradis et al., 2012; Purushothaman et al., 1998). The dynamics of horizontal connections depending on these stimulus parameters are represented in Figure 6.

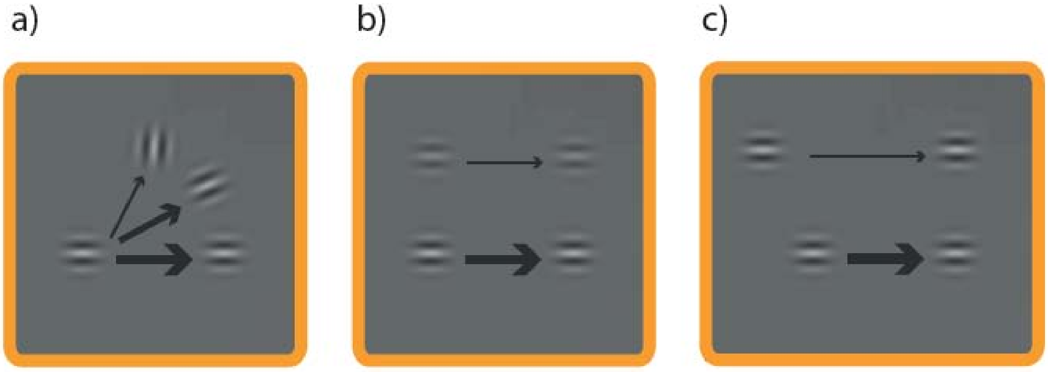


Figure 6. Graphic representations of the horizontal connections strength depending on stimulus characteristics between two neurons with close RFs. Arrows represent the strength of the horizontal connection. **(a)** When both stimuli have the same orientation the connection is strong and facilitates detection of the second stimulus; **(b)** When contrast is low horizontal

connections spread information with less strength and the second stimulus would not be facilitated (or in less degree); **(c)** When the distance from the two stimulus increases connections are less strong and thus the stimuli would not be facilitated as when it is closed to the second stimulus.

Considering moving objects, it is also very likely that lateral connections have a determinant role in anticipating moving objects future positions. These connections are faster compared to forward connections, i.e., connections from higher areas as MT which may introduce important delays (Kaplan et al., 2013). The horizontal spread of neural activity constitutes a travelling wave along horizontal connections with an anisotropy connectivity pattern that influences spike responses and thus, influences V1 output as well (Kaplan et al., 2013; Sato et al., 2012). Moreover, this travelling wave is progressively delayed as distance increase at both trailing and leading edges (motion onset and motion offset, respectively). There is ample evidence that these trailing waves are facilitatory, i.e., depolarize neurons and elicit spikes, covering ample regions of space and are selective for orientation (Sato et al., 2012).

Therefore, trajectories of moving objects prompt a fast travelling activity wave that extend far behind the classical receptive field (Bringuier et al., 1999; Jancke et al., 2010, 2004; Nijhawan, 2008; Paradis et al., 2012; Sato et al., 2012). Accordingly, there is psychophysical evidence for a lower threshold for stimuli located at the leading edge of motion that is hypothesized to be mediated by horizontal connections providing facilitatory signals for further positions along the path (Arnold, Thompson, & Johnston, 2007; Roach, McGraw, & Johnston, 2011). These connections modulate neurons responses providing a possible role on anticipation of the future positions of a moving object. Accordingly, physiological studies provide strong evidence for the importance of horizontal connections to enhance neural speed processing (as will see in detail in the next section) which may be the mechanism that anticipates future positions of moving objects.

However, the question how horizontal connections spread information causing travelling waves is still unsolved. There are two main hypothesis regarding this question (Prechtl, Bullock, & Kleinfeld, 2000; Sato et al., 2012), see Figure 7. The first hypothesis states that a single neuron sends information through horizontal connections to other neurons causing sub-threshold activity in those neurons. This scenario argues in favour of a delayed excitation of the excited neuron. Another hypothesis refers that a neuron propagates spikes for the wave to go further, that is, pulses are propagated in an excitable network information about a stimuli located far from their RF.

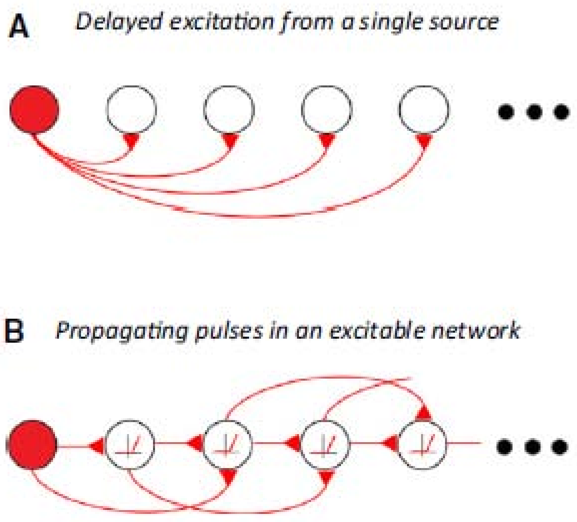


Figure 7. Likely network scenarios that could lead to travelling waves. Red circle indicate where the wave starts, whereas white circles represent neurons or population of neurons that receive subthreshold activity. **(a)** A simple model in which a unique neuron transmits passively information to other neurons. On the contrary, **(b)** a more complex model and more costly as well; assumes that each neuron receives information and then, sends the output to their neighbours. Note, that in this case, neurons would only transmit information if their activity reaches a threshold. This latter model appears to be more cooperative. Image retrieved from Sato et al. (2012)

1.3. Anticipation dynamics for visual moving objects

Summary

Taking into account the findings reported in the previous sections, we now intend to review throughout this Chapter neurophysiological and psychophysical evidence on anticipation dynamics of moving objects. In Chapter 1.3.1 we will consider a predictive coding that predicts incoming sensory information based on previous information which may underlie motion processing as well. Next, in Chapter 1.3.2 we will report psychophysical evidence for the role of prediction and anticipation mechanisms on motion perception. With all these outcomes in mind we hypothesize that the area next to motion will be affected by anticipatory mechanisms, and facilitatory effects should occur for an object presented in that area.

Some research report an anticipation of moving object's trajectory that starts earlier in the retina (Berry, Brivanlou, Jordan, & Meister, 1999; Palmer et al., 2015). There is evidence showing that when a moving object is presented at constant speed, ganglion cells fire for a more extended period and start earlier comparing to the presentation of a static object (Berry et al., 1999; Hosoya, Baccus, & Meister, 2005; Palmer et al., 2015). It could be the case that this compensation or anticipation mechanism may be present at all levels of the visual processing. Shorter latencies on salamander retina, cat's LGN and area 17 and macaque MT neurons were found for moving bars compared to flashed bars (Jancke et al., 2004; Orban, Hoffmann, & Duysens, 1985). Moreover, in the neural image that is transmitted to the brain, the moving object is clearly ahead in space compared to a flashed object as previously seen in Figure 4.

An excellent investigation using electrophysiological recordings was able to show that cortical activation (in cat area 17) for moving stimulus is ahead in space comparing to a flash

(Jancke et al., 2004). About fifty milliseconds after stimuli presentation it was observed a spatial lag between the moving stimulus and the flash (see panel 50 ms at Figure 8.). This latency difference between both stimuli was of approximately 16 ms, being the moving object processed earlier in time. It is very possible that neural latency reduction is related to the fact that motion trajectories are internally represented by a travelling wave in position space shaped by neurons (Jancke et al., 2004; Kaplan et al., 2013; Sato et al., 2012). This facilitatory travelling wave of activity in the network elicits higher probability of firing action potentials resulting in preactivation of neurons. The most probable candidate mechanism for this preactivation is the long-range horizontal connections.

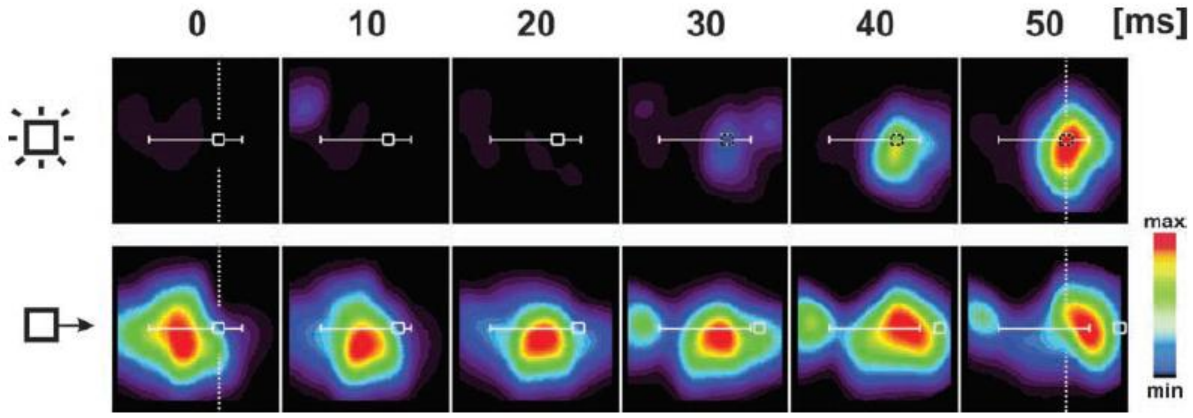


Figure 8. Representation of the cortical activation in cat area 17 for moving and for flash stimuli; data from Jancke et al. (2004). Soon as the stimuli is displayed at time 0, a clear propagating peak for the moving stimulus is observed. On the contrary, no cortical activation is observed for the flash at time 0. Moreover, after 50 ms cortical representation of the moving stimuli is also clearly ahead regarding the flash (static stimulus).

Hence, when a stimulus moves, neurons with RF at the “real” position of the stimulus are the most active, and importantly, these neurons send modulatory information regarding the stimulus (through long range horizontal connection) to the neighbouring neurons causing a subthreshold activity. The preactivation by travelling waves may be the mechanism by which the system implements the anticipation of future positions of moving objects.

Moreover, when the stimulus appears in the RF of a preactivated neuron, the stimulus is detected earlier in time with a higher peak response, because that neuron was already closed to firing threshold and then, would react faster. In sum, subthreshold activation leads to the preactivation of neurons where the moving stimuli will be located in the future. Accordingly, neurophysiological studies show that motion produces a facilitation wave; these studies reported spatial shifts in the activity patterns in early visual areas (Fu, Shen, Gao, & Dan, 2004; Fukiage & Murakami, 2013; Jancke et al., 2004; Maus, Ward, et al., 2013), which could be related to the perceived position shift of the moving object in the Flash Lag, Fröhlich Effect and Representational Momentum effects (Chappell, Potter, Hine, Mullen, & Shand, 2013; Fukiage & Murakami, 2013; Jancke et al., 2010, 2004). The visual system might compute the future position of a moving object in order to compensate for neural processing delays. The brain actively makes predictions about the future values of sensory inputs anticipating future positions of the moving object (Berry et al., 1999; Jancke et al., 2010; Kaplan et al., 2013; Nijhawan, 2008; Palmer et al., 2015).

1.3.1. Predicted coding for motion stimuli

The brain needs to constantly update and predict incoming sensorial information, but how these goals are achieved remains unclear. It is improbably that the brain processes all the possibilities and weights one against the other to find the optimal solution because this would be computationally inefficient. Instead, prediction estimation would occur at every level of processing, converging to the solution with higher probability of being true. The existence of predictive coding for motion stimuli is emergent. Motion stimuli may be processed by a predictive coding so that probabilities of future locations are computed (Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010; Eriksson, Wunderle, & Schmidt, 2012; Roach et al., 2011; Schellekens, Ramsey, & Raemaekers, 2015). The idea of prediction in visual processing is not new and in the last decades it became the most probable explanation for several phenomena like visual illusions. Starting with the Flash Lag Effect (FLE) soon the word predictive was prominent in the field. Findings from the study by Jancke and colleagues (2004) mentioned in the previous section provided data that can be implemented by a predictive coding for future positions of the moving object.

At the same time, bayesian models and predictive coding models for visual brain computation also started to give further evidence that the visual brain predicts future occurrences. Since then, predictive coding has elicited interesting debate and research work. Predicted coding models highlight that predictions play a central role in visual processing. The brain is able to learn from its own computations and from the statistical regularities of the external world to only signal error to those predictions saving neural activation. The brain is thus “*a statistical organ predicting worldly states that generates its sensory inputs*” (Kanai et al., 2015, p.1). The main idea of these predictive coding models is that prediction is handled in each stage of visual processing for all sensory inputs including predictions of individual neurons or populations of neurons (Clark, 2013; Eriksson et al., 2012; Huang & Rao, 2011; Palmer et al., 2015). In fact, predictive coding was found earlier in the retina (Palmer et al., 2015). These predictions are computed towards likely scenarios minimizing prediction and representation of sensory input (Friston, Daunizeau, Kilner, & Kiebel, 2010; Lee & Mumford, 2003; Rao & Ballard, 1999; van der Helm, 2015). However, how the brain computes all the incoming information in relation to its predictions experience-based is still unsolved.

Research on predicted coding for motion has been conducted using functional magnetic resonance imaging (fMRI). Alink and colleagues reported different blood-oxygenation signals (BOLD) responses for predictable and unpredictable motion trajectories (Alink et al., 2010). The predictable object moved along positions ordered in space in time whereas the unpredictable object moved along the same trajectory, but some positions were changed, and hence, positions were unpredictable within that trajectory. Particularly, these authors found greater V1 responses for unpredictable motion trajectories and on the contrary, less V1 responses for predictable ones. The authors explained their findings based on a predictive coding; i.e. when predictions are in accordance with the processed stimulus the system reduces their neural responses. Interestingly, previously psychophysical findings from the same authors regarding predictable stimuli revealed that these stimuli were detected more often than stimuli under unpredictable trajectory; using the same stimuli parameters in both studies (Schwiedrzik, Alink, Kohler, Singer, & Muckli, 2007).

Similarly, Wang and colleagues showed that responses in V1, V2 and V3 were biased with higher responses at the edge of the stimulus aperture, i.e. motion origin (Wang et al., 2014). Following the same investigation line, higher BOLD signals were found at the trailing edge of motion dots, whereas moving dots at the leading edge suppressed BOLD responses (Schellekens et al., 2015). These authors explained their findings also based on a predictive coding as well, where BOLD amplitudes decrease as consequence of prediction errors decreasing, which in turn, decrease as accuracy increases (Huang & Rao, 2011; Rao & Ballard, 1999).

The excitatory activity decreasing from trailing to leading edge is proposed to be a result of a motion-induced predictive suppression mechanism (Wang et al., 2014). It might be the case that this predictive coding by means of decreasing BOLD signals amplitude is the consequence of an efficient coding through short-distance neuronal interactions, possibly through horizontal connections (Angelucci et al., 2002; Gilbert & Wiesel, 1989). Accordingly, lower detection thresholds near the leading edge could be due to a relative increase in available resources. The visual system may employ forward modelling to maintain its ability to detect predictable moving objects that counteract surround suppression (Roach et al., 2011). The activity reduction in early sensory cortex could be related to an improved sensory representation, that is, expectation might sharpen the population response (Kok, Jehee, & de Lange, 2012). Nonetheless, when an object moves, the visual system may employ forward predictions based on sensory accumulation of the trajectory and neural responses may be suppressed when stimulus location is predicted from the responses of neighbouring neurons (Lee & Mumford, 2003; Rao & Ballard, 1999; Roach et al., 2011). These hypotheses suggest that neural responses are evidence-based on sensory accumulation (Mazurek et al., 2003). In the case of an object that moves across the visual field, neural responses might be suppressed when stimulus location can be predicted from the responses of neighbouring neurons near the location of motion onset, a form of predictive coding (Rao and Ballard, 1999; Lee and Mumford, 2003).

Hence, evidence for enhancement of psychophysical sensitivity at locations further along the motion trajectory than at motion onset, with higher facilitation at leading edge may be explained by input summation or by a forward predictive coding of motion signals (Arnold, Marinovic, & Whitney, 2014; V. Doorn & Grind, 1989; Roach et al., 2011; Verghese, Watamaniuk, McKee, & Grzywacz, 1999). However, it is important to note that activation measured by BOLD responses at the leading edge is reduced regarding the trailing edge of a motion trajectory. While some authors propose that the system propagate predictive information (i.e., probabilities, population activity, spikes) as travelling waves allowing an earlier and higher neural activity for motion (Jancke et al., 2004; Kaplan et al., 2013; Paradis et al., 2012); others claim a predictive coding by a decreasing in neural activity because the input matches the prediction (Alink et al., 2010; Schellekens et al., 2015; Wang et al., 2014). What is more, both views emphasize the role of horizontal connections on anticipating and predicting motion trajectories. It is unlikely that both views are in disagreement; differences between the techniques used in these studies may generate different results. Moreover, neurocomputational mechanisms are still in debate and the lack of correspondence between the proposed predicted code and empirical data such as fMRI, electroencephalography (EEG) and extracellular and single cell records highlights discrepancies (Clark, 2013; den Ouden, Kok, & de Lange, 2012; Eriksson et al., 2012; Gotts, Chow, & Martin, 2012; Kok et al., 2012; Rauss, Schwartz, & Pourtois, 2011; Summerfield & de Lange, 2014). Additionally, BOLD signal and underlying neuronal activity are not fully understood; besides the fact that new quantitative data-analyses techniques are emerging to extract more information from fMRI signals (Dumoulin, 2015; Ekstrom, 2010; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Logothetis, 2003). At this date, it is not possible yet to determine whether recorded neuron responses are signalling predictive errors or solely stimulus information or both; or if there are specialized neurons for prediction signalling. To this end, electrophysiological recordings should be combined to ascertain the mechanism underlying such predictive coding (Logothetis et al., 2001; Logothetis, 2003; Matthews et al., 2014).

1.3.2. Psychophysical evidence for anticipation

Behavioural studies have been yielding controversial results as well and the implications of shorter processing latencies and anticipation dynamics for moving objects are still a matter of debate (Hubbard, 2014; Mate, Pires, Campoy, & Estaún, 2009; Maus, Ward, et al., 2013; Nijhawan, 2008). Several illusionary effects illustrate the possible implication of motion on perceptual detection. Some effects are generated by motion stimuli along their trajectory, as for instance, the Fröhlich effect (FE), the Flash Lag Effect (FLE) and the Representational Momentum (RM). The former; i.e. FE, is an effect that when participants are asked to locate the stimulus at the *beginning* of the trajectory they perceive the location of the moving object shifting forward in the direction of motion. On the other hand, the FLE occurs when a static object is presented near the *middle* of the trajectory of a moving object; participants perceive the moving object as shifting forward in motion direction. The latter, i.e. RM, is the effect in which participants perceive the final location of a moving object to shift forward when the moving object *ends* its trajectory. These effects reveal similar dynamics that may be accomplished by the mechanism of horizontal connections spread of information by travelling waves (Jancke & Erlhagen, 2010). That is, the travelling wave induced by motion starts immediately after the moving stimulus appear (and may lead to the Fröhlich effect), being stronger at the middle (leading to FLE) and disappearing some milliseconds after motion offset (representational momentum effect).

Regarding the Flash Lag Effect (FLE) it has been tested using different types of trajectories: continuous, reversal and onset. Studies show incongruent results on whether the FLE is increased or decreased in the condition of onset trajectory compared to a continuous trajectory (Chappell et al., 2013; Eagleman & Sejnowski, 2000; Linares, López-Moliner, & Johnston, 2007; Oğmen et al., 2004). As for the previously mentioned effects (FE and RM) the observed increasing in the FLE for these types of trajectories could also be explained by a travelling wave along horizontal connections. Moreover, in support of anticipation for moving objects by travelling waves, Maiche and collaborators reported that the FLE was increased when two objects moved toward the spot where the moving object was presented few milliseconds later (Maiche et al., 2007). The shorter perceptual delay induced by moving objects that converged into that spot, was hypothesized to be the result of a spatial propagation of activity in the visual cortex that has facilitative effects on the response to stimuli presentation in the RF (as mentioned previous in this Chapter).

Similarly, psychophysical results are also controvert in whether influence of motion on targets detection is enhanced (by facilitatory mechanisms) or decreased (by motion masking) along motion trajectory, at the leading or at the trailing edge of motion (Arnold et al., 2014; Lenkic & Enns, 2013; Liu, Ashida, Smith, & Wandell, 2006; Roach et al., 2011; Schwiedrzik et al., 2007; Whitney et al., 2003; Yantis & Nakama, 1998). One possible reason may be related to the timing and spatial configuration of experiments. That is, it seems critical to consider when and where should occur the presentation of the probe target along motion trajectories. This finding was imminent in the study of Schwiedrzik et al. (2007) who reported different results depending on the timing and spatial presentation (predictablilty) of the probe target within motion trajectories. In this case, if a target was located in time and position with the estimated spatiotemporal positions of the moving object, its detection was facilitated (Schwiedrzik et al., 2007). On the contrary, targets detection was impaired when the target did not coincide in time (too early or too late) as well as in space with positions of the moving object. Further evidence for anticipation comes from the study by Hogendoorn and colleagues that revealed that when a disc reversed its position and the target was located in positions ahead after motion reversal, lower reaction times (RTs) were found (Hogendoorn, Carlson, & Verstraten, 2008). However, somehow counter-intuitive, when motion did not reversal its direction, RTs were higher for the locations ahead of motion.

Other studies reported a higher detection at the leading edge of motion regarding the trailing edge when target was presented in spatiotemporal phase as the inducer (Arnold et al., 2007; Roach et al., 2011). These findings revealed also that target visibility was enhanced when the probe target could be predicted by the trajectory matching prediction. These outcomes are inconsistent as well with motion masking (detection impairment), but are consistent with predictive accounts. It may be that impairment along motion trajectory is due to the spatiotemporal presentation of the target, as mentioned previously, and also to the fact that the target to be detected differs in shape with relation to motion. Accordingly, Kanai et al. reported that sensitivity to detect an irregularity (change in contrast, colour, shape or gaps) is impaired in motion trajectories (Kanai, Carlson, Verstraten, & Walsh, 2009). On the contrary, facilitatory effects are most likely to happen when the target and moving object do not differ. In this case, targets presentation are predictive, and hence, its visibility is enhanced as expectancies or predictions match reality (Lenkic & Enns, 2013). This might reflect the notion that stimulus position is determined by combining sensory input with a predictive signal (Nijhawan, 2008; Roach et al., 2011).

On the other hand, psychophysical research on collinear facilitation has often used static stimuli and explored variables such as spatial frequency, orientation, phase, timing, location and distance between flankers and targets (eg: Huang & Hess, 2008; Huang, Mullen, & Hess, 2007; Lev & Polat, 2011; Polat & Sagi, 1993; Polat & Tyler, 1999). However, to the best of our knowledge, little has been investigated using coaligned moving objects. Whether coaligned moving Gabor patches can facilitate target detection located next to the leading edge of motion remains unexplored. A study by Georges et al. (2002) is a precedent on this issue reporting a "speedup" illusion in which a Gabor patch moving along its orientation is reported to move faster than a Gabor patch oriented orthogonal to the motion axis. Also of a great relevance is another study by Paradis et al. (2012) who found that the amplitude and latency of magnetoencephalography (MEG) signals varied according to the contrast and orientation of moving Gabor patches, and thus proposed that long range horizontal connections may contribute to spread activity modulating perceptual saliency or contrast detection (Paradis et al., 2012; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Seriès et al., 2002).

In conclusion, when an object moves, neurons that code the initial segment of motion, may spread a fast neural activity to neighbouring neurons, through horizontal connections, preactivating and prompting them to fire earlier when the object arrives at their RF (Jancke et al., 2004; Jancke & Erlhagen, 2010; Paradis et al., 2012). Hence, this sub-threshold activation of neurons may cause an enhanced detection of targets located in the leading edge of movement. Thus, we can speculate that system is able of predicting the subsequent target location by anticipating future positions due to the data gathered (by the system) along the previous trajectory of the moving object.

2. Aim of the current research

Chapter 2

2. Aim of the current research

Motion signals prepare neighbouring neurons likely to be activated in the future by the moving object. Thereby, they may influence perception of static objects that are located in the area next to the leading edge of motion (motion offset). Given the above considerations we aimed to test whether positions next to the leading edge of motion would be facilitated regarding locations distant of motion.

Therefore, we varied motion stimuli parameters known to underlie facilitatory modulations through horizontal connections to obtain psychophysical data on perceptual facilitation in the area next to the leading edge of motion. We hypothesized that higher detection probabilities, reduced reaction times, earlier onset detection and higher perceived brightness would be observed for targets presented near and after a predictable trajectory comparing to targets located far.

2.1 Specific objectives:

(1) We aimed to test whether the facilitatory effect (induced by motion) would depend on the predictability of motion trajectory in the following hypotheses (Preliminary empirical work; Chapter 3.1). Specifically, we tested whether:

1.1. Detection probabilities would be higher for targets presented near the predicted trajectory compared to targets near the unpredictable trajectory (Experiment 1);

1.2. Reaction times (RTs) would be lower for targets presented near the predicted trajectory compared to targets near the unpredictable trajectory; and RTs would increase with the distance to the predicted trajectory whereas no such influence would be observed for the unpredictable trajectory (Experiment 2).

(2) We aimed to test facilitatory effects on a target located ahead of motion by manipulating motion parameters in the following hypotheses (Empirical work; Chapter 3.2). Therefore, we specifically tested whether:

> **2.1.** Temporal facilitation would increase as a function of the *number of trajectories* (Experiment 3);
>
> **2.2.** Brightness facilitation would increase as a function of the *number of trajectories* (Experiment 4);
>
> **2.3.** Temporal facilitation would decrease for trajectories composed by Gabor carrier *orientation* orthogonal to the trajectory (Experiment 5);
>
> **2.4.** Temporal facilitation would decrease by increasing the *distance* between target location and the leading edge of motion (Experiment 6);
>
> **2.5.** Temporal facilitation would increase as a function of trajectory *contrast* (Experiments 7);
>
> **2.6.** Temporal facilitation would increase as a function of trajectories *length* (Experiments 8);
>
> **2.7.** Temporal facilitation would increase as a function of trajectory *length and contrast*. (Experiment 9);
>
> **2.8.** Temporal facilitation observed in the previous experiments may be a specific effect due to motion and thus, we expect to not observe temporal facilitation as a function of the number of *static Gabor patches* (Experiment 10)

3. Methods and Results

Chapter 3

3. Methods and Results

3.1. Preliminary empirical work: Spatial facilitation by predictable motion

Abstract

We provide behavioural evidence for the existence of a spatial facilitation wave that enhances detection of targets located near motion. We assessed detection and forced-choice localization for static targets that appeared near the predicted trajectory of a moving object. In **Experiment 1**, participants had to detect the target when it was preceded by one of two different types of apparent motion: predictable and unpredictable (random). Participants showed higher detection probability when targets were presented near the predicted trajectory of a moving object than when they were presented following an object that moved with an unpredictable (random) trajectory. In **Experiment 2**, participants performed a forced-choice localization task and reaction time (RT) was measured. Lower RTs were observed for targets located near the predicted trajectory of the moving object, while no such difference was found for targets preceded by an unpredictable trajectory. Moreover, the spatial facilitation by the predictable trajectory decreased with distance to the moving object. Together, these experiments show that perception of a static object is enhanced when presented near the predicted trajectory of a moving object, providing further evidence for a facilitatory influence of motion in nearby locations.

Experiment 1: Detection task

The first experiment explored whether apparent motion facilitates visual detection of targets presented near the predicted trajectory of the moving object. We compared detection when a target was presented near the predicted trajectory of a single-direction (left to right) moving object versus when the same target was presented after a moving object that changed direction randomly (left to right and right to left), so that the trajectory was unpredictable.

Methods

Participants

Ten individuals (aged between 20 and 32 years old) volunteered to participate in this experiment and written informed consent was obtained. They all reported normal or corrected-to-normal visual acuity and did not receive compensation for their participation. The experiment was conducted with the approval of the local Ethics committee and in accordance with the 2008 Declaration of Helsinki.

Apparatus and Stimuli

The experiment was carried out using a Pentium IV computer and a 21” CRT monitor with a resolution of 1024 x 768 pixels and a refresh rate of 100 Hz. DirectRT software version 2010.2.103 (Jarvis, 2010) was used for stimuli presentation and data collection.

The moving objects were grayscale luminance modulations around the mean luminance of the screen (black screen with mean luminance of 0.07 cd/m²). They consisted of rectified Gabor patches with a profile described by the following equation:

$$G(x,y) = c.exp\left(-\frac{x^2+y^2}{2\sigma^2}\right) - \left|\cos\left(\frac{x-y}{\sigma-\sqrt{2}}\right)\ \right|$$

where c is a contrast constant and σ is the space constant of the Gaussian envelope. The spatial frequency of the Gabor patches was 1.06 cpd, c= 0.132, with 99% Michelson contrast, σ=22.5 arc min and 1.2° of visual angle. Gabor carrier orientation was always horizontal, i.e. parallel to the trajectory. Both types of trajectories were composed by a Gabor patch presented at four horizontally aligned positions for 10 ms each with an interstimulus interval of 80 ms. The four positions were located to the left of a fixation point (FP) and separated by 2.4º visual angle from the adjacent ones. In the predictable condition, the Gabor was presented sequentially in the positions from left to right along a path of 4.8º visual angle (Figure 9a). In the random (unpredictable) condition, the Gabor was presented in a random order within the same four positions.

The target consisted of a Gaussian profile (σ= 22.5 arc min) with 1º visual angle with one of three different levels of luminance: (1) low (mean luminance of 0.25 cd/m^2); (2) mid (mean luminance of 1.02 cd/m^2); and (3) high (mean luminance of 3.08 cd/m^2). It was presented for 300 ms with equal probability in one of four possible positions. The four possible positions had equal eccentricity from the fixation point (1.2º visual angle in both horizontal, left and right, and vertical, up and down, directions). The left column was 2.4º visual angle to the right from the closest position of the Gabor patch.

Procedure

Participants sat 57 cm away from the screen in a dark room with their heads placed on a chinrest to restrict head movement. They were habituated to the dark room for about 5 minutes. Each trial started with a black screen (Figure 9b). After 1200 ms, the FP (“+” sign) appeared at the centre of the screen and remained present until the end of the trial. Participants were asked to fixate the FP and were reminded to do so all along the experiment (Figure 9b). After 1200 ms, the moving object (sequence of Gabor patches) was presented (duration: 280 ms) in either a predictable or a random trajectory sequence (see section Apparatus and stimuli). In most of the trials, 30 ms after the offset of the last Gabor patch, the target appeared at one of the four possible positions during 300 ms (75% of the trials). In the rest of the trials (25%), no target was presented. Participants were asked to report, as fast and as accurately as possible, whether they saw the target or not by pressing the corresponding key (S for “Yes” and N for “No”) on a keyboard.

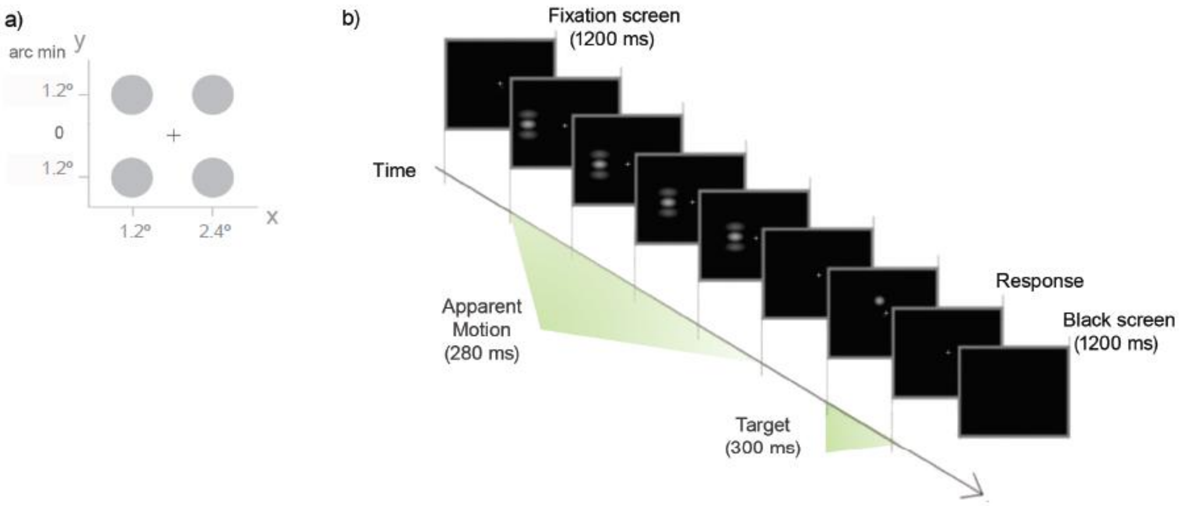


Figure 9. (a) Spatial representation of the four possible positions of the target in Experiment 1. All targets had the same eccentricity from the FP. **(b)** Schematic representation of the time course of a predictable trajectory trial in Experiment 1. First, the FP appeared (1200 ms). Then, the moving object (Gabor patch) was presented sequentially within four positions. After 30 ms, in 75% of the trials, the target appeared at one of four possible positions and participants had to indicate whether or not they had seen it. In the rest of the trials (25%), no target was presented.

After 20 practice trials, participants performed a total of 320 experimental trials divided into 4 blocks between which they were allowed to take a short break. Of the total number of trials, 240 were target-present trials and there were 10 trials per condition: trajectory (predictable and random), target position on the horizontal axis (left and right), target position on the vertical axis (up and down) and target luminance (low, mid and high). The target was absent in 80 of the 320 trials, 40 of them corresponding to the predictable trajectory condition and 40 to the random trajectory condition. The experiment lasted approximately 30 minutes (including practice trials).

Results and Discussion

We performed a repeated-measures ANOVA for detection probability (defined as number of hits divided by total number of target-present trials) with trajectory (predictable and random), target position relative to fixation point on the horizontal axis (left and right), target position relative to fixation on the vertical axis (up and down) and target luminance (low, mid and high) as within-participant factors. This analysis revealed main effects of trajectory ($F(1, 9) = 6.48$, $p = .031$), position on the vertical axis ($F(1, 9) = 8.59$, $p = .017$) and luminance ($F(2, 18) = 47.18$, $p < .0001$). The interaction between luminance and position on the vertical axis reached significance ($F(2, 18) = 3.83$, $p = .041$), indicating some differences in probability between upper and lower targets for lower luminance (post-hoc paired t-tests for upper versus lower targets for low luminance: $p = .024$; mid luminance: $p = .002$; and high luminance: $p > .1$). More interestingly, the interaction between trajectory and position on the vertical axis also reached significance ($F(1, 9) = 21.57$, $p = .001$), indicating that the effect of the moving object trajectory depended on target position on the vertical axis (Figure 10a). Indeed, for the predictable trajectory, detection probability was higher for targets presented in lower than the upper positions (post-hoc paired *t*-test upper versus lower for predictable trajectory: $p < .0001$) while, for the unpredictable trajectory, detection probability did not differ between upper and lower targets (post-hoc paired *t*-test upper versus lower targets for unpredictable trajectory: $p > .1$). Furthermore, lower targets showed higher detection probability for predictable than unpredictable trajectories (post-hoc paired *t*-test lower targets predictable versus unpredictable: $p = .006$). In agreement with this finding, psychophysical studies have shown a dominance of the lower visual field for motion processing of lower eccentricity targets (Fuller, Rodriguez, & Carrasco, 2008; Karim & Kojima, 2010; Levine & McAnany, 2005; Portin, Vanni, Virsu, & Hari, 1999; Thomas & Elias, 2011).

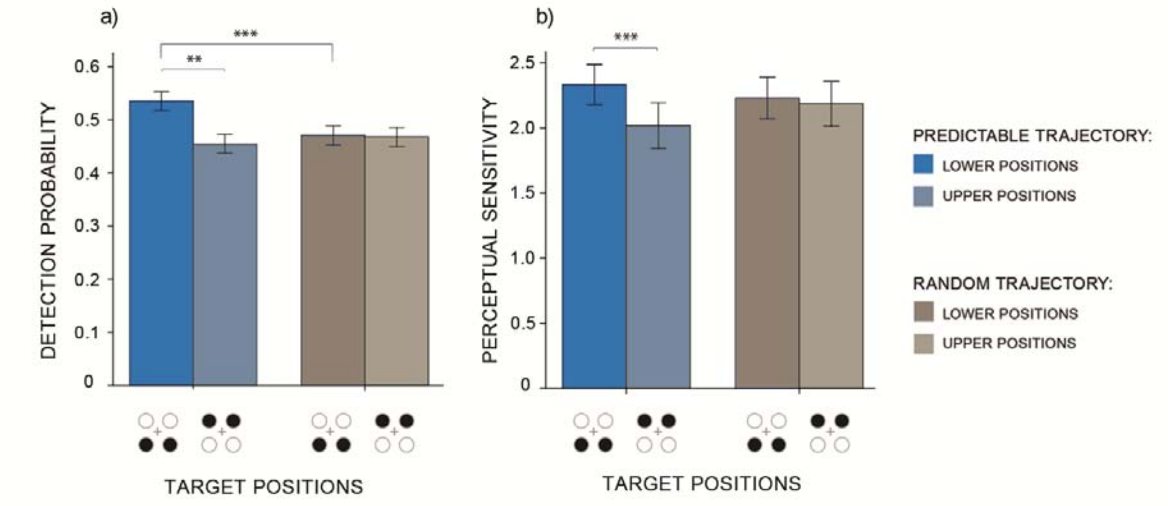


Figure 10. Detection probability **(a)** and perceptual sensitivity **(b)** (mean ± standard error) for predictable and random trajectories for upper and lower targets in Experiment 1. The predictive trajectory condition as compared to the unpredictable (random) condition led to higher detection probabilities, particularly for targets located in the lower visual field. This effect did not reach significance for perceptual sensitivity. ** $p < .01$, *** $p < .001$.

In order to explore the possibility of changes in response criterion, we used Signal Detection Theory to assess perceptual sensitivity and response bias. A repeated-measures ANOVA was performed on perceptual sensitivity with the same factors as the detection probability analysis. This analysis revealed main effects of target position on the vertical axis ($F(1, 9) = 9.93$, $p = .012$) and luminance ($F(2, 18) = 51.20$, $p < .0001$). Similarly to the results observed for detection probability, the interaction between luminance and target position on the vertical axis reached significance ($F(2, 18) = 4.67$, $p = .023$), indicating a difference in perceptual sensitivity between upper and lower targets for low luminance (post-hoc paired t-tests for upper versus lower targets for low: $p = .014$; mid luminance: $p > .1$; and high luminance: $p > .1$). Also similarly to probability, the interaction between target position on the vertical axis and trajectory also reached significance ($F(1, 9) = 22.18$, $p = .001$), indicating that the effect of trajectory depended on target position on the vertical axis (Figure 10b). Indeed, for the predictable trajectory, sensitivity was higher for targets presented in the lower than the upper positions (post-hoc paired *t*-test upper versus lower targets for predictable trajectory: $p < .0001$) while, for the unpredictable trajectory, perceptual sensitivity did not differ between upper and lower targets (post-hoc paired *t*-test upper versus lower targets for unpredictable trajectory: $p > .1$). Sensitivity scores for lower targets did not significantly differ across trajectories (post-hoc paired *t*-test for lower targets predictable versus random trajectory: $p > .1$). This difference did not reach significance for upper targets either (post-hoc paired *t*-test for upper targets predicable versus random trajectory: $p > .1$). The same repeated-measures ANOVA was performed for response bias (beta). Only a main effect of luminance reached significance ($F(2, 18) = 7.76$, $p = .004$).

In summary, detection probability was improved for targets displayed near the predicted trajectory of a moving object particularly in the lower visual field, while the effect diluted when using signal detection theory (i.e. taking into account false alarms).

Experiment 2: Forced-choice localization task

In order to explore how far ahead of the movement the facilitated area extended and whether perceptual facilitation occurred for forced-choice (‘awareness-independent’) tasks, we performed Experiment 2 in which more and higher eccentric target positions were tested. We hypothesized that facilitatory effects (i.e. lower RTs) would decrease with distance to moving object with a predictable trajectory.

Methods

Participants

Eight individuals (aged between 20 and 32 years old, 1 left-handed) took part in this experiment; the exact same conditions as in Experiment 1.

Apparatus and Stimuli

We used the same set up as in Experiment 1. The stimuli used were the same of Experiment 1, except for the following: (a) mean luminance was always high (4 cd/m^2) and the target was slightly bigger (1.2º visual angle); (b) there was only one trajectory condition (predictable): (c) a higher number of positions and higher eccentricity levels were tested (6x3 positions). In addition to the 4 positions tested in Experiment 1, 14 positions were added. These positions corresponded to 2 more positions above and below (6 total positions on the vertical axis) and one more column to the right (3 total positions in the horizontal axis) (Figure 11a).

Procedure

The procedure was the same as in Experiment 1, except for the following: (a) For each trial, the FP appeared at one of three possible positions (Figure 11b) (at the centre of the first, the second or the third column) and it indicated the column in which the target would appear. This was done to facilitate the task, given the increased difficulty of a high number of possible positions; (b) The target appeared in all trials, with equal probability in one of the 18 possible positions.

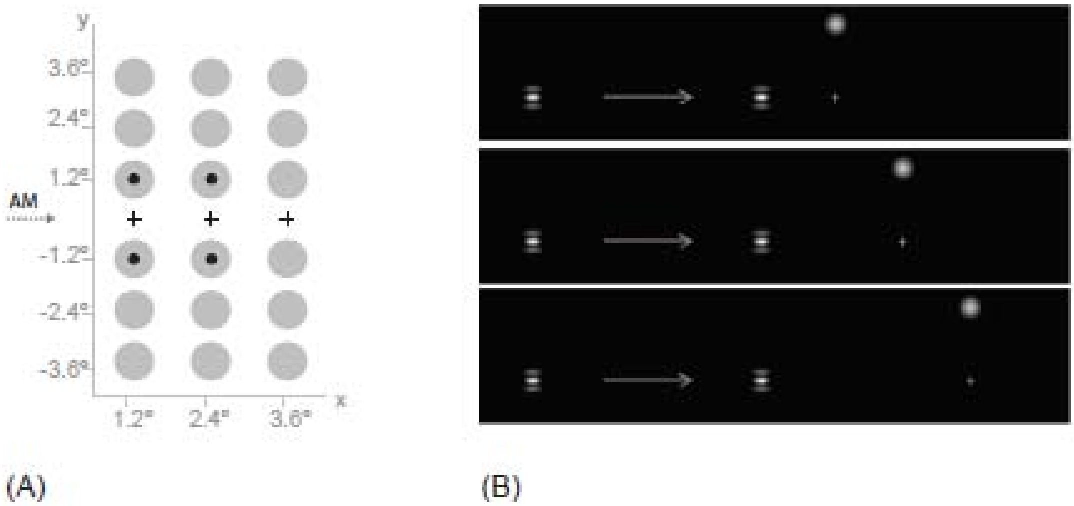


Figure 11. (a) Schematic representation of the 18 target positions in Experiment 2. The arrow indicates the moving trajectory in the predictable condition (left to right). Circles indicated with a black point in the middle correspond to the same positions used in Experiment 1. **(b)** Schematic representation of the three possible positions of the FP in Experiment 2. The position of the FP indicated, in each trial, the column where the target would subsequently be displayed.

Participants were instructed to fixate the FP along the trial. They were asked to indicate as fast and accurately as possible whether the target appeared above or below the FP by pressing the corresponding key on the keyboard. The experiment was divided in 2 blocks. In one block, participants responded by pressing with their right hand the key “P” for above and with their left hand the key “Z” for below. On the other one, they responded by pressing with their left hand the key “Q” for above and with their right hand the key “M” for below. The order of the two blocks was randomized across participants.

The experiment lasted about 30 minutes (20 practice trails included). Each target position was repeated 12 times, resulting in 216 trials performed in a randomized order.

Results and Discussion

Participants showed high levels of performance and error rates were less than 5% (we excluded errors from further analyses). RT above or below 3 standard deviations from the mean (mean ± SD: 322 ± 74 ms) were also excluded.

RT was subjected to a repeated-measures ANOVA with target position on the vertical axis (6 positions) and target position on the horizontal axis (3 positions) as within-participant factors. A main effect of target position on the horizontal axis reached significance ($F(1, 7) = 35.16$, $p = .001$), indicating a linear increase of RT from closest to furthest positions from the moving object ($F(1, 7) = 35.17$, $p = .001$).). These findings indicate that perceptual facilitation decreases with distance to the moving object. No other main effects of interactions were observed.

To further confirm that this effect was specific to the predictable trajectory, we performed a control experiment (5 participants aged between 20 and 41 years old) in which we tested the random trajectory condition used in Experiment 1. Again, error trials and RT above and below 3 standard deviations from the mean (*M* ± *SD*: 372±84 ms) were excluded from the analyses. RT was subjected to a repeated-measures ANOVA with target position on the vertical axis (6 positions) and target position on the horizontal axis (3 positions) as within-participant factors. No main effects or interactions reached significance. Thus, RT facilitation appeared to be specific for the predictable trajectory (Figure 12a).

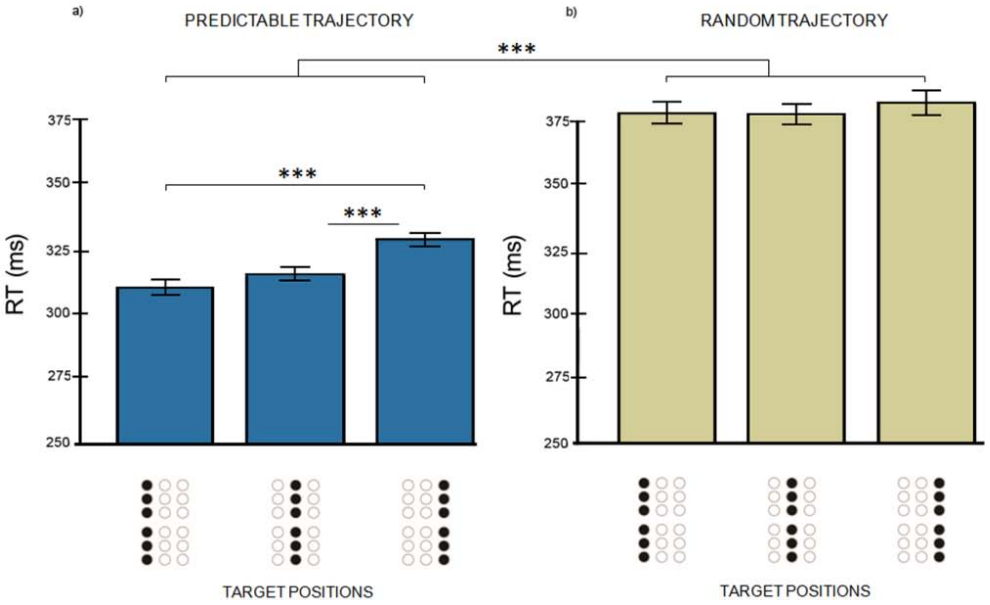


Figure 12. RT (mean ± standard error) for **(a)** predictable and **(b)** random trajectories along the horizontal axis (vertical columns) in Experiment 2 for the predictable and random conditions. The predictable trajectory of a moving object facilitated target localization decreasing RT. * $p < .05$, ** $p < .01$, *** $p < .001$.

To further prove this finding, we subjected all RT data to a repeated-measures ANOVA with target position on the vertical axis (6 positions) and target position on the horizontal axis (3 positions) as within-participant factors and trajectory (predictable and unpredictable) as a between-participant factor. A main effect of trajectory reached significance ($F(1, 11) = 7.38$, $p = .02$), indicating that RT for the random trajectory condition were higher than for the predictable trajectory condition, thus further showing that the latter facilitated perception (Figure 12b). A main effect of target position on the horizontal axis also reached significance ($F(2, 22) = 9.39$, $p = .001$). More importantly, the interaction between position in the horizontal axis and type of trajectory was also significant ($F(2, 22) = 4.53$, $p = .023$), indicating that only for the predictable trajectory RT depended on distance (planned comparisons paired *t*-tests for the predictable trajectory: first vs. second column: $p > .1$; first vs. third column: $p = .001$; second vs. third column: $p = .001$; planned comparisons paired *t*-

tests for the random trajectory: all $p > .1$). No other main effects or interactions reached significance.

These findings indicate that perceptual facilitation is specific to the predictable trajectory and decreases with distance.

Summary of results

These experiments were designed to provide our first behavioural evidence of spatial facilitation, i.e. perceptual facilitation in spatial positions near the predicted trajectory of a moving object. Our results support the hypothesis that a moving object affects perception in future positions near the predicted trajectory of motion. The facilitation could result from a preactivation of those visual cortex neurons coding for the regions of the space near the predicted trajectory, as a preparation of the system for processing subsequent input (Jancke et al., 2004; Maiche et al., 2007; Paradis et al., 2012; Yilmaz et al., 2007).

Findings from Experiment 1 showed higher detection probability for targets that were preceded by a predictable trajectory of a moving object as compared to those preceded by a random trajectory. This effect does not reach significance when taking into account false alarms using signal detection theory, suggesting that, although there is a significant increase in detection probability, there might also exist a non-significant effect in the false alarms preventing changes in perceptual sensitivity from reaching significance. Moreover, perceptual facilitation was observed only for targets located in the lower visual field, which is in agreement with some psychophysical findings that also reported dominance of the lower visual field for motion processing (Fuller et al., 2008; Karim & Kojima, 2010; Levine & McAnany, 2005; Portin et al., 1999; Thomas & Elias, 2011).

In Experiment 2, a moving object with a predictable trajectory also yielded perceptual facilitation assessed through RT. In this case, higher eccentricity positions were tested, and results showed that facilitation depends on the distance to the moving object: the further a target presented on the predicted trajectory of a moving object is the lower the effect. No differences were observed in the dimension perpendicular to the movement (vertical), indicating that eccentricity along this axis was enough to erase any difference between lower and upper visual fields but not enough for a decrease of the facilitatory effect with eccentricity to be observed. Importantly, RTs for the random trajectory condition were significantly higher and did not show any difference along this axis.

The spatial facilitation reported here may reflect specific anisotropic cortical preactivation produced by motion (Kaplan et al., 2013). In the random (unpredictable) trajectory, neighbouring neurons may have been more diffusely preactivated, which may have led to a weaker non-significant facilitation. The observed effect along the direction of the movement in Experiment 2 supports the hypothesis that this facilitation mechanism may be implemented by long-range cortical horizontal connections that spread subthreshold activation and lead to the preactivation of neurons at future positions along the path of motion (Jancke et al., 2004; Nijhawan, 2008; Paradis et al., 2012; Yilmaz et al., 2007). Our results also allowed us to roughly estimate the size of the facilitated window. It seems clear that this facilitation window depends mostly on the horizontal dimension, with RTs increasing linearly along this axis. Our findings are in agreement with those of Roach and colleagues (2011), who observed facilitation for targets located at the leading edge of motion. Our conclusions also find support in neurophysiological data showing faster processing for moving stimuli that may be caused by the subthreshold activation of neurons at positions further along the motion trajectory (Jancke et al., 2004; Jancke & Erlhagen, 2010; Maus, et al., 2013).

Notwithstanding, the present preliminary work had a series of limitations which we tried to overcome in the next set of experiments in Chapter 3.2. In the next series of experiments we will test one target that is located at the same axis as the trajectory.

3.2. Empirical work: Motion stimuli parameters and spatial facilitation

Abstract

In the preliminary empirical work formerly presented we found psychophysical evidence for spatial facilitation: targets where more often perceived and with lower reaction times (RTs) if preceded by nearby predictable motion (Experiments 1 and 2). However, targets were not displayed in the same horizontal axis as motion. Therefore, we designed a series of experiments, fully described in this section, in which one target was displayed in the subsequent position after motion and another target was displayed at a distant position. Gabor patches moved along different linear trajectories toward one of two static targets, according to the constant stimuli method. The Gabor carriers were oriented parallel to the direction of motion, as in Experiments 1 and 2. The present study aimed to test whether spatial facilitation varied with the contrast, distance, orientation, number and length of motion trajectories. Our results showed that the target presented next to the leading edge of motion was perceived earlier and as brighter compared to the target displayed in a distant location (Experiments 3 and 4). Moreover, the facilitatory effect was also observed for all the (motion - target) distances tested (Experiment 6). We also observed that by increasing contrast temporal facilitation was enhanced (Experiment 7). On the contrary to the expected, short trajectories (Experiments 8 and 9) and trajectories with Gabor carrier orientation orthogonal to the trajectory (Experiment 5) induced a facilitatory effect as well. To be ascertain that such facilitatory effect is specific of motion stimuli, we tested whether the presence of static Gabor patches next to the location of the subsequent target would also facilitated target detection (Experiment 10). Indeed, presentation of static Gabor patches did not yield a significant facilitatory effect indicating that the effect is specific to moving objects. In conclusion, our data showed that a target located next to the leading edge of a moving object is perceived

earlier and as brighter than a target located in a distant position. These findings may be related to horizontal connections, which are thought to be responsible for a fast and enhanced spreading activity of neighbouring neurons preactivating neurons at future positions of the moving object.

General Methods

We used the same methodology in the following 8 experiments (i.e. Experiments 3-10), and thus, we will not enter into details in each experiment regarding the method. If there are differences they will be detailed in each experiment.

Participants:

All individuals participated voluntarily in these experiments and signed the consent form. They all reported normal or corrected-to-normal visual acuity and did not receive any economic compensation for their participation. Experiments were conducted with the approval of the local Ethics committee of the University of the Republic (Uruguay) in accordance with the 2008 Declaration of Helsinki.

Apparatus and Stimuli

All stimuli were presented on a CRT monitor (resolution: 1920 x 1080, refresh rate: 60 Hz). All the experiments were programmed using MATLAB with Psychtoolbox (Brainard, 1997; Pelli, 1997) for stimuli presentation and data collection. Analysis were computed using R studio software (RStudio Team, 2015) and lme4 package (Bates, Maechler, & Bolker., 2011).

Stimuli

Motion stimuli were composed by a Gabor patch presented during 16 frames (total duration: 0.267 sec) along a path of 9° visual angle, with a speed of ~23°/sec. Motion was presented for brief periods of time duration to ensure that participants would not have enough time to track the trajectory with smooth pursuit when the object starts to move. The moving object (Gabor patch) was a grayscale luminance modulations around the mean luminance of the screen (grey screen with mean luminance of 38 cd/m²). It consisted of a Gabor patch with a profile described by the following equation:

$$\mathbf{G}(x, y) = c\_\exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right)\_|\cos\left(\frac{\pi\_y}{\sigma\_\sqrt{2}}\right)|$$

where *c* is a contrast constant and σ is the space constant of the Gaussian envelope. The spatial frequency of the Gabor patch was 0.35 cpd, *c*= 0.97, with 3 % Michelson contrast, σ= 0.12 degrees and 0.57º visual angle of diameter. Gabor carrier orientation was always horizontal. Trajectories were composed by a Gabor patch with carrier orientation parallel to the trajectory (i.e. coaligned Gabor). Gabor moved during 16 frames and stopped at 0.57º of visual angle to the right, left or below the fixation point (FP).

In order to test whether detection is facilitated in the area next to the leading edge of coaligned moving objects, we presented a target in that location – nearby target – and another target further away - distant target. Both targets were equal and consisted of a Gaussian profile (σ= 0.12 degrees) with 11% Michelson contrast and a size of 0.57º visual angle and appeared on the screen for just one frame (~17 ms) (see Figure 13).

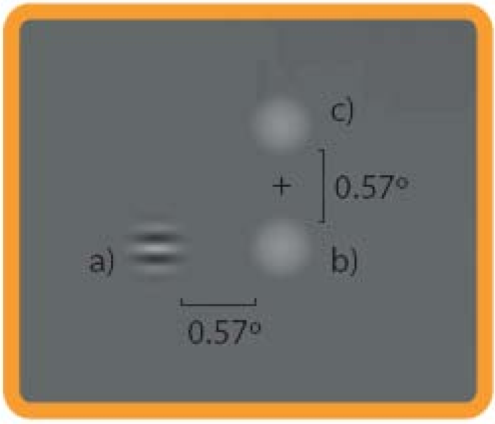


Figure 13. Stimuli distance and size in visual angles. Motion was composed by **(a)** Gabor patch that stopped at 0.57º visual angle to the left of the **(b)** subsequent nearby target. The fixation point ("+" sign) was located between the nearby target and the **(c)** distant target. All stimuli had the same size of 0.57º visual angle. Note that additional moving objects may be presented moving right to left and/or upwards and stopping at 0.57º visual angle to the right or below the nearby target.

Design and Procedure:

Four conditions were tested in **Experiments 3, 4 and 5**: (a) One motion trajectory. In half of the trials the moving object followed the left-to-right trajectory and in the other half the moving object followed the right-to-left trajectory; (b) Two motion trajectories. One object followed left-to-right and the other right-to-left trajectories; (c) Three motion trajectories. In addition to the two objects presented in the previous conditions, a third object moved upwards; (d) Baseline condition; no moving objects were presented. The objects moved from periphery to centre (conditions: a, b and c).

The same design was employed in **Experiment 10** but with static Gabor patches.

For **Experiments 6, 7, 8 and 9** objects always moved across three motion trajectories - the previous condition (c) - to further explore other variables.

All the experiments were equal regarding the constant stimuli method (except Experiment 4):

After motion offset, target could appear according to the constant stimuli method. The distant target (standard stimulus) always appeared 3 frames (~50 milliseconds) after motion offset. On the other hand, the nearby target (comparison stimulus) could appear at 6 possible onset times: 1 (~16.67 ms), 2 (~33.34 ms), 3 (~50 ms; the same as the distant target), 4 (~67.17 ms), 5 (~83.34 ms) and 6 (~100 ms) frames after motion object offset (see Figure 14). Pilot data indicated that participants reported more often the target moving up (i.e. they saw the nearby target earlier regarding the distant). So, to equilibrate probability of Yes/No responses we added a sixth frame (~100 ms); so the nearby target could appear (~50 ms) after the distant target. By doing this we were able to compensate the strong illusion due to movement, which produced more often the perception of the target moving upwards.

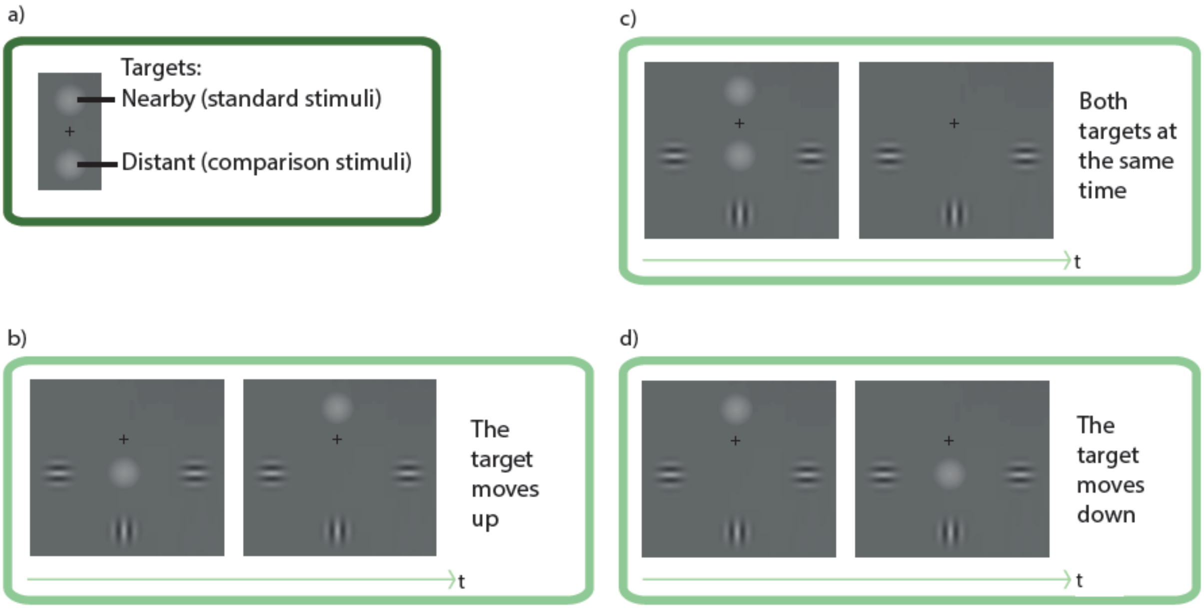


Figure 14. Conditions according to the constant stimuli method. **(a)** Target classification by location (nearby or distant). Onset times after motion object offset were the following: **(b)** the nearby target appeared first (17 or 30 ms) and the distant after (50 ms); **(c)** the nearby and distant targets appeared at the same time (50 ms); **(d)** the distant target appeared first (50 ms) and the nearby after (67, 83 or 100 ms). Note that Gabor and fixation point are shown for simplification, because they were never presented on the screen at the same time as targets.

A within-subjects design was employed for **all the experiments**. Before starting each experiment, participants were habituated to the dark room and a training block was performed (or several, according to their psychophysical performance). Each experiment consisted in two separate sessions with three randomized blocks between which participants were allowed to take a short break. They were seated 114 cm away from the screen in a dark room with their heads placed on a chinrest to restrict head movement. Each trial started with a grey screen during 1200-2000 ms (see Figure 15 for a single-trial example). Then, the fixation point ("+" sign) appeared on the screen and one, two or three Gabor started to move from periphery-to-centre (duration: 16 frames; see section Apparatus and stimuli). Then, the Gabor patches and the fixation point disappeared and the targets (nearby and distant) were displayed during 1 frame (~17 ms) at varying onset times according to the constant stimuli method (Figure 14).

After target's offset, participants were asked to report, as fast and as accurately as possible, whether they saw the target moving down by pressing the corresponding key (S for "Yes" and N for "No") on a keyboard. The total number of trials was 528, including 22 trials per condition (6 nearby target onset times x 4 moving object conditions). The order of trials was randomized across participants.

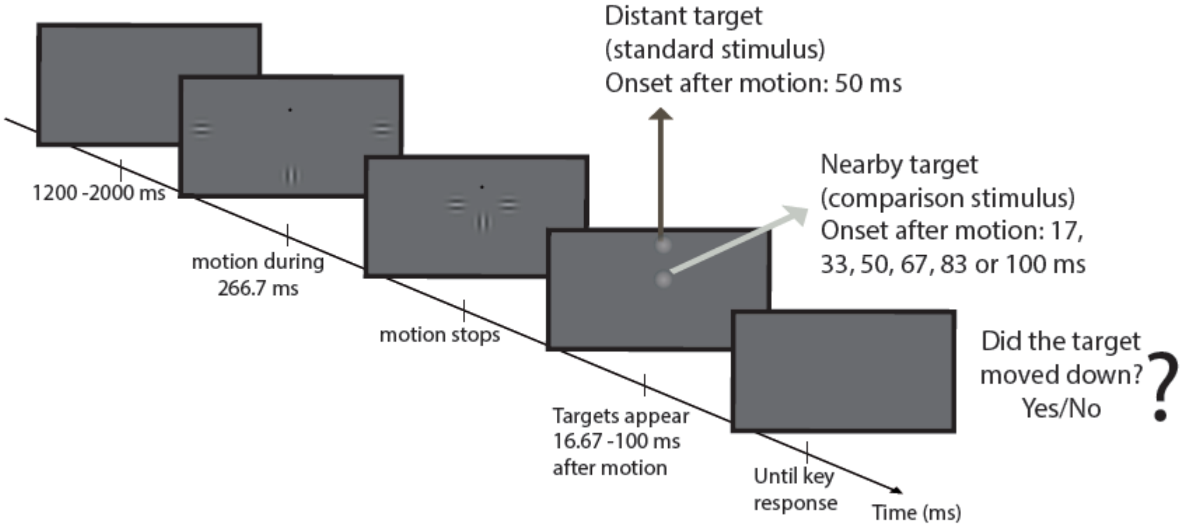


Figure 15. Example of a single trial for three motion trajectories. Collinear moving Gabor patches moved during 267 ms and 17 or 30 or 50 ms after, the target appeared on the screen, according to the constant method stimuli. Participants were asked to indicate as fast as possible if the target moved down (yes/no).

General Analyses

The same type of analysis was conducted in the following 8 experiments, i.e. Experiment 3 to 10. Responses for each participant in each experimental condition were fitted by a Maximum likelihood estimation using the following function:

$$P(Yj = 1) = \frac{1}{1 + e^{-(\beta + \alpha x)}}$$

In each trial, j, if the response variable (Y_j) had the value 1 it indicates that the participant responded “target moved down” and on the contrary, the value 0 indicates that participants responded “target moved up”. The parameter χ indicates the target onset time. We analysed the data of all participants with a Generalized Linear Mixed Model (GLMM), using the lmer function of R package lme4 (Bates et al., 2011). This hierarchical model extends the psychometric function to the group level with the advantage of variance estimation of the distribution and so, the effect it is not due to a specific participant (Lacquaniti et al., 2014; Moscatelli, Mezzetti, & Lacquaniti, 2012). Participants’ factor was modelled as a random effect on slopes and intercepts whereas conditions were estimated as fixed effects in the GLMM model. We analysed if these variables could be considered numerical by using a likelihood ratio test. The saturated model was used for all the experiments when significantly lower Akike Information Criterion (AIC) values were observed in order to perform the following factor analyses and bootstrap. Moreover, we used the Wald test to analyse if the fixed effect (conditions tested) significantly varied the slopes and intercepts of participants’ psychometric curves.

We evaluated the probability of responses to address our main research question, i.e. whether motion induced facilitatory effects in targets detection. To this end, we estimated the Point of Subjective Equality (PSE), i.e., the value of the comparison stimulus (nearby target), for a probability of 0.5 ($PSE= -\beta/\alpha$) with 95% confidence intervals (CI). The distribution of the difference in PSEs was estimated by using a semi-parametric bootstrap procedure to estimate variance of the parameters (sampled data sets = 2000) (Moscatelli et al., 2012). PSEs values represents the onset time of the nearby target (comparison stimulus) that it is perceived as equal to the onset time of the distant target (standard stimulus). Then, if PSE was higher than the value of the distant target (standard stimulus) it indicates that participants perceived before the nearby target (comparison stimulus) than the distant target and psychometric curves would be shifted to the right. In the case that motion did not influence detection of nearby target onset time, psychometric curves should be centred at the 50 ms point. Experiment 4 was slightly different and tested brightness perception instead of onset times as it will be specified in Experiment 4, however analysis were exactly the same.

After the bootstrap, we analysed temporal facilitation (ΔPSE = PSE – standard stimulus). We will refer as temporal facilitation to this facilitatory effect because the nearby target onset is perceived earlier (only in Experiment 4 was different). Nevertheless, the effect is spatial given that facilitation occurs at a specific spatial location (next to the leading edge of motion).

We expected that motion conditions would be capable of inducing a facilitatory effect. In this regard, temporal facilitation should be significantly above 0 and the confidence interval should not contain a 0 value. Moreover, differences across conditions were also analysed. Although this type of methodology analysis does not usually use p-values, we decide to include it in this doctoral dissertation. In addition, we also corrected p-values for multiple comparisons using the Benjamini-Hochberg correction method. We assumed a standard normal distribution and so, the t statistic was treated as if it were a z statistic.

Experiment 3: Number of trajectories

The current experiment tests the hypothesis that by increasing the number of trajectories it should increase temporal facilitation as well.

Methods

Participants:

Seven participants (1 author and 6 naïve), aged between 20 and 34 years old.

Independent variable

The number of motion trajectories: 0,1, 2 and 3.

Results and Discussion

Individual psychometric curves corresponding to 0, 1, 2 and 3 moving objects were fitted using the GLMM model (AIC = 469) and are represented in Figure 16. Psychometric curves corresponding to the conditions with motion trajectories appear shifted to the right as compared to the baseline curve (0 moving objects). This indicates that participants perceived the nearby target onset earlier for motion trajectories conditions regarding the baseline condition, which implies that moving objects facilitated onset detection. Average of all data and of PSEs values are shown in Figure 17. For instance, when three moving objects preceded the onset of the nearby target, PSE mean was 65 ms. This indicates that the nearby target was seen 15 ms before than the distant target (50 ms).

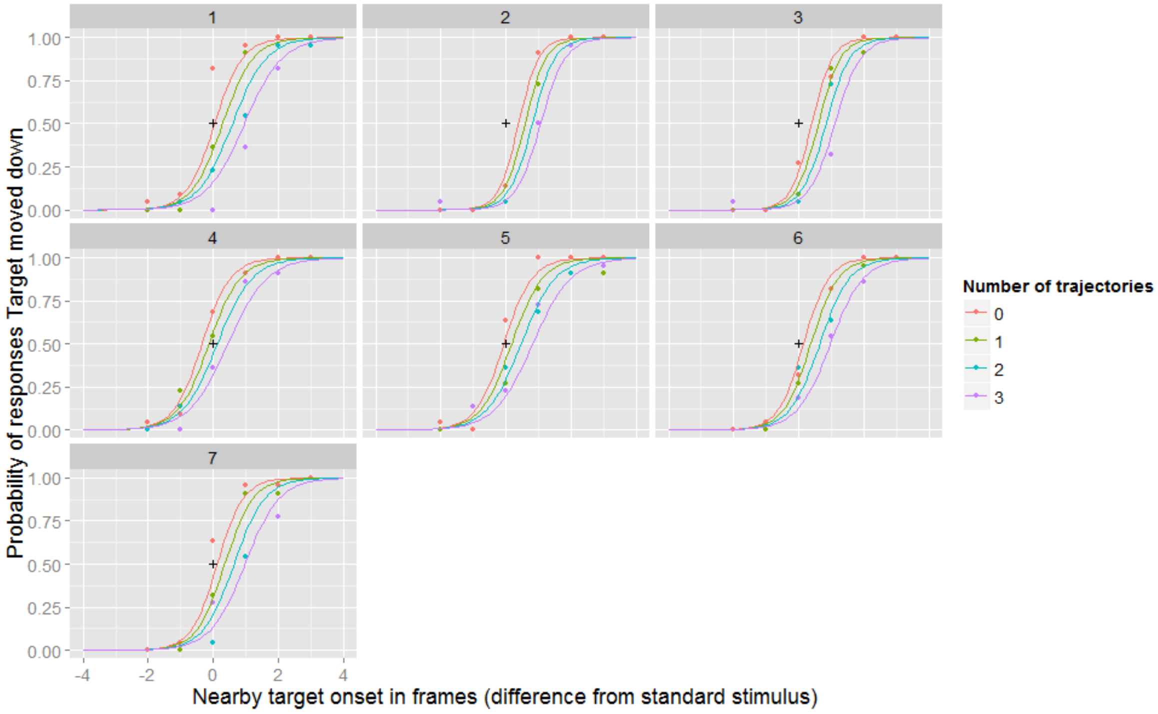


Figure 16. Probability of responses "Target moved down" as a function of target onset time in frames. For the condition with three motion trajectories all participants perceived the target moving up more often. On the contrary, in the baseline condition participants tended to be accurate and to respond that the target moved down or up 50% of the time. The black "+" sign indicates the theoretical PSE.

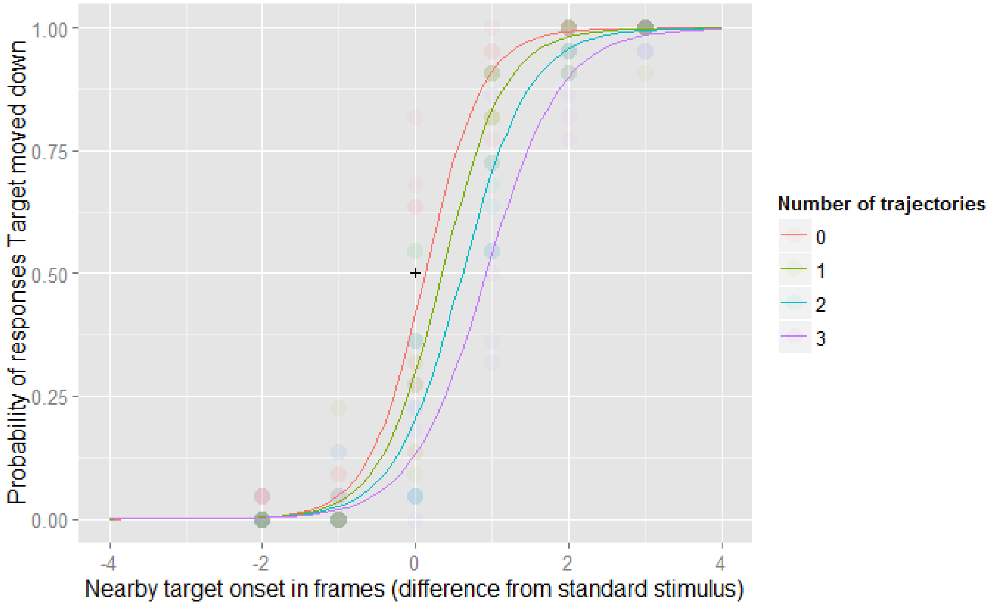


Figure 17. Averaged probability of responses "Target moved down" as a function of the onset time in frames. On the right, PSEs in ms according to the number of moving objects. All conditions with motion trajectories (green, blue and purple curves) were shifted to the right with regards to the psychometric curve for the baseline condition (red), which was centred in

the theoretical PSE ("+" sign) revealing that participants accurately perceived the target onset time. For example, in the condition with three trajectories, when both targets were presented at the same time, in average, participants perceived the nearby target 15 ms before, and as a consequence, they saw the target moving up.

To test the hypothesis that the nearby target onset time detection would vary as a function of motion trajectories, the GMML model was applied as indicated in the "General Methods" section, revealing that the fixed factor "number of motion trajectories" was significant (Wald test, *p* <.001). Then, we applied a bootstrap procedure with 95% CI to estimate PSEs variance (see Figure 18). For simplification we analysed whether temporal facilitation (PSE minus standard stimulus) was significantly different across conditions as well as whether each condition was significantly different from 0. Indeed, temporal facilitation was significantly above 0 for all the conditions with motion trajectories. Temporal facilitation for three motion trajectories was equal to 15 ms, 95% CI ranging from 13.8 to 16.8 ms, *p* <.001; for two motion trajectories was equal to 10 ms, 95% CI ranging from 8.6 to 11.6 ms, *p* <.001; for one motion trajectories was equal to 6 ms, 95% CI ranging from 4.1 to 7.2 ms, *p* <.001 and finally, baseline was equal to 2 ms, 95% CI ranging from 0.3 to 3.7 ms, *p* >.05.

Temporal facilitation was enhanced by as much as 15 ms. Moreover, two and three motion trajectories were significantly different from the baseline condition (*ps* <.001). Additionally, three motion trajectories were significantly different from two motion trajectories (*p* <.032) and from one motion trajectory (*p* <.001).

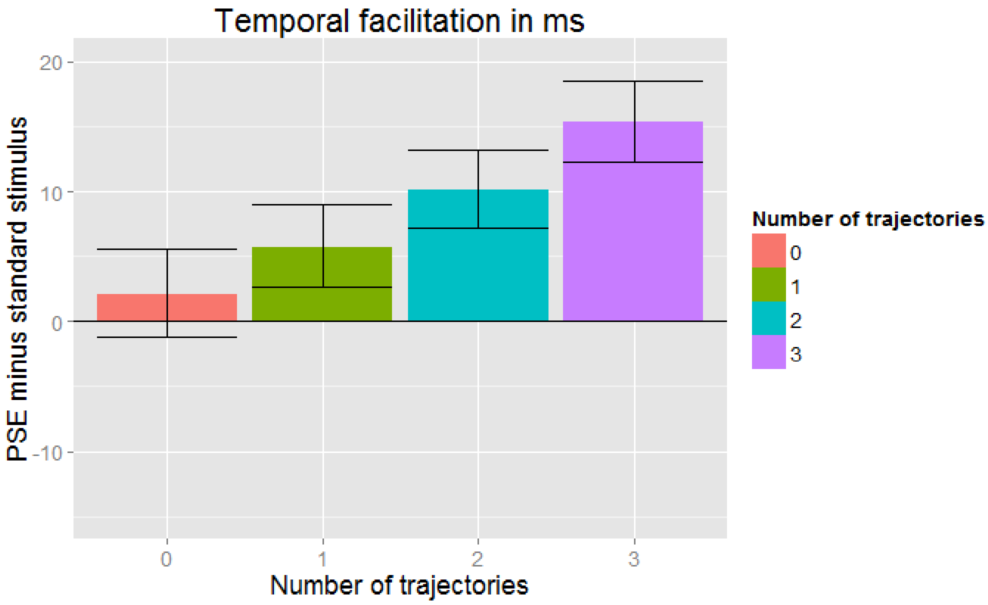


Figure 18. Temporal Facilitation + 95% CI in ms for Experiment 3. The onset of the nearby target was perceived earlier in all the conditions with motion trajectories. A greater facilitation was observed for the condition with three motion trajectories.

Results bring evidence that coaligned moving Gabor patches (oriented parallel to the trajectory) generated a temporal facilitation at the position next to the leading edge of motion in agreement with previous findings reporting enhanced detection at the leading edge of motion (Experiment 2; Roach et al., 2011. Remarkably, temporal facilitation increased with the number of trajectories, such that visual processing was faster when more moving objects were observed, which may be related to the hypothesis that long range-horizontal connections mediate neural latency (Georges et al., 2002; Jancke et al., 2004; Paradis et al., 2012).

Experiment 4: Perceived Brightness

Taking into consideration the results of Experiments 3, it may be possible that perceptual facilitation increases temporal detection as increases brightness perception if the target is preceded by coaligned moving Gabor patches. It is known that horizontal connections might also provide the subtract for a higher perceived brightness to an object when preceded by other stimuli (Rossi et al., 1996). In the current experiment, we decide to test the hypothesis if facilitation would also increase perceptual saliency of the nearby target preceded by motion trajectories. This would able us to gather more information about the mechanism of such facilitatory effect at the leading edge of motion.

Methods

Participants:

Five participants (1 author and 4 naïve), aged between 20 and 32 years old.

Apparatus and Stimuli

Apparatus and stimuli were identical to "General Methods" section, except target contrast that varied across trials. The distant target (standard stimulus) had always the same Michelson contrast of 11.1% whereas the nearby target (comparison stimuli) could varied in five contrast levels (8.3%, 9.9%, 11%, 12.3% or 13.8% Michelson contrast). The values used were tested in pilot experiments to ensure an appropriate level of task difficulty.

Independent variable

The number of motion trajectories: 0,1, 2 and 3.

Design and Procedure:

The same within-participants design and the constant stimuli method were employed as detailed in the "General Methods" section, except for the (a) target onset time was fixed (50 ms); (b) target contrast varied in five levels and (c) question at the end of the trial: "Is the top target less bright?" (see Figure 19).

Participants were instructed to answer a different question from the previous experiments, which was: *"Was the top target less bright?"* and to indicate Yes ("s") or No ("n"), as quickly as they could.

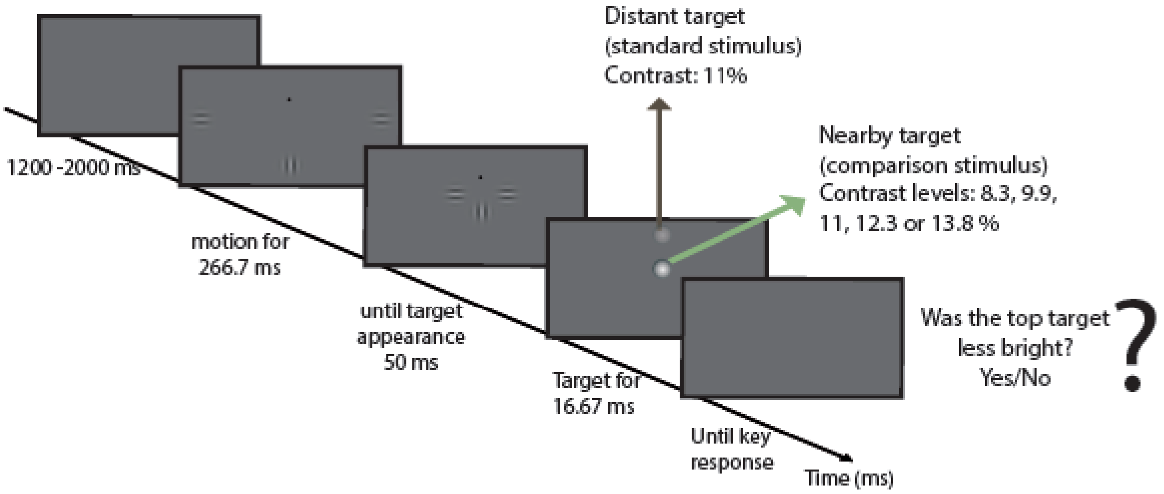


Figure 19. Example of a single trial in Experiment 4. A trial started with a blank screen and then, Gabor patches started to move (in the exact same conditions as in Experiment 3). After the offset of motion, both targets appeared during 17 ms, and participants had to respond as fast as they could whether the distant (top) target was less bright as compared to the nearby target (yes or no).

Results and Discussion

Four psychometric curves were fitted using the GLMM model (AIC = 397) for each participant (Figure 20) and average of probability of responses “top target less bright” for each condition is represented in Figure 21. In the case that motion did not influence perceived brightness of the nearby target, psychometric curves should be centred at the theoretical PSE point. However, if motion facilitated perceived brightness of the nearby target, we should observe a leftward shift of psychometric functions. Moreover, we should find a higher leftward shift as a function of the number of trajectories. It can be observed that psychometric curves are displaced to the left regarding the theoretical 11% Michelson contrast level (the value of standard stimulus). In this case, curves leftward displacement indicates that participants responded more often that the nearby target was brighter if preceded by motion trajectories.

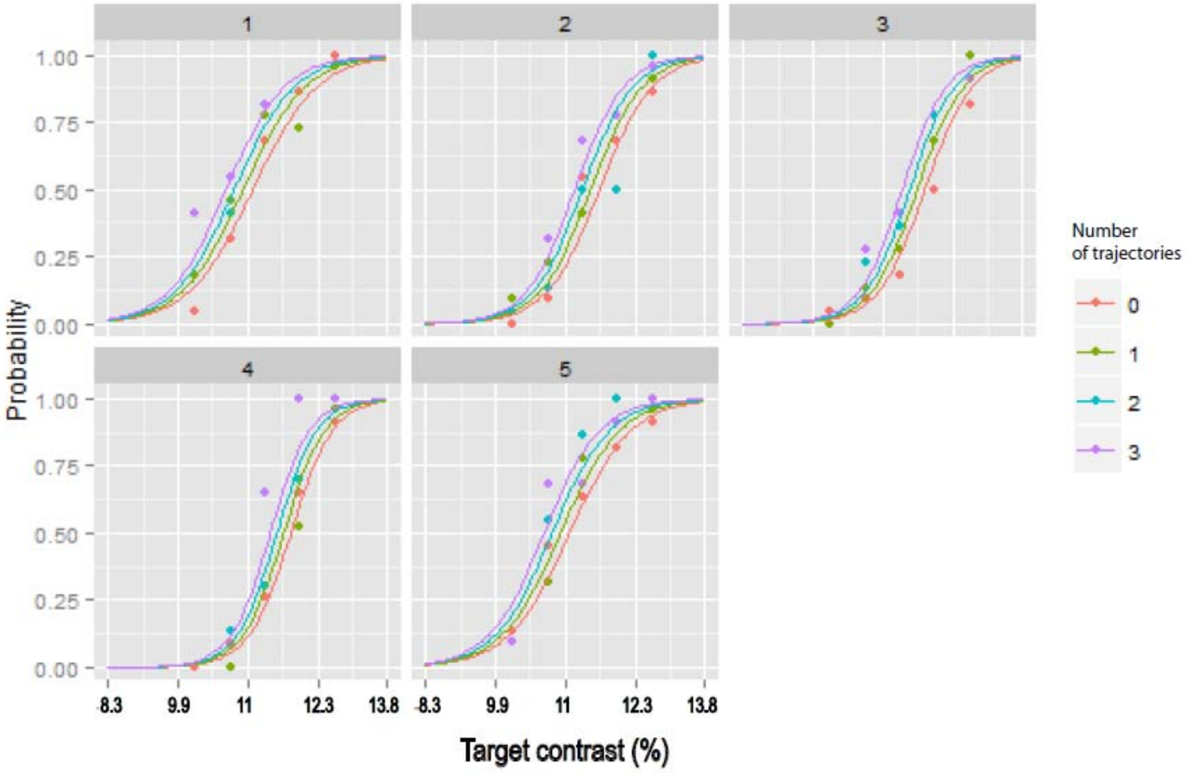


Figure 20. Probability of responses “top target less bright” for Experiment 4 as a function of nearby target contrast (Michelson contrast in %). Almost all of the participants perceived the nearby target as brighter when preceded by three and two motion trajectories (curves are shifted to the left), whereas they perceived the nearby target as dimmer in the baseline condition (red psychometric curve).

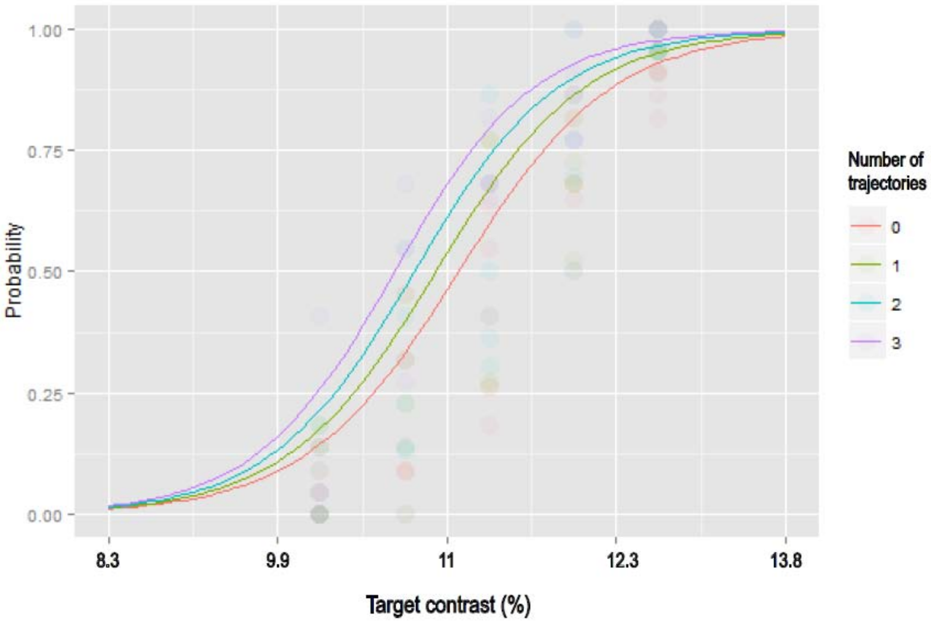


Figure 21. Average of probability of responses “top target less bright” for Experiment 4 as a function of target nearby contrast. The psychometric curve for three and two motion trajectories are shifted leftwards which means that the nearby target was perceived as brighter

compared to the distant target. On the other hand, it seemed that for baseline condition (no motion), the nearby target was perceived as dimmer, and the curve is shifted rightward.

The number of trajectories significantly influenced participants responses (GLMM model, Wald test, $p < 0.001$). Then, we applied a bootstrap procedure to test if PSEs variance at 95% CI were significantly different across conditions. We analyse brightness facilitation (PSE minus standard stimulus) to test if conditions were significantly different from 0 (0= no brightness facilitation). In fact, two and three motion trajectories significantly improved perceived brightness of the nearby target (three trajectories: *TF* =3.6%, *CI* = [1.6 – 5.7] %, $p < .001$; and two trajectories: *TF* = 2.5 %, *CI* = [0.5 – 4.7] %, $p < .001$). Moreover the condition with three motion trajectories significantly differed from baseline (one trajectory: *TF* = 1.5%, *CI* = [-0.5 – 3.7] %; and baseline *TF* = 0.5%, *CI* = [1.6 - 2.9] %, $p = .48$. No other significant effects were observed. Hence, individuals perceived the nearby stimulus (comparison stimulus) as brighter compared to the distant target (standard stimulus) when preceded by two and three motion trajectories (Figure 22).

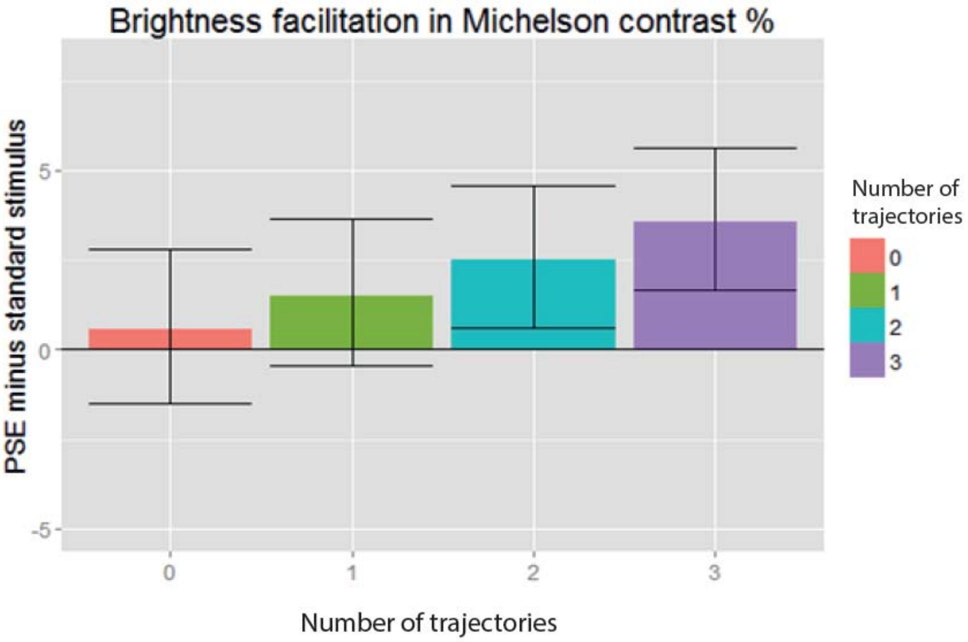


Figure 22. Brightness facilitation (BF + 95% CI) for the nearby target as a function of the number of motion trajectories (bootstrap with 2000 samples). For the condition with three and two motion trajectories participants perceived the nearby target as brighter compared to baseline condition.

Our results are in agreement with our previous findings in Chapter 3.1 that showed facilitatory effects as well. Other studies revealed lower detection threshold for objects located in the leading edge of motion (eg., Roach et al., 2011) which may be related to the perceptual effect found here. Therefore brightness perception is affect by the presence of previously displayed stimuli which underlie horizontal connections spreading of activation along adjacent neurons (Rossi et al., 1996). Moreover, perceptual saliency of a stimulus can be enhanced if located at the leading edge of at least more than one trajectory. This implies that the facilitation observed in this paradigm is not limited to the temporal domain, instead, it increases saliency of a stimulus as well enhancing its brightness perception.

Experiment 5: Orientation

Gabor carrier orientation parallel to the trajectory has been argued to induce a faster propagating of information through horizontal connections (Georges et al., 2002; Paradis et al., 2012). Based on this assumption, we decided to test Gabor carrier orientation orthogonal to the trajectory, in Experiment 5, to observe it the effect would decrease.

Methods

Participants:

Five participants (1 author and 4 naïves) aged between 22 and 30 years old.

Independent variable

In Experiment 5, in which we manipulated Gabor carrier orientation we used Gabor carriers oriented orthogonal to trajectories (i.e. non-coaligned) of 0, 1, 2 or 3.

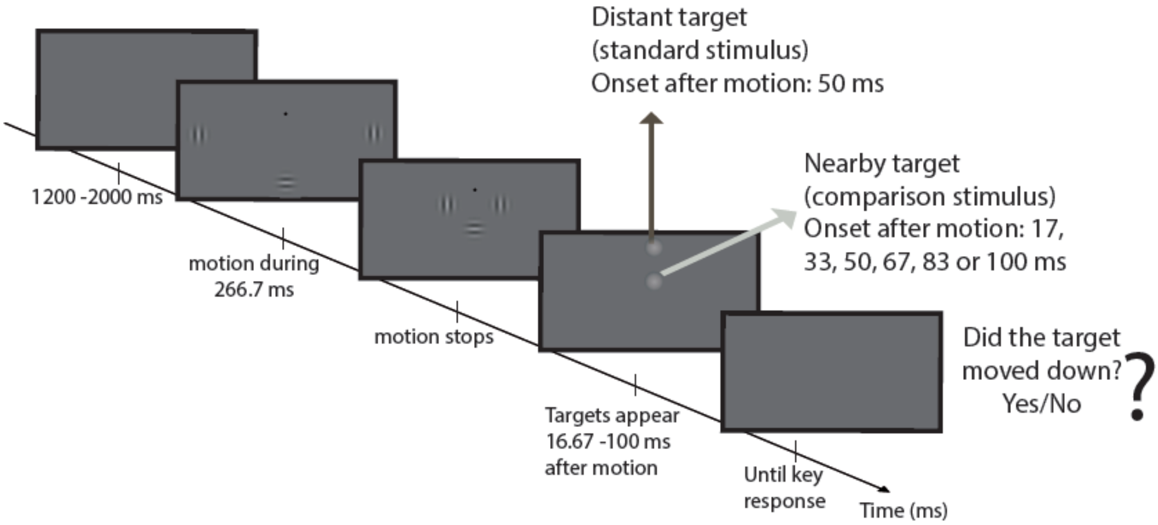


Figure 23. Single-trial example for Experiment 5. Moving Gabor patches were orthogonal to the trajectory. All the rest was equal to Experiment 3.

Results and Discussion

Individual psychometric functions fitted accordingly with the GMML model (AIC = 525) (see “General Analysis” section in this Chapter) are presented in Figure 24. Averaged psychometric functions and PSEs are shown in Figure 25. The purple psychometric curve for three non-collinear moving objects is shifted to the right, which means that participants perceived the target in an average of 11 ms seconds before its onset time (50 ms). On the contrary, the control condition represented by the red curve was centred at the theoretical PSE point ("+" sign), which indicates that participants accurately perceived the onset of the nearby target in time.

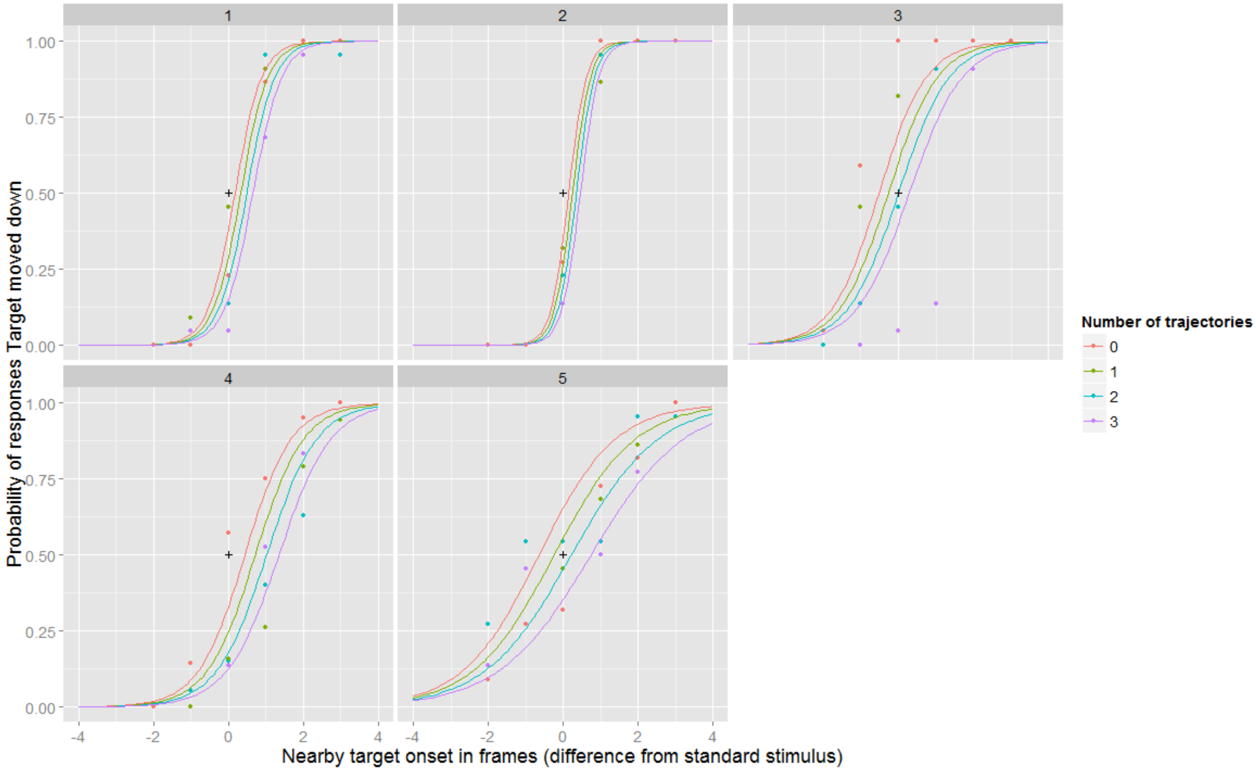


Figure 24. Probability of responses "Target moved down" for Experiment 5 as a function of the target onset time. Almost all participants accurately perceived the onset of the nearby target in the baseline condition, whereas in conditions with two or three non-collinear trajectories almost all participants perceived the onset earlier.

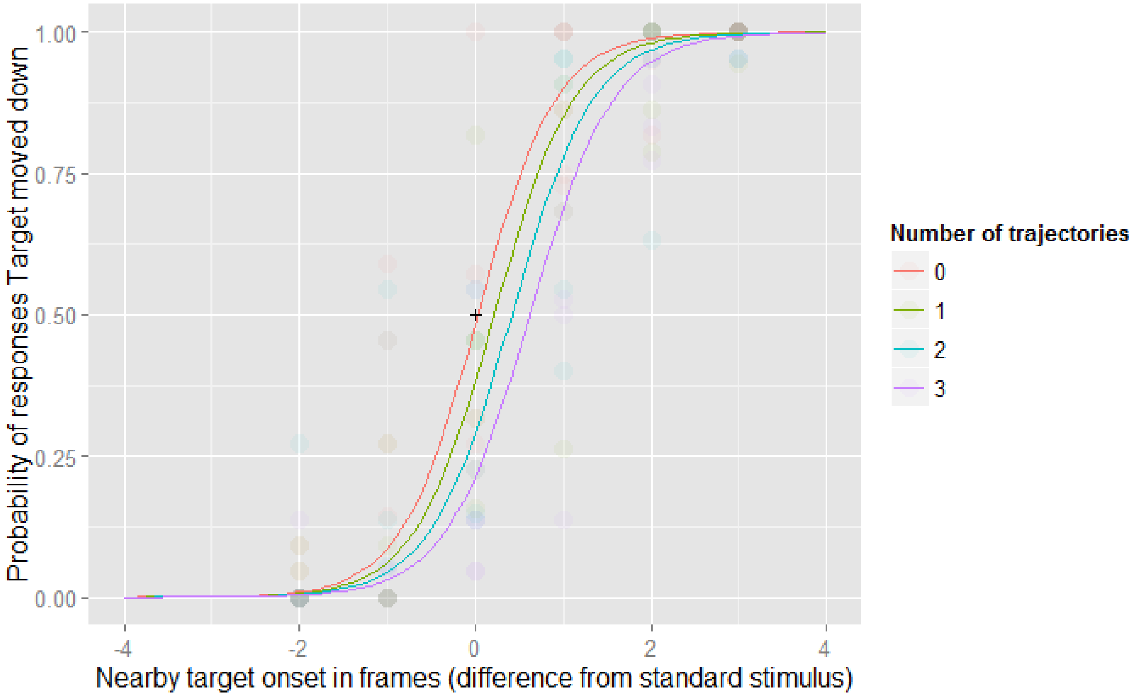


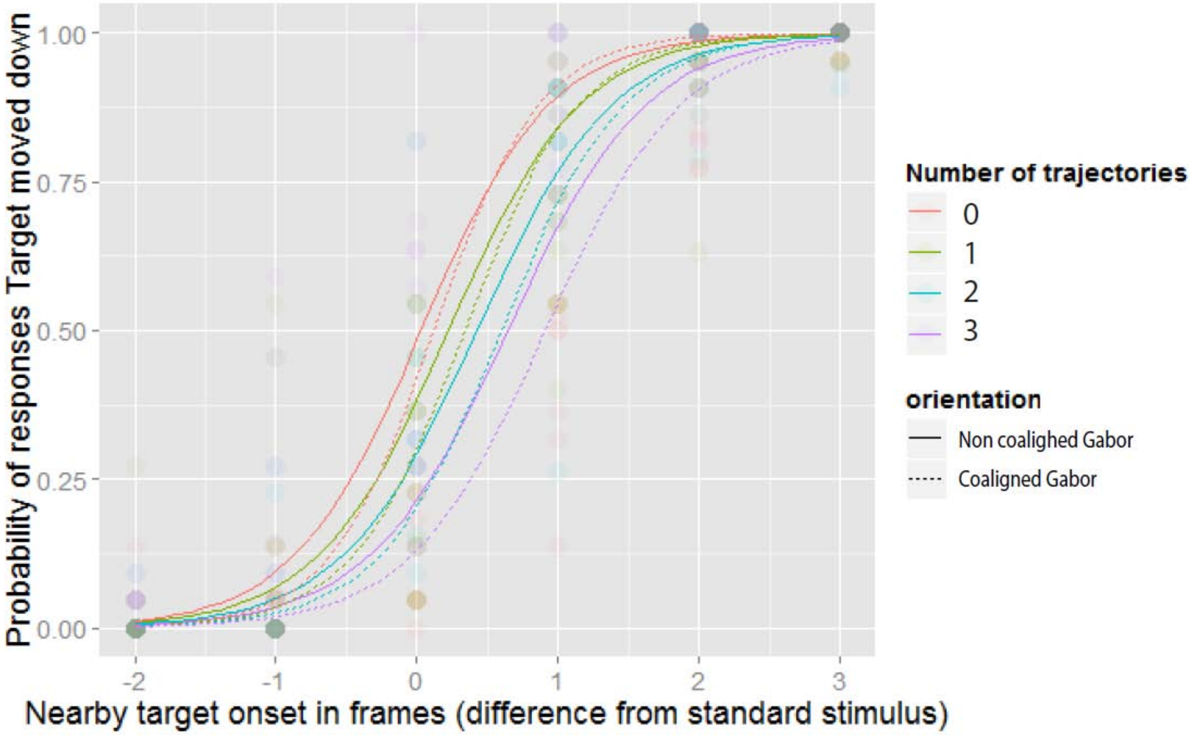
Figure 25. Average of probability of responses "Target moved down" for Experiment 5 as a function of the nearby target onset time regarding the distant stimulus onset time. Psychometric curves representing the conditions with motion stimuli are displaced to the right regarding the red psychometric curve corresponding to baseline condition.

Participants responses varied significantly with the number of trajectories (Wald test, $p = 0.29$). After the bootstrap with 2000 samples we analysed whether temporal facilitation (TF: PSE minus standard stimulus) was significantly above 0 for each condition and significantly different across conditions. TF was significantly different from 0 for the condition with three trajectories ($TF = 10.4$ ms, $CI = [3.8 – 16.2]$ %, $p < 0.001$; and two trajectories ($TF = 5.9$ ms $CI = [2.2 – 11.5]$ %, $p = 0.02$) while such significance was not found for the other conditions (see Figure 25). However, non coaligned (1, 2 or 3) motion trajectories were not significantly different from baseline condition.

In order to compare if orientation significantly influenced temporal facilitation we used the same GMML model and bootstrap samples to compare Experiments 3 and 5. However, we must be cautious in this comparison as the experiments were between-participants. For this reason, we also conducted a repeated measure ANOVA with the number of objects as within-factor and Orientation (coaligned and non-coaligned moving objects) as between-participants factor. Results revealed that the number of trajectories influenced the perceived onset significantly ($F(3, 27) = 9.8$, $p<.001$, $\eta^2_p = .52$) and TF increased linearly with the number of motion trajectories ($F(1, 9) = 15.4$, $p = .003$, $\eta^2_p = .63$). However, neither the factor Experiment nor the interaction reached significance ($p> .05$).

Additionally, using the bootstrap analyses with 95% CI we arrived to the same conclusions using *t*-tests corrected for multiple comparisons.

a)



b)

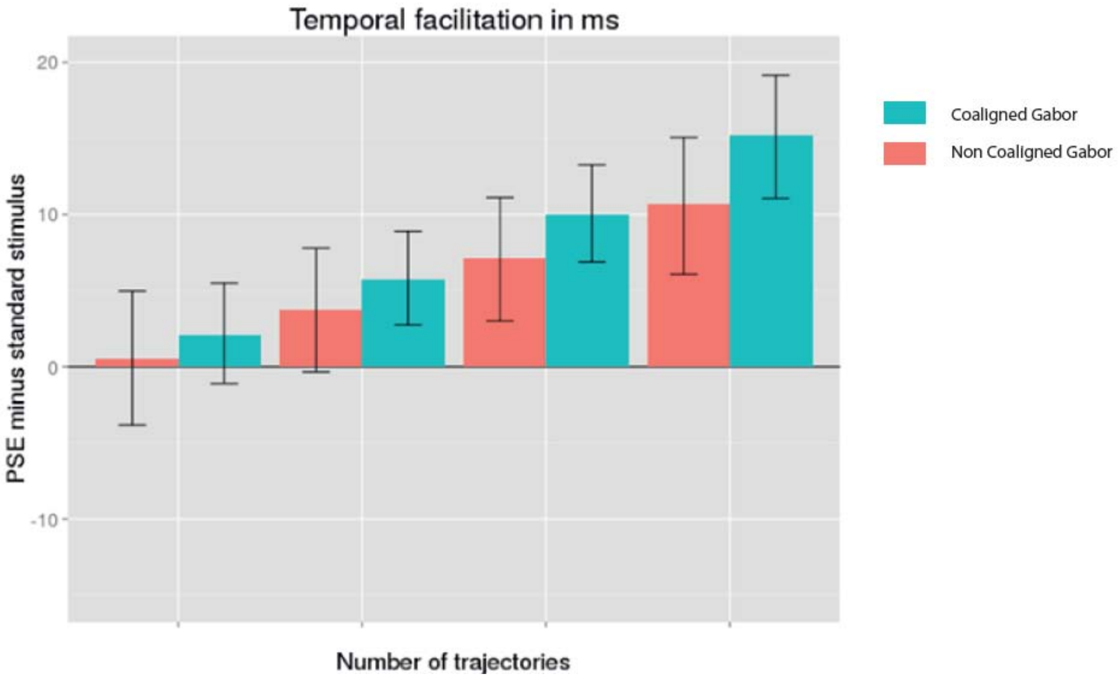


Figure 26. (a) Average of probability of responses “Target moved down” for Experiment 3 and 5 as a function of the nearby target onset time. The (dashed purple) psychometric curve for three trajectories with coaligned Gabor is shifted to the right in higher degree than trajectories with no-coaligned Gabor (continuous purple curve), which means that participants perceived the target before under the condition with coaligned moving objects, although it was not significant. **(b)** Temporal facilitation + 95% CI after a bootstrap (2000 samples). As it can be observed, TF increases with the number of trajectories and that higher TF values are observed for the condition with coaligned Gabor patches regarding condition with non coaligned Gabor patches.

These results indicate, on one hand, that non-coaligned Gabor patches may generate enough strength on the visual input to produce a significant TF. Moreover, the comparison between Experiment 3 and Experiment 5 did not reach significant differences. Taken together, these results it can be suggested that moving objects enhance detection at positions further ahead of their leading edge. A stronger effect for coaligned Gabor patches was expected, in line with findings showing collinear facilitation using static Gabor as flankers (Georges et al., 2002; Lev & Polat, 2011; Paradis et al., 2012) but it may be that at this speed, orientation of Gabor patches are not so relevant as the number of trajectories presented in the visual field. On the other hand, a possible facilitatory modulation by MT may explain why facilitation was prompted as well for non-coaligned configurations.

Experiment 6: Distance from motion leading edge

The series of experiments in this chapter were based on **condition (c) of Experiment 3** (see ‘General Methods” section). If such facilitatory effect previously observed was due to horizontal propagation of stimuli information from periphery to centre, we expected that it would be influenced by the distance between the leading edge of motion and the location of the subsequent target. Thus, we conducted Experiment 6 to give additional data on this matter.

Methods

Participants:
Six (naïve) individuals voluntarily participated, aged from 22 to 34.

Design and Procedure:
For the following experiments (except for Experiment 10), we used the condition with three motion trajectories (coaligned Gabor patches moving left-to-right, right-to-left and upwards), given that it led to a significantly higher perceptual facilitation in Experiment 3.

Independent variable
Four different distances between the leading edge of motion and the subsequent nearby target were manipulated across trials: (a) 0.6° visual angle (condition (c) of “General Methods” section), (b) 1.1°, (c) 1.7°, and (d) 2.3° visual angle (see Figure 27).

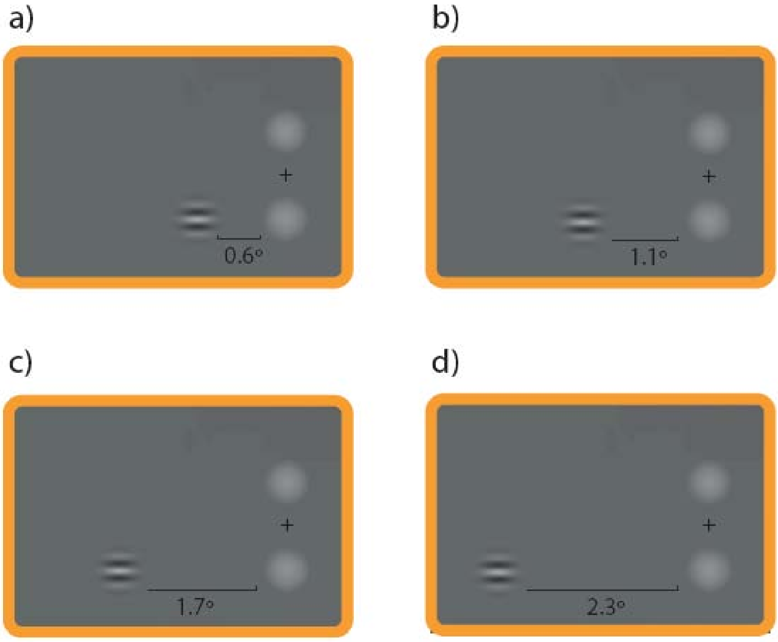


Figure 27. Schematic representation of distance conditions. The nearby target could be located at **(a)** 0.6º (same size as stimuli), **(b)** 1.1º, **(c)** 1.7º or **(d)** 2.3º visual angle from the leading edge of collinear Gabor patches that moved along three trajectories. Note that only the

left-to-right trajectory is represented in this Figure.

Results and Discussion

Four psychometric functions per participant (one for each distance) fitted by GLMM (AIC = 525) are represented in Figure 28 and averaged data across the six participants are shown in Figure 29, where nearby target onset times are plotted as a function of distance from motion trajectories. In the case that motion did not influence detection of nearby target onset time, psychometric curves should be centred at the theoretical PSE value (“+” sign). However, if motion facilitates detection of nearby target onset times, we should observe a rightward shift of psychometric functions. Moreover, we could expect a higher rightward shift as a function of distance. For instance, in the condition of 0.6º visual angle distance participants perceived the nearby target at 59 ms, which means that they perceived target onset 9 ms before than the onset of the distant target (presented always at 50 ms).

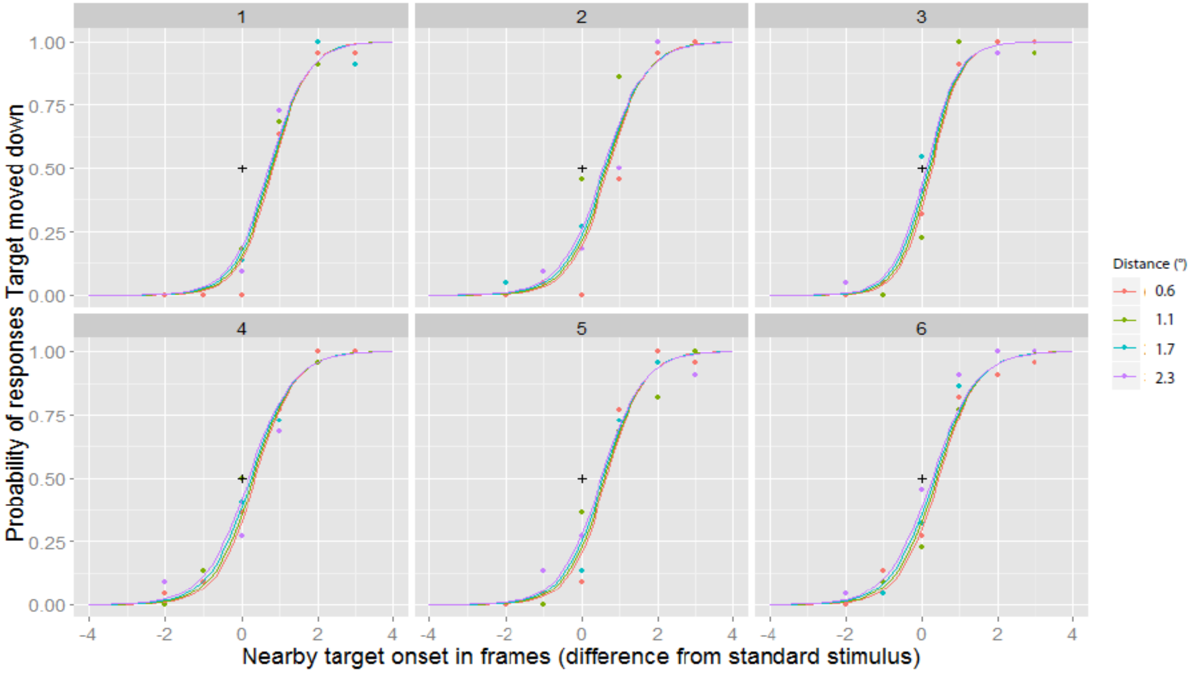


Figure 28. Probabilities of answers “Target moved down” as a function of nearby target onset times in frames. The “+” sign represents the theoretical PSE value. Each psychometric function per participant represents distance conditions. The four psychometric curves are shifted to the right in almost all the participants, which means that they perceived the nearby

target onset earlier compared to the onset of the distant target.

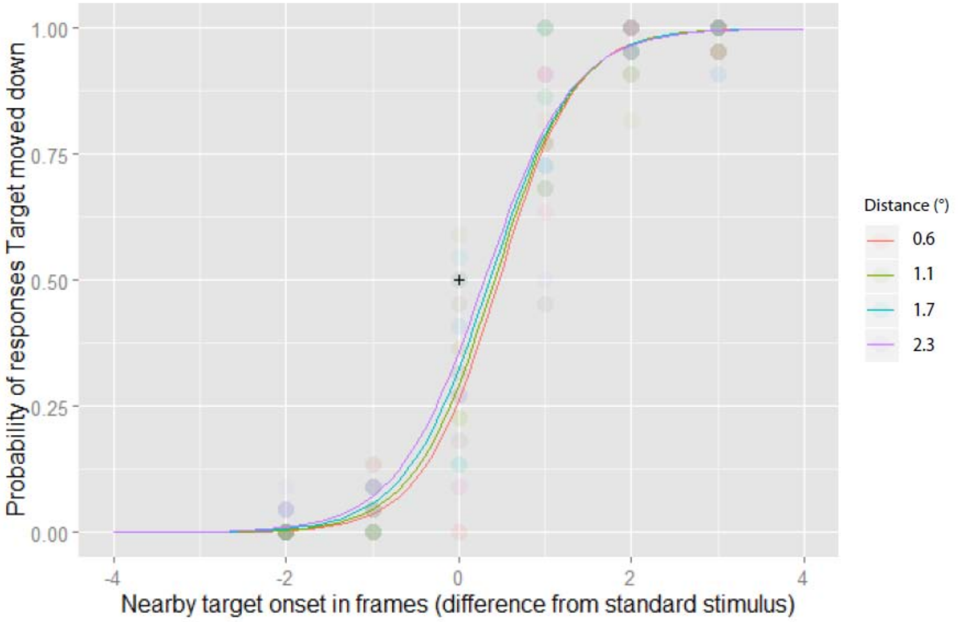


Figure 29. Average of probability of answers "Target moved down" as a function of nearby target onset time in frames. The "+" sign represents the theoretical PSE value. All psychometric curves are shifted to the right, which means that participants perceived the nearby target moving up more often. That is to say, participants perceived the nearby target onset earlier compared to the onset of the distant target. In addition, the effect seems to decrease with distance from the motion trajectory and thus, psychometric curves are shifted rightward in a higher degree.

Participants responses varied significantly with distance conditions (Wald test, *p* = .029). After the bootstrap procedure (2000 samples) where we estimated PSE's variance, we analysed if temporal facilitation (TF: PSE minus 50 ms) across conditions was statistically significant. Results revealed no significant differences across distance conditions. Additionally, if distance conditions induced temporal facilitation, the mean of temporal facilitation should differ significantly above a hypothetical 0 (i.e. no facilitation). Analyses revealed temporal facilitation was significantly different from 0: distance 0.6° visual angle: *TF* = 7.6 ms, *CI* = [3.9 – 11.2] ms, *p* < .0001; distance 1.1° visual angle: *TF* = 6.8 ms, *CI* = [3.1 – 10.3] ms, *p* < .0001; distance 1.7° visual angle: *TF* = 5.9 ms, *CI* = [2.1 – 9.5] ms, *p* = .003; and distance 2.3° visual angle: *M* = 4.8 ms, *CI* = [0.5 – 9.7] ms, *p* = .018, see Figure 30.

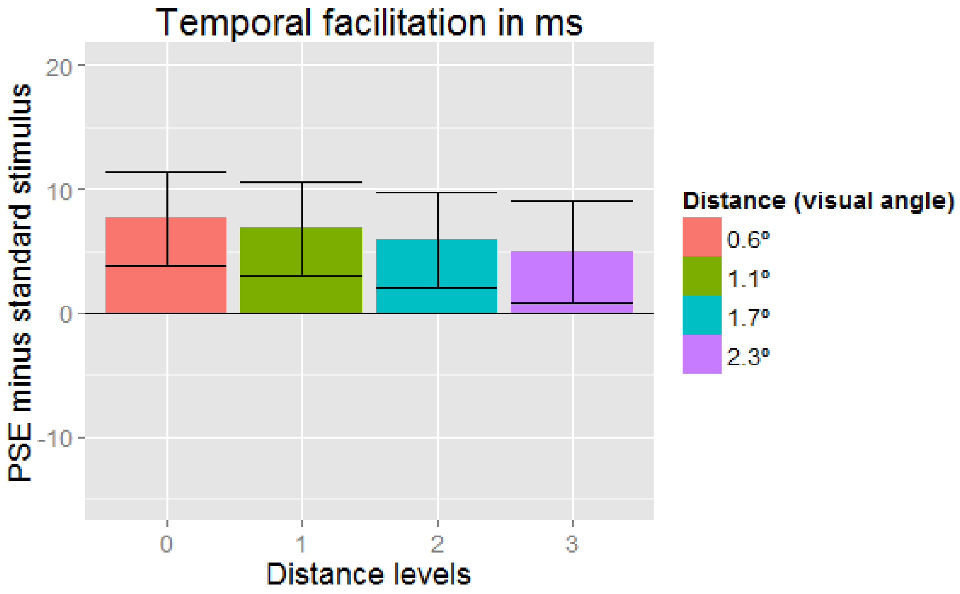


Figure 30. Temporal Facilitation (TF + 95% CI) in ms as a function of the distance between the leading edge of motion and the subsequent nearby target. Each condition was significantly above 0 and no significant differences across conditions were observed.

Our results indicate that the effect of motion was strong in all the distances tested. Temporal facilitation did not significantly varied across conditions showing that motion might had provided a predictive input that enhances target detection at least for the next four future positions of the moving object (distance of 2.3º visual angle). Data from electrophysiological studies show that increasing stimuli distance decreases the strength of V1 neurons responses increasing the delay of these responses (Bringuier et al., 1999; Chavane et al., 2000). Our results might be related to the horizontal connectivity to neighbouring areas of the visual cortex that propagates information even at a distance of 10º visual angle (Chavane et al., 2000). Hence, greater distances may need to be tested in order to observe significant decreases on temporal facilitation.

Experiment 7: Trajectory contrast

Objects with higher contrast are processed faster compared to objects with low contrast and hence, stimuli contrast influences neural latency (Purushothaman et al., 1998). Given that temporal facilitation may be the result of faster neural latency, we might also expect that by changing the contrast of a moving Gabor, temporal facilitation will vary accordingly as well.

Methods

Participants:
Seven (naïve) participants (aged between 18 and 37 years old).

Independent variable
Four contrast levels of three motion trajectories were used: ~3.5%, ~1.8%, ~1.2% and ~0% ($1x10^{-9}$) Michelson contrast.
Three motion trajectories correspond to condition (c) in the “General Methods” section.

Results and Discussion

The psychometric curves were fitted using the GMML model (AIC = 655) as indicated previously, for each participant are represented in Figure 31 and averaged psychometric functions for all the participants are shown in Figure 32.

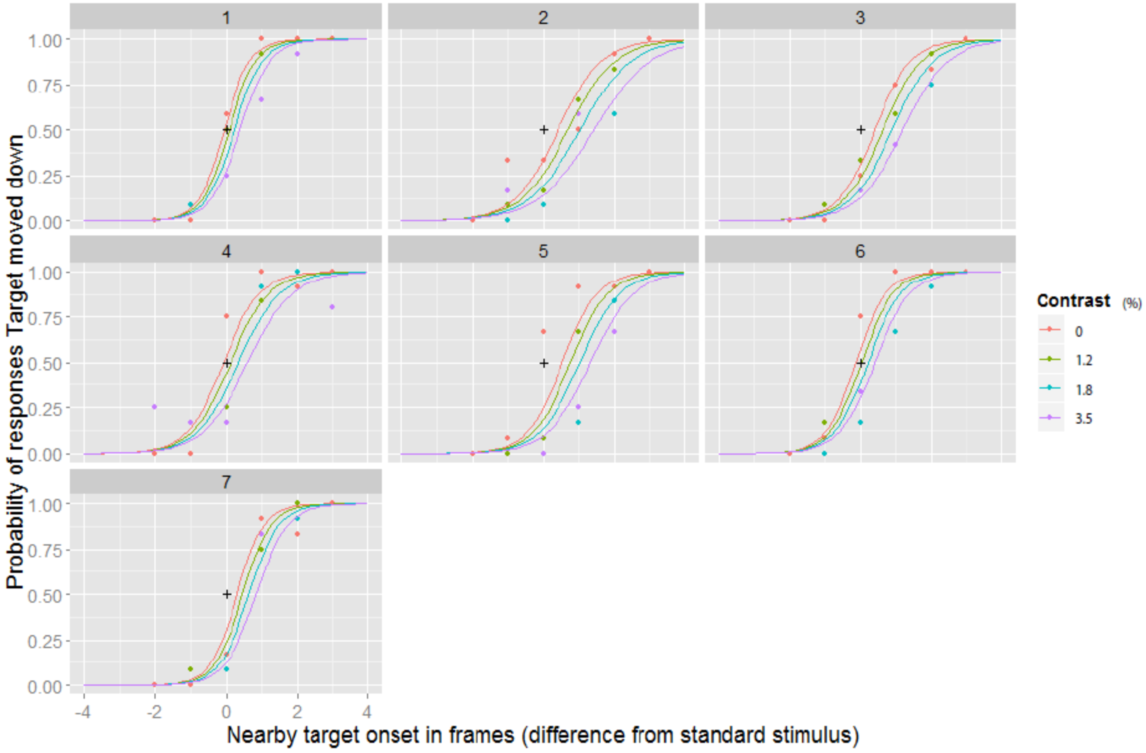


Figure 31. Probability of responses "target moved down" for each participant as a function of nearby target onset time in frames. Participants perceived the target moving down less often when contrast of the motion trajectory was higher, and thus, blue and purple curves are shifted to the right, revealing temporal facilitation. This means that participants perceived the nearby target onset earlier (target moving up more often).

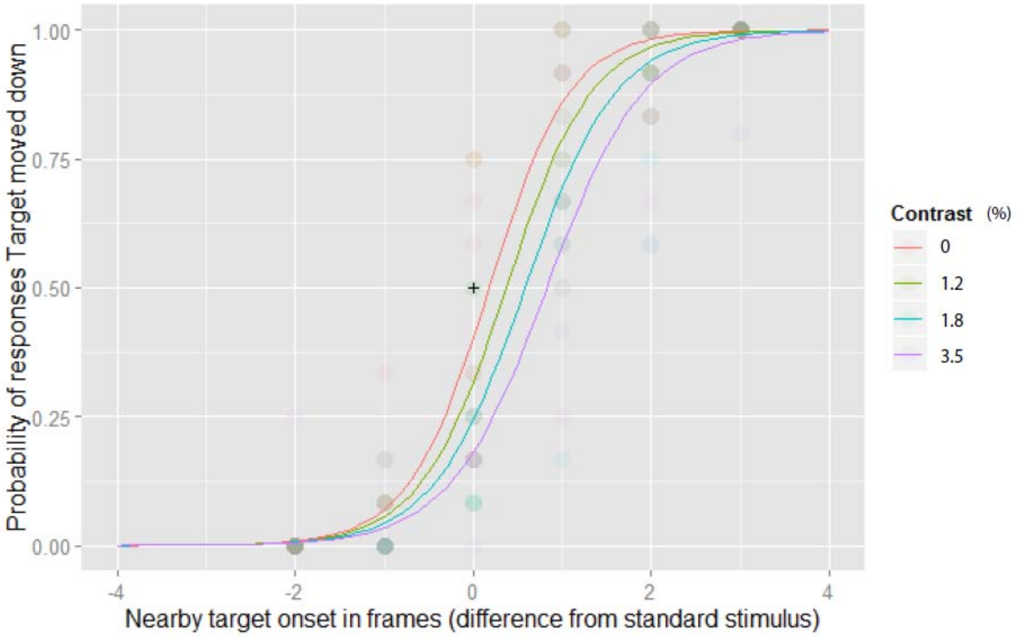


Figure 32. Average of probability of responses "target moved down" across participants. The axis of abscissas indicates the nearby target onset time in frames. The nearby target was perceived earlier when preceded by motion with higher contrast (represented by blue and

purple curves); and thus, curves are shifted rightward. In contrast, when the nearby target was preceded by motion with very low contrast, participants accurately perceived the onset time (red curve), i.e. the psychometric curve is centred on the theoretical PSE value (”+” sign) exhibiting no shift.

Contrast levels revealed to significantly influence participants responses (Wald test, $p < .001$). After the bootstrap procedure with 2000 samples we analysed whether temporal facilitation (TF: PSE minus 50 ms) varied significantly between conditions and if they were significantly above 0. As expected, temporal facilitation was not observed for the condition with contrast 0, that is, the condition where actually no moving object could be visualized (see Figure 33). In contrast, all conditions with motion trajectories significantly increased temporal detection for the nearby target (it was perceived earlier): 3.5 % contrast (*TF* = 12 ms, *CI* = [6.1- 17.4], $p < .001$), 1.8% contrast (*TF* = 12.2 ms, *CI*= [7.9-16.4], $p < .001$) and 1.2% contrast (*TF* = 6.3 ms, *CI*= [2.4-10.1], $p = .0012$). This means that participants perceived the nearby target onset earlier. Temporal facilitation was enhanced by as much as 12 ms.

It seems that above 1.8% contrast temporal facilitation reached its maximum. Importantly, conditions with contrast above 1.2% were significantly different from the condition without motion (condition with contrast equal to 0): 3.5% contrast, $p = .003$; 1.8% contrast, $p = .009$).

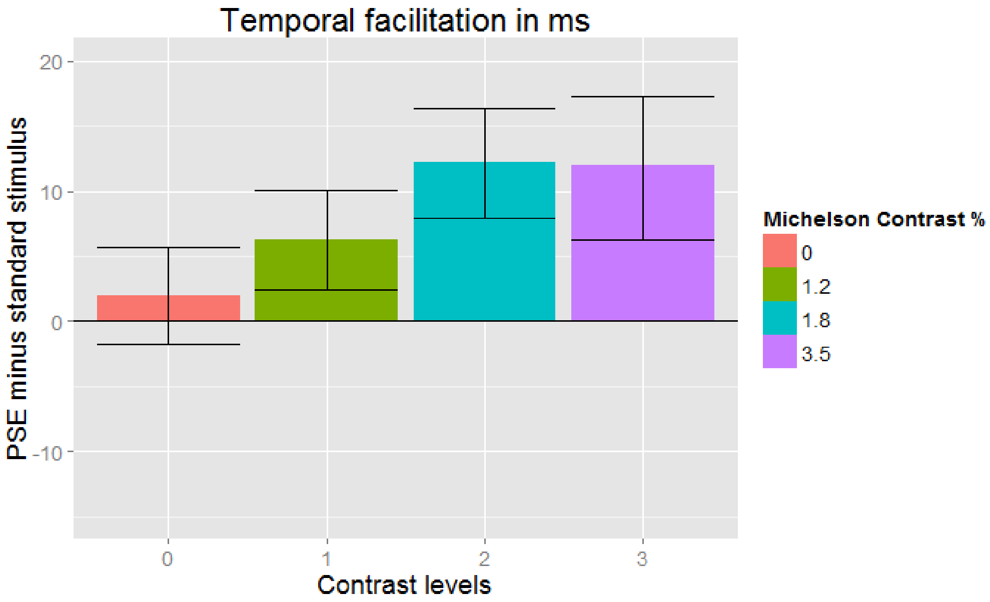


Figure 33. Temporal Facilitation (TF + 95% CI) in ms as a function of trajectory Michelson contrast.

Results revealed that trajectories with contrast above 0 facilitated targets detection, whereas those with lower contrast did not. This is in accordance with previous research that shows that RF properties are highly contrast dependent with slower onset latency for low contrast stimuli (Bair, Cavanaugh, & Movshon, 2003; Cass & Spehar, 2005; Kapadia et al., 1999; Paradis et al., 2012; Seriès et al., 2002). Our data also support that neural sub-threshold preactivation may facilitate detection for higher contrast stimulus (Nijhawan & Khurana, 2010).

Experiment 8: Trajectory length

In the present experiment, we investigated the impact of trajectory length on temporal facilitation. Taking into consideration a predictive coding perspective for motion, a longer trajectory would reduce prediction error because the system is able to predict with higher probability positions of the object in the next future. In addition, it is plausible that more neurons would be preactivated along the motion trajectory, and thus, spread activity to neighbouring neurons with RF close to the leading edge of motion.

Methods

Participants:

Four (naïve) participants voluntarily decided to participate in the experiment, aged between 18 and 35 years old.

Independent variable

The length of three motion trajectories was manipulated across trials as follows (see Figure 34): (a) A Gabor patch was sequentially presented during 16 frames in 16 positions (same condition as in the previous experiments; trajectory duration: 267 ms); (b) 8 positions during 8 frames (trajectory duration: 133 ms); (c) 4 positions during 4 frames (trajectory duration: 67 ms); (d) 2 positions during 2 frames (trajectory duration: 33 sec).

The last Gabor was always presented 0.6º away from the future location of the nearby target as in the previous experiments. The tree motion trajectory corresponds to condition (d) in "General Methods" section.

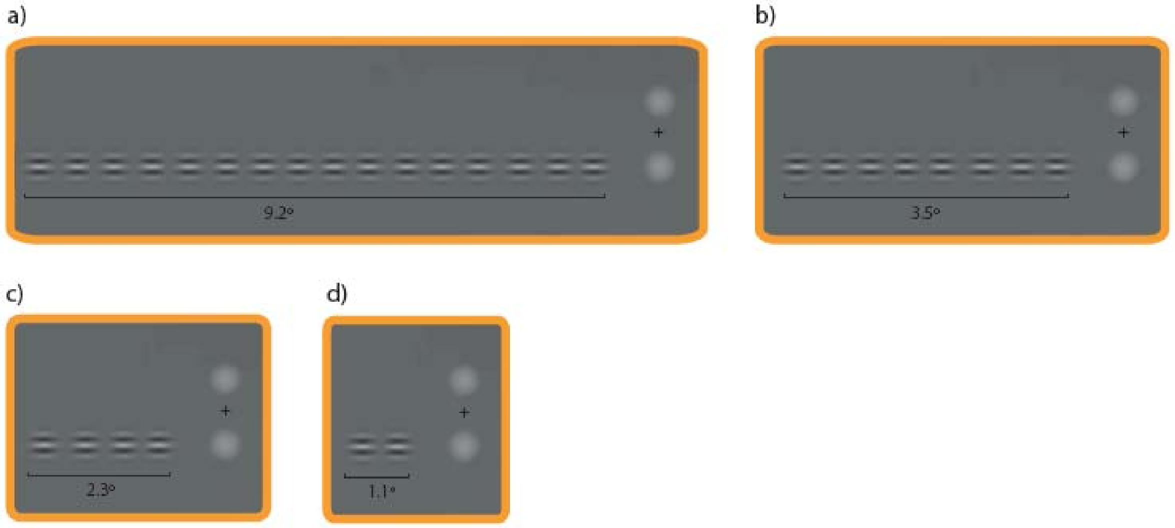


Figure 34. Trajectory length conditions in Experiment 8. Gabor moves along **(a)** 16 positions during 16 frames, **(b)** 8 positions during 8 frames, **(c)** 4 positions during 4 frames and **(d)** 2

positions during 2 frames. Note that for simplification all stimuli are represented in this figure, but Gabor and targets were never displayed at the same time in the experiment. Also note that three motion trajectories were always presented.

Results and Discussion

Individual psychometric functions were fitted accordingly with the GMML model (AIC = 317) and are represented in Figure 35 whereas averaged psychometric functions and PSEs are shown in Figure 36. All psychometric curves are shifted to the right, which means that participants perceived the target before its onset time (50 ms).

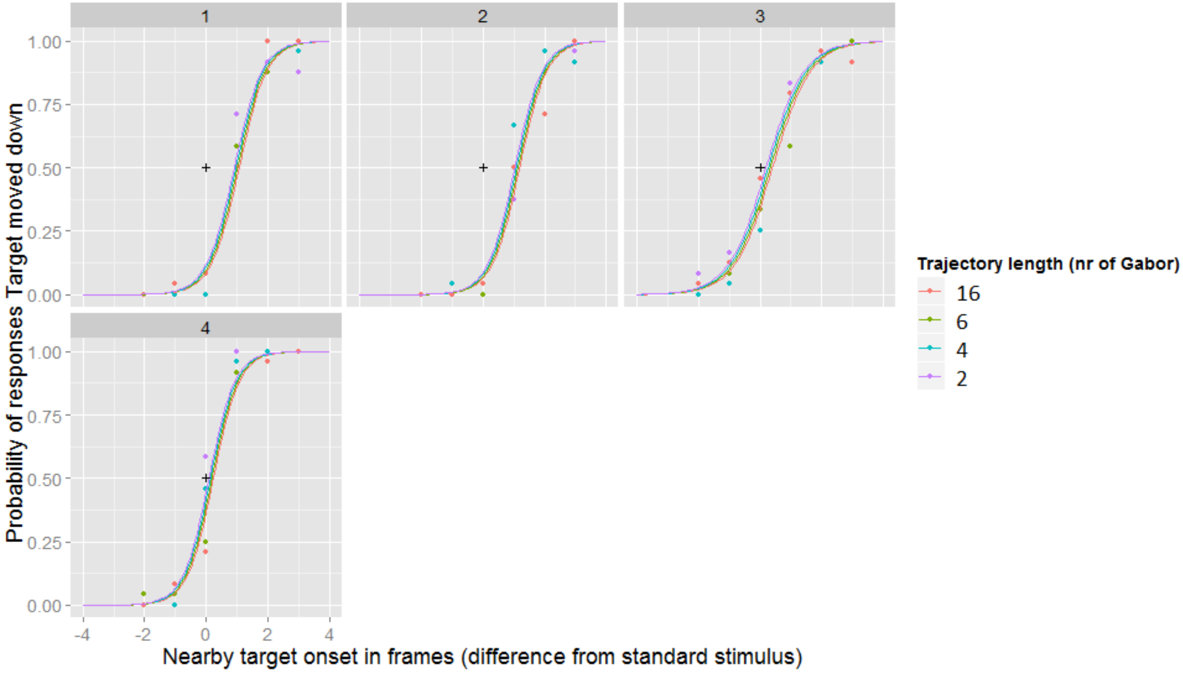


Figure 35. Proportion of responses “Target moves down” for Experiment 8 as a function of the target onset time (in frames) regarding the standard stimulus onset. Psychometric curves of all the participants are displaced to the right which means that they perceived the nearby target onset before the onset of the standard stimulus.

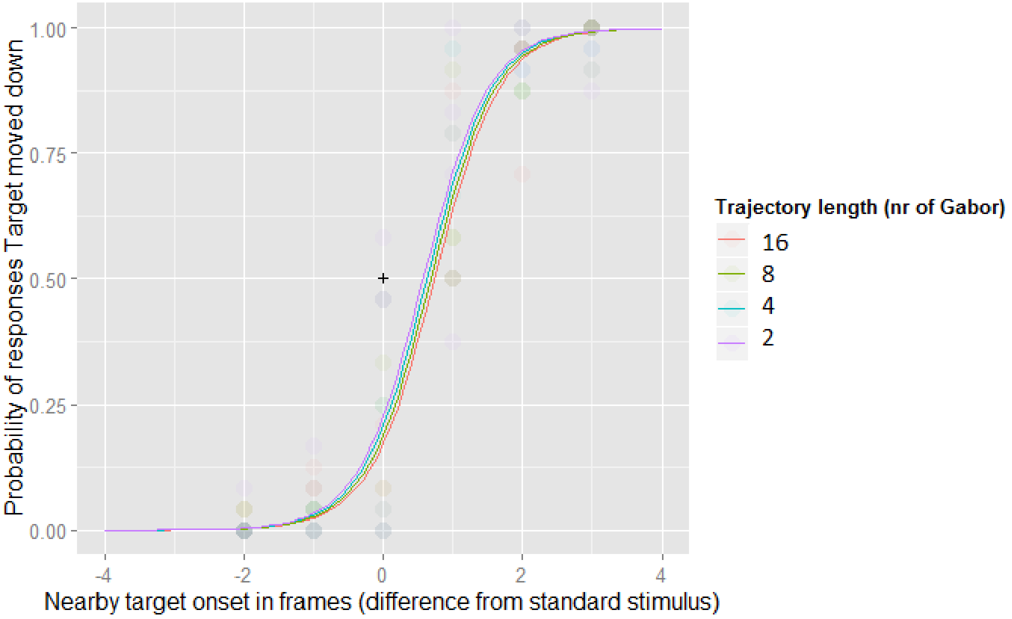


Figure 36. Average of proportion of responses “Target moved down” as a function of the target onset time (in frames) regarding the standard stimulus. Curves represent length conditions: red curve represents 16 Gabor patches, green curve represents 8 Gabor patches, blue curve 4 Gabor patches and purple curve 2 Gabor patches. As it can be observed all the curves are displaced to the right which indicates that participants perceived the target to move up more often.

Participants’ responses did not vary across length conditions (Wald test, *p* > .05). After the bootstrap procedure with 2000 samples, we intend to analyse whether temporal facilitation (TF: PSE minus 50 ms) was significantly above 0 for each condition. Indeed, all trajectories length yielded a facilitatory effect above 0: 16 Gabor trajectory: (*TF* = 11.5 ms, *CI* = [4.6-18.8] ms, *p* = .002), 8 Gabor trajectory (*TF* = 12.0 ms, *CI*= [5.6-18.7] ms, *p* = .001), 4 Gabor trajectory (*TF* = 11.1 ms, *CI*= [5.1-17.4] ms, *p* < .001) and 2 Gabor trajectory (*TF* = 8.8 ms, *CI*= [1.5-16.4] ms, *p* = .020), see Figure 37.

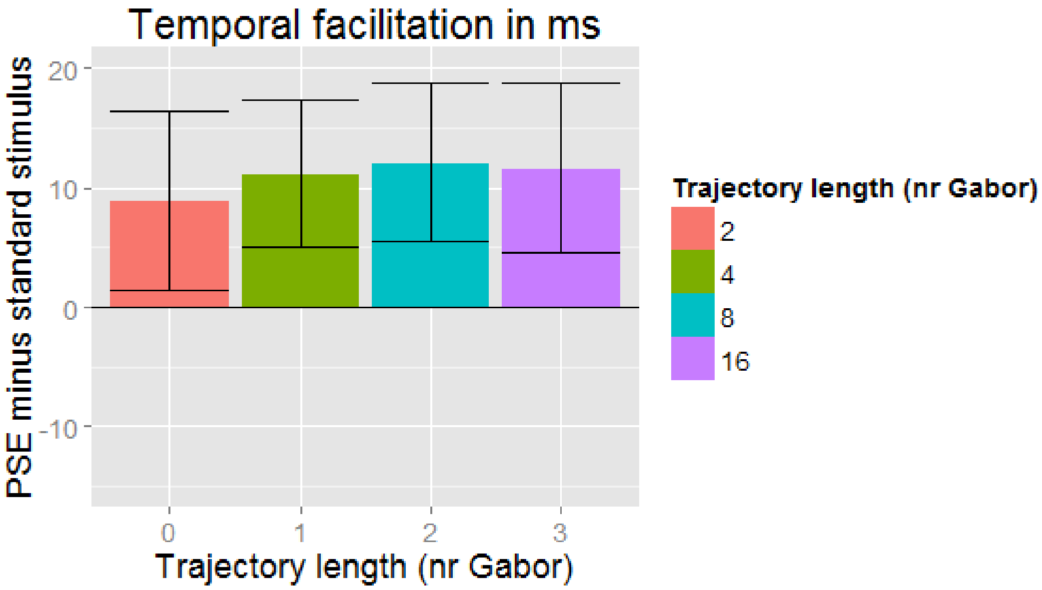


Figure 37. Temporal facilitation + 95% CI as a function of trajectory length (number of Gabor displayed). As it is observed all the conditions led to a facilitatory effect above 0.

These findings were unexpected; instead, we were expecting to observe a facilitatory effect for short trajectories as well, but in lesser degree regarding longer trajectories. Due to these findings we decided to run another experiment and test trajectory length with different contrast levels to see if this relation would change the relevance of trajectory length. See “Results and Discussion” section of Experiment 9.

Experiment 9: Trajectory length and contrast

This experiment was designed to test the impact of trajectory length on temporal facilitation using higher contrast motion trajectories. We decided to use the contrast conditions that led to a stronger facilitatory effect in Experiment 7.

Methods

Participants:
Seven participants (1 author and 4 naïve), aged between 20 and 39 years old.

Independent variable
The length of three motion trajectories was manipulated across trials as in Experiment 8. Additionally, each trajectory length was tested under two conditions of motion contrast: (1) high: 3.5 % Michelson contrast (condition (c) from Experiment 7) and (2) mid: 1.8% Michelson contrast (condition (d) from Experiment 7).

Design and Procedure:
The total number of trials was 1046, including 22 trials per condition (6 nearby target onset time x 4 trajectory length x 2 motion contrast). The order of trials was randomized across participants.

Results and Discussion

Individual psychometric functions are represented in Figure 38 and averaged psychometric functions for all the participants in Figure 39. All psychometric curves appear shifted to the right regarding the theoretical PSE value (“+” sign). Moreover, psychometric curves for the higher contrast (continuous curves) appear shifted to the right with regards to the curves corresponding to mid contrast (dashed curves). This finding suggests a strong effect for higher contrast motion, i.e. participants perceived the nearby target onset earlier (compared to the distant target).

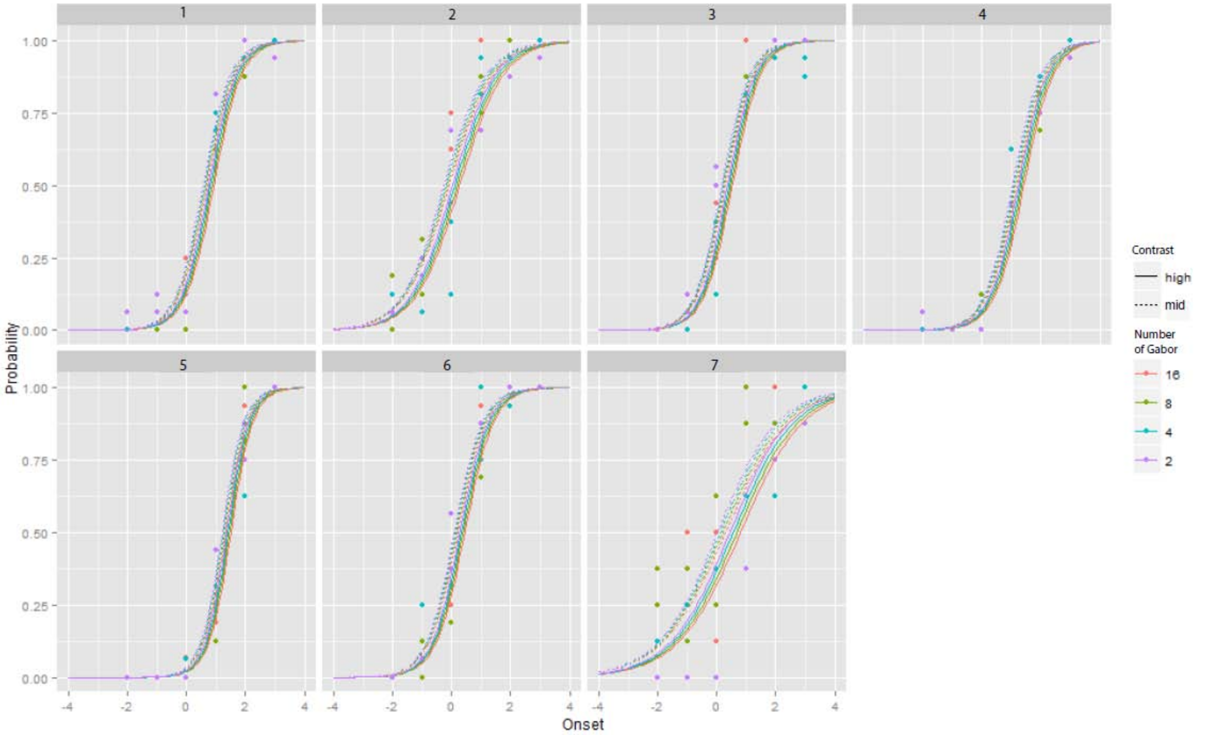


Figure 38. Eight individual psychometric functions as a function of nearby target onset time. Dashed curves represent conditions of mid contrast while continuous curves represent conditions with higher contrast. Colour represents the number of Gabor patches/trajectory length. As it can be observed, mid contrast curves compared to higher are displaced to the left for most participants, which indicates that they perceived target onset more accurately, i.e. there was less temporal facilitation for mid vs. higher contrast.

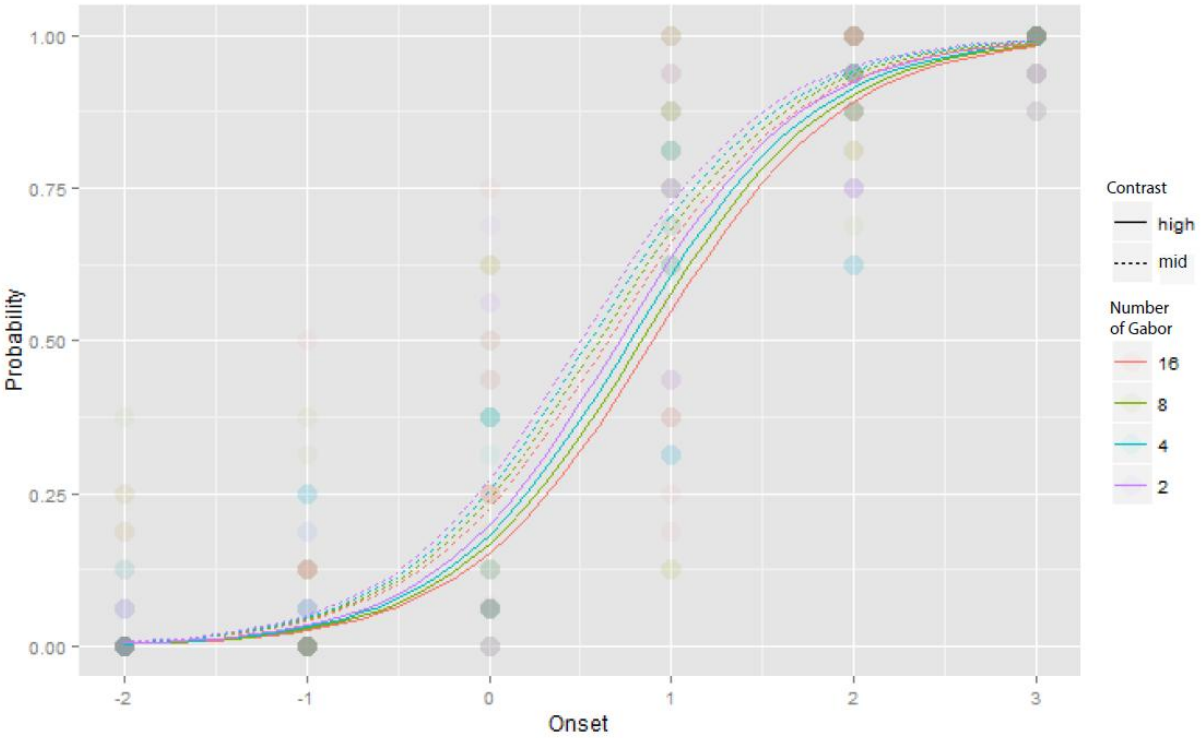


Figure 39. Average of probability of responses “Target moved down” for Experiment 9 as a function of nearby target onset time in frames. Dashed lines represent condition with lower

contrast whereas continuous curves represent the higher contrast condition. Colours represent the length of the trajectory by means of the number of Gabor patches presented along the trajectory.

Analyses revealed a main effect of contrast (Wald test, *p* <.005). However, neither the factor trajectory length nor the interaction of length and contrast were observed. Hence, temporal facilitation increased as a function of contrast but not as a function of length (see Figure 40). Then, we analysed whether temporal facilitation (PSE minus standard stimulus) varied across conditions and whether conditions were significantly above 0 (0: no temporal facilitation).

All higher contrast trajectories facilitated the perceived onset of the nearby target, i.e. temporal facilitation was significantly above 0: Gabor patches moving along 16 positions (*TF* = 10.9 ms, *CI*= [5.3 – 16.7] ms, *p* = .007); 8 positions (*TF* = 10.3 ms, *CI*= [4.6 – 5.8] ms, *p* = .013); 4 positions (*TF* = 9.2 ms, *CI*= [3.7 – 15.1] ms, *p* = .016); and 2 positions (*TF* = 8.4 ms, *CI*= [2.6 – 4.6] ms, *p* = .048). All *p* values were corrected using with Benjamini-Hochberg for multiple comparison as in all previous experiments. For the mid contrast lengths, no effects reached significance after correction. Moreover, we did not observe significant differences across trajectory length under both conditions of contrast.

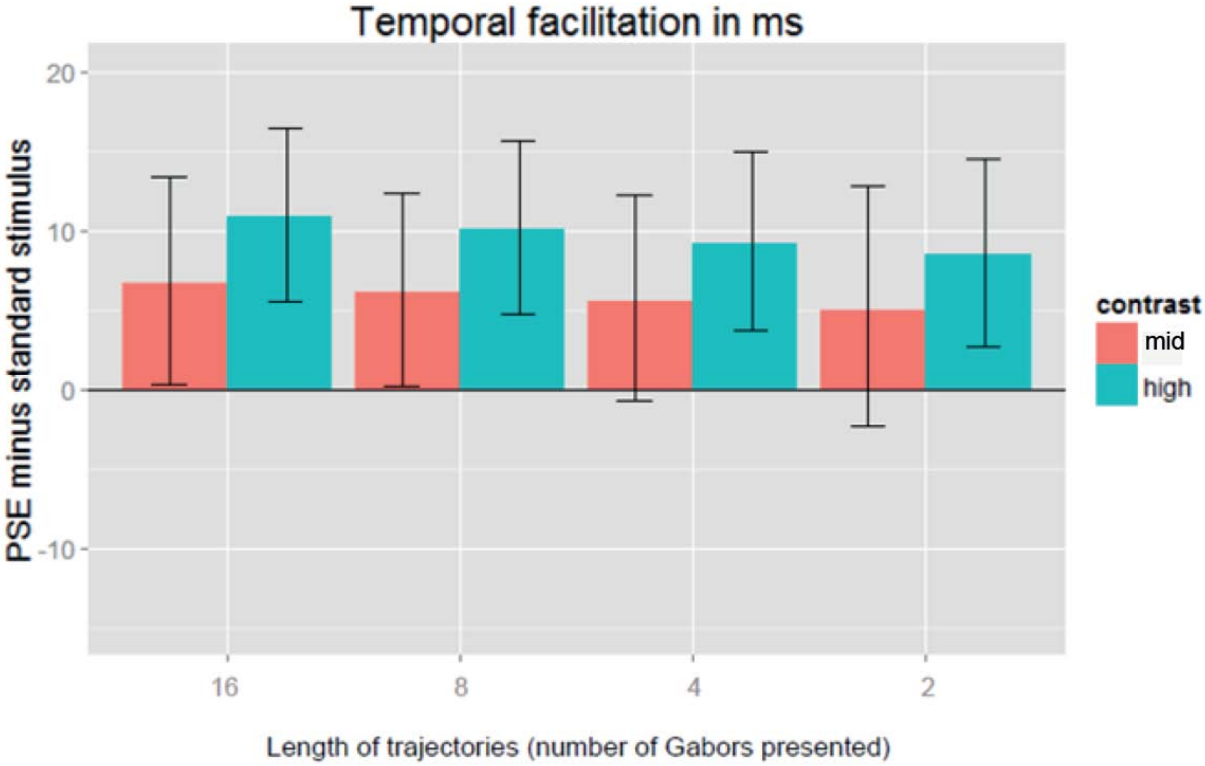


Figure 40. Temporal Facilitation (TF + 95% CI) in ms as a function of the length of the trajectory (number of Gabor). Temporal facilitation was found for higher contrast Gabor despite its trajectory length.

In Experiment 7 these two levels of contrast were not significant different, contrary to the present experiment. This may be due to the fact that in Experiment 7 four types of contrast were interleaved during the experiment and thus, differences across them were reduced. Moreover, these results revealed again that contrast was a determinant variable capable to elicit temporal facilitation.

Accordingly with findings of Experiment 8, the present results indicate the same perceptual speed for short and long trajectories. This implies that short trajectories are sufficient to prompt faster neural spread of activity that allows a rapid processing and preactivation of neurons with RF close to the leading edge of motion. In fact, electrophysiological data show that in response to a moving objet, population of neurons elicit a higher propagating peak of activity already at 30 ms, compared to a static object. This time may be sufficient to lead to the perceptual facilitation found here. On the contrary, our results about length might be not in agreement with some psychophysical findings that show that perceived speed increases with bar length (Castet, Lorenceau, Shiffrar, & Bonnet, 1993). However, other findings on localization judgements, showed that forward displacement was not affected by the trajectory of a disk or a line moving along 2º, 4º or 6º which would be in line with our results (Kerzel, 2003).

By assuming a predictive coding framework, one should not expect the same perceptual facilitation for short trajectories considering that the prediction error is higher in the initial segment of motion. However, a predictive coding explanation is possible if we consider the proposal by Eriksson and colleagues (Eriksson et al., 2012) in which a sole neuron process error coding and stimulus coding as it follows. A moving Gabor first elicits an error coding (predictions minus actual signal) because the system is not expecting a sudden appearance of a moving object, and then, the stimulus coding occurs. Accordingly, a low contrast stimulus elicits a higher error coding and a later and weaker stimulus coding. Given these findings, we hypothesize that in case of a Gabor moves along two positions, the same error coding (as for a Gabor that moves along 4 positions) would be computed and then, stimulus coding would be processed. Respectively, independently of the trajectory length the system would rapidly enhance stimulus coding for moving objects (see Figure 41).

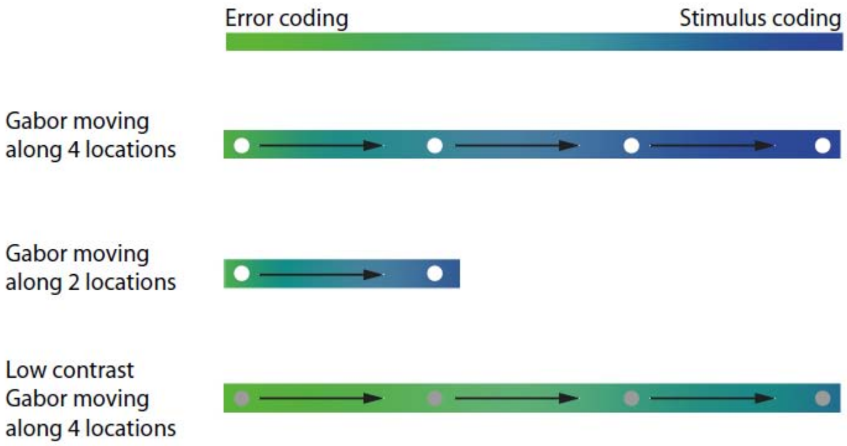


Figure 41. Illustration of predictive coding for some conditions of Experiment 9 adapted from Eriksson et al. (2012). It can be observed the hypothesized coding difference between high and low contrast Gabor patches that move along four positions. For the low contrast Gabor, error coding is higher and lasts longer, whereas stimulus coding is lower. We hypothesized

that for a higher contrast Gabor that moves only in two positions, error coding would be lesser compared to a lower contrast Gabor, and just after, neurons would rapidly start to compute stimulus coding leading to the same activity as with a high contrast Gabor that moves in four positions.

The fact that there were no differences between the presence of an object moving along 16, 8, 4 or 2 positions casted us with the need to test temporal facilitation using static Gabor patches. This would able us to disentangle if it is an effect of collinear flankers (that can be static) or, as expected from the beginning of our research, a specific effect due to motion processing.

Experiment 10: Control for coaligned static Gabor patches

We decided to run this experiment as a control to ascertain that our results were due to the visual processing of moving objects and not to collinear facilitation (with static flankers). With this aim we presented 1, 2 or 3 collinear static Gabor as flankers (to see if there was a linear relation between the number of static Gabor patches and TF).

Methods

Participants

Seven participants (naïve), aged between 19 and 32 years old.

Independent variable

The number of static Gabor were manipulated as follows: (a) baseline condition: no stimuli was presented, (b) 1 Gabor patch: half of the trials presented at the right and the other half at the left of fixation point, (c) 2 Gabor patches: one presented at the right and the other at the left of the fixation point; and last, (d) 3 Gabor patches: located at the left, right and bellow of fixation point. See Figure 42 for a single trial example.

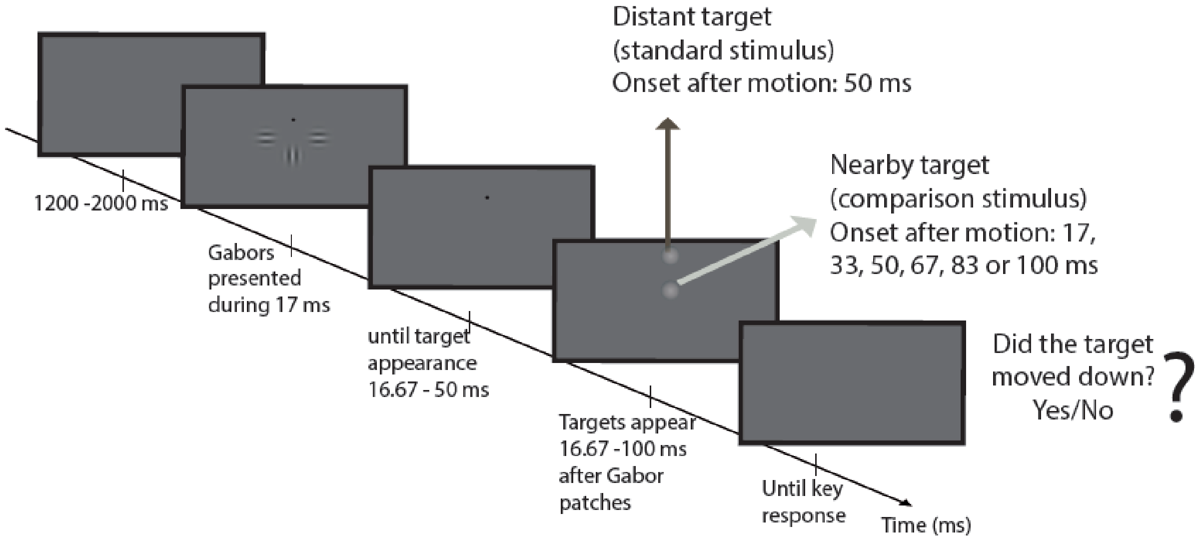


Figure 42. Single-trial example. A blank screen is presented for 1200-2000 ms and after fixation point is presented for 250 ms (15 frames) and then one static Gabor is displayed for 17 ms (one frame). One frame after target is displayed according to the constant stimuli method. Note that this example shows the condition for three Gabor patches, but Gabor patches could also appear either at right and left or right or left.

Results and Discussion

Data were fitted using the same method as in the previous experiments (AIC = 308). Four individually psychometric curves are represented per each participant in Figure 43 and average of probability of responses “Target moved down” and PSE are represented in Figure 44.

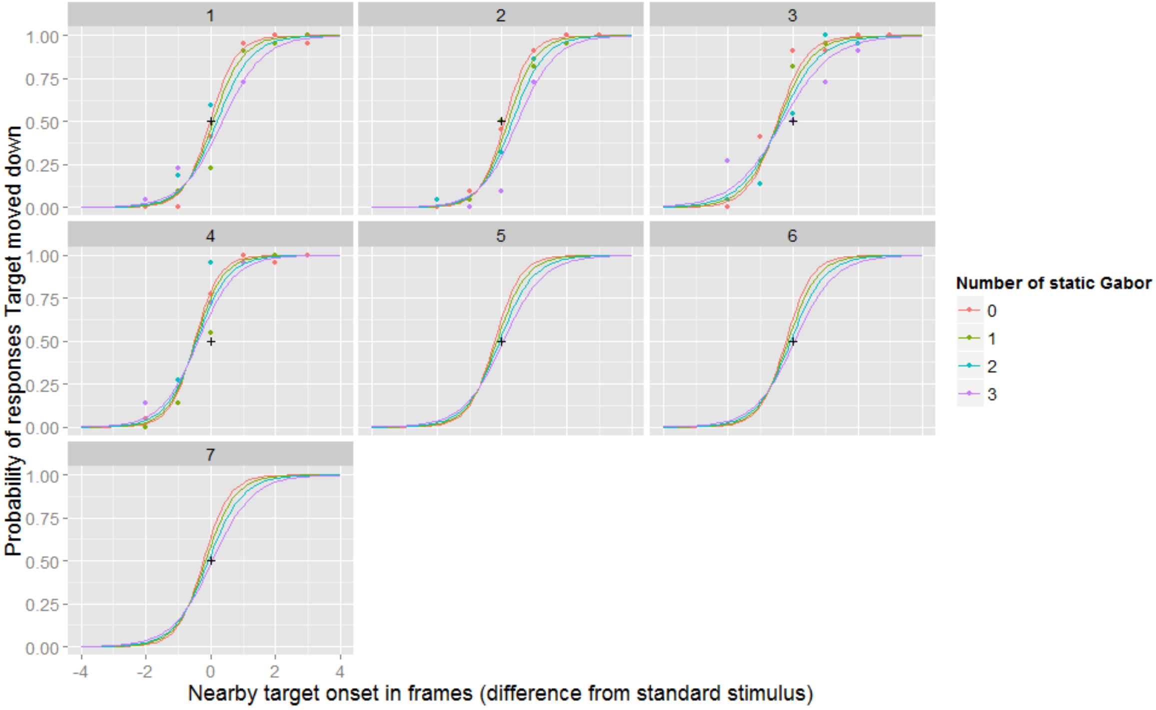


Figure 43. Individual psychometric functions as a function of target onset time in frames. Psychometric curves appear centred at the theoretical PSE point (“+” sign).

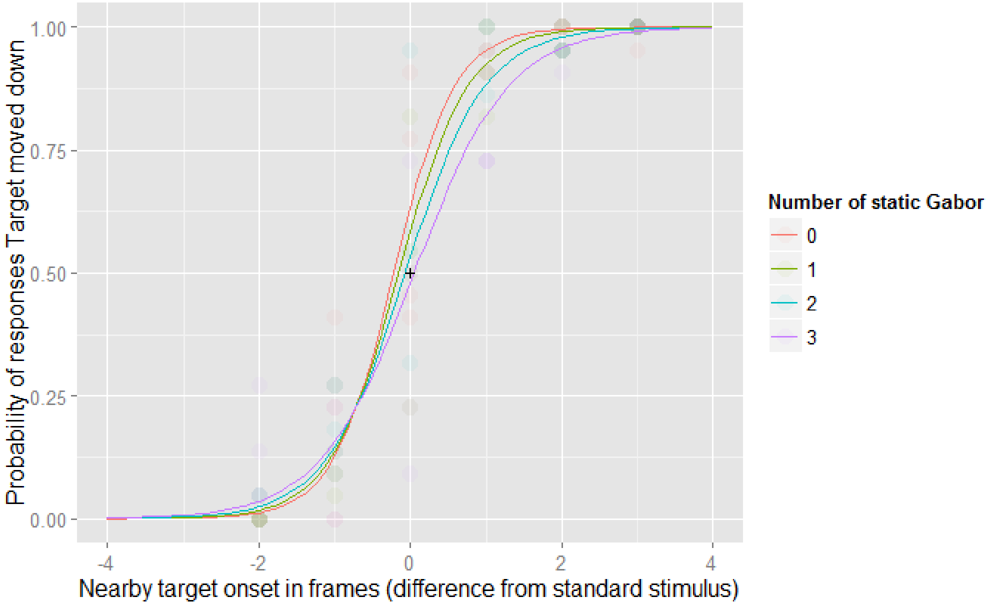


Figure 44. (a) Average of probability of responses “Target moved down” in Experiment 10. The abscissa indicates nearby target onset time in frames. Except for the condition with three static Gabor patches, psychometric curves are not displaced to the right, instead, curves are centred on the theoretical PSE value (“+” sign), with a small displacement to the left.

Using the GLMM we found that static Gabor significantly change participants responses (Wald test, *p* = .003). Then, a bootstrap (2000 sampled) with 95% CI was used to estimate variance of PSEs. For further analyses, we analysed Temporal Facilitation (PSE-standard stimulus). Indeed, as expected, neither conditions were significantly different and nor were significantly different above 0. Thus, these outcomes indicate that the presence of static objects before target onset do not generate any facilitatory effect.

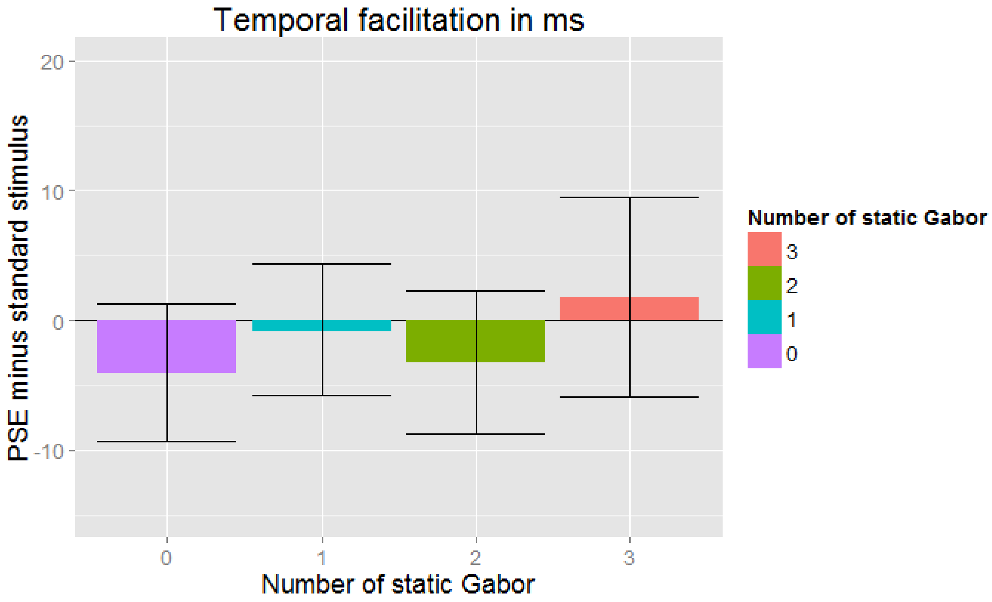


Figure 45. Temporal Facilitation (TF + 95% CI) in ms as a function of the number of static Gabor patches, after bootstrap procedure (2000 samples).

In conclusion, presenting static Gabor patches had no significant effect on temporal facilitation. Research on collinear facilitation report evidence on lower target detection threshold when Gabor patch (target) is aligned with the surrounding Gabor patches (flankers) However, it is worth noting that normally studies use as a target a Gabor patch, and manipulate the contrast or the carrier orientation. For instance, it maybe that the contrast between flankers and target suppressed temporal facilitation in a similar manner as in study of Chen and Tyler (2008) where lower contrast collinear flankers increased threshold for a higher contrast target (as in our experiment: targets have higher contrast than motion stimuli).

Another difference in our study is that our target was a Gaussian profile with equal distribution of wavelength. Hence, besides these comparisons we must be cautious in ascribing the same mechanisms to either these results given the different stimulus conditions and experiment design used in each of these experiments.

Importantly the present Experiment (i.e. Experiment 10) supports evidence that the spatial facilitation effect is due to motion trajectories and that the presence of static Gabor patches does not affect perception as motion trajectories do.

Summary of results

Motion perceptually facilitates a target located next to the leading edge of motion. In particular, the nearby target is perceived earlier and brighter in agreement with previous findings showing that detection is facilitated at the leading edge of motion (Arnold et al., 2007; Roach et al., 2011). Such facilitatory effect proved to depend strongly on the contrast of motion and the number of trajectories. Orientation of Gabor patches and trajectory length appear to play a less determinant role that may need further exploration.

Findings from **Experiments 3 and 4** revealed that a target next to the leading edge of motion was facilitated, i.e., perceived earlier and brighter compared to a target located distant from motion. Moreover, temporal facilitation increased with the number of trajectories in agreement with the hypothesis that more trajectories would induce a faster processing. The sum of several inputs for moving objects (through long-range connections) should provide neurons with RF close to the target position to fire before and to process the target onset earlier when it appears in their RF. This is in agreement with the hypothesis that the context affects brightness perception, being that coaligned moving stimuli enhance perceptual saliency for the subsequent target (Rossi et al., 1996; Seriès et al., 2002). In addition, the sum of inputs by moving objects presented in the periphery may preactivate neurons with RF close to the target position. The strength of this preactivation may depend on the number of trajectories, as expected, taking into consideration our psychophysical results.

On the other hand, we tested the role of carrier orientation of Gabor patches in **Experiment 5**. Results revealed that non coaligned Gabor patches, that is, Gabor with carrier orientation orthogonal to the trajectory, led to significant results on temporal facilitation as well. We were expecting that temporal facilitation would be more influenced by Gabor patches carrier orientation. However, we found that the number of motion trajectories were more important than orientation to create a temporal bias.

All the distances between motion leading edge and the nearby target location tested in **Experiment 6** led to temporal facilitation. Though, no differences between distances were found. That is, motion elicited temporal facilitation when the target was located four positions further ahead of the leading edge of motion. However, if the facilitatory effect is related to motion, it is reasonable to believe that distance should be a key factor. Hence, further investigation using longer distances are needed in order to clarify its role on temporal facilitation.

Contrast is known to affect neural latencies and to be related to horizontal connections that might spread activity faster (probably, by a predictive coding). Results from **Experiment 7** showed a pronounced facilitation effect depending on motion contrast. Given the fact that neural latency highly depends on stimulus contrast, it is not surprising to find a strong relation in this experiment: by increasing the motion contrast, there is an increased temporal facilitation for the location where the object will be in the next future.

The impact of trajectory length was also tested in **Experiment 8** and results revealed no differences across different trajectories length, although all induced facilitatory effects. Instead, we were expecting to observe higher facilitation when the target was preceded by longer trajectories and, on the contrary, to find lower facilitation for shorter trajectories. Additionally, we decided to conduct **Experiment 9** to test trajectory length with different contrast levels. Contrast did vary temporal facilitation whereas length did not.

Experiment 10 finally served to further confirm that temporal facilitation was related to movement itself rather than the presence of nearby static objects preceding target onset. In this experiment we presented static Gabor patches (as flankers) next to the nearby target. We found that static Gabor patches were not able to produce a facilitated effect.

These outcomes suggest that the system does not linearly predict objects future position and maybe uses heuristics strategies that prompt for any trajectory length. Thus, a stimulus that moves in visual space in two coordinates or in 16 coordinates would have equal high priority in processing, and it would result in a temporal facilitation. One possible explanation is that error coding for both stimuli (moving in 16 or two coordinates) are almost the same, as also the subsequent stimulus coding, that is prompted faster, which may be sufficient to enhance a perception in the predicted location (where the object would be in the future), following the predictive coding hypothesis proposed by Eriksson et al (2012), see Figure 41 in Experiment 9, page 106.

Anticipation dynamics for motion are well established, however, it remains unknown which exact parameters of motion trajectories are most importance and the interplay between them.

4. General Discussion

Chapter 4

4. General Discussion

The aim of this doctoral dissertation was to provide behavioural evidence for a spatial facilitatory effect induced by moving objects. Our results support the hypothesis that a moving object affects perception in future positions near the predicted trajectory of motion. Additionally, we had extensively studied some relevant variables akin to an anticipatory coding for motion by which cortical cells are preactivated along the trajectory. These facilitatory modulations (neurons' preactivation) triggered by horizontal connections in the primary visual cortex may be the responsible for faster processing and integration of moving objects. These modulations prepare the cortex for the object's future trajectory which may underlie spatial facilitation in future positions of motion.

Preliminary findings from Experiments 1 and 2 demonstrated that motion led to higher detection probabilities and less reaction times (RTs) means for objects located next to the leading edge of an object that moved along predictable locations. Accordingly, an object moving in predictable locations, one after the other in space and time, enhanced target detection in positions further ahead of its trajectory. On the contrary, an object that randomly moved in the same space positions was not able to produce such facilitation. Moreover, we observed that for the predictable trajectory condition facilitation followed an anisotropic pattern being that horizontal locations were more facilitated (less RTs) regarding vertical locations. This finding is in agreement with an anisotropic travelling wave induced by moving objects (Kaplan et al., 2013).

We went further on testing this facilitatory effect and build an experimental paradigm that was able to boost an illusion of movement for static objects located next to the leading edge of motion (Chapter 3.2). If motion trajectories preceded a static target, that target would be perceived earlier compared to a distant target; i.e. participants would perceive one static target first and then the other. Based on this paradigm, we found that the number of motion trajectories enhanced perceptual facilitation (Experiments 3 and 4). Orientation of Gabor patches carrier revealed not to be a determinant factor and facilitatory effects were observed for this type of orientation as well (Experiment 5). On the other hand, increasing distance between the leading edge of motion and target reduced the facilitatory effect, although we were not able to suppress facilitation with the distances tested in our experiment (Experiment 6). Results also indicated that by incrementing the contrast of motion the facilitatory effect also increased (Experiment 7). A surprising finding was the one related to the length of trajectories as we were expecting that by decreasing the length the facilitatory effect would also be reduced (Experiments 8 and 9). Nevertheless, we found that a stimulus that moves in only two locations was sufficient to led to a perceptual facilitation. Moreover, the presence of static Gabor patches did not yield a significant facilitatory effect indicating that the effect was specific to motion (Experiment 10).

In the following sections we will discuss and relate the main conclusions of our findings with psychophysical and physiological outcomes with the aim to shed light into the anticipatory dynamics underlying moving objects perception.

4.1. Anticipation dynamics and spatial facilitation ahead of the leading edge of motion

Nervous fibre information transport imposes some delays for perception and for that reason some sort of compensation should be handled by the visual system, especially for moving objects. Physiological and anatomical studies using optical imaging and intracellular recordings demonstrate that horizontal connections between neurons in the primary visual cortex (V1) mediate neural latency for moving objects (Bringuier et al., 1999; Chavane et al., 2011; Grinvald, Lieke, Frostig, & Hildesheim, 1994; Jancke et al., 2010). Hence, when a stimulus is presented in a neuron’s receptive field (RF), a spatial spread of its activation occurs, which allows other neurons to integrate contextual information about such stimulus. In addition, moving stimuli presented one after the other change cortical activation dynamics in a way that could explain faster processing; i.e. neurons are preactivated in the presence of moving images across the retina (Jancke et al, 2004). Motion signals are computed quickly and may produce a predictive anticipation of the probable trajectory, preactivating those neurons coding for that region of the space enhancing processing speed (Maiche et al., 2007; Purushothaman et al., 1998; Yilmaz et al., 2007). It has been argued that this fast spread of neural activity through long-range horizontal connections of nearby neurons reduces their time-to-fire threshold when a stimulus appears in their RF (Jancke et al, 2004, 2010; Sato, 2012).

Our findings strongly support physiological data by means of preactivation of neurons induced by a moving object in the primary visual cortex (V1). We confirmed that stimuli known to influence neural spread of information through horizontal connections had influence in perceptual facilitation as well. In this regard, higher *contrast* motion trajectories induced a perceptual facilitatory gain. This outcome is related to findings showing that increasing stimuli contrast decreases the neural latency of neurons in the lateral geniculate nucleus (LGN) and cat area 17 (analogous to V1) (Gawne, Kjaer, & Richmond, 1996, Jancke 2004). Moreover, our results are in accordance with psychophysical results that show an increased latency when decreasing contrast (Solomon & Morgan, 1996, as cited in Cass, 2006; Purushothaman et al., 1998; Yilmaz et al., 2007).

Increasing the *number of motion trajectories* enhanced perceptual facilitation of a target located next to the leading edge of trajectories, despite Gabor carrier orientations. Based on a predictive coding (maybe mediated by horizontal connections) it is not surprising to find facilitatory effects as a function of the number of trajectories. If trajectories are displayed converging to the spot where the target will be located, it is therefore expected that there would be an improvement on target perceptual detection. That is, more input through horizontal connections would arrive to neurons facilitating their firing threshold when the stimulus arrives at their receptive field (RF). Further experiments should be conducted to disentangle when does the effect saturates according to the number of motion trajectories.

Neural latency is also known to be influenced by *orientation* of stimuli as V1 architecture is highly orientation dependent. Stimuli oriented in the same fashion preactivate cells with similar orientation preferences, and thus, when the stimulus appear at their RF they would show a higher peak of activation and a faster response to such stimulus (Paradis et al., 2012; Seriès, Lorenceau, & Frégnac, 2003). Neurons may not facilitate each other by horizontal connections for non-coaligned Gabor as they do for coaligned ones (Gilbert, Ito, Kapadia, & Westheimer, 2000; Kapadia, Ito, Gilbert, & Westheimer, 1995; Kapadia et al., 1999; Polat, Mizobe, Pettet, Kasamatsu & Norcia, 1998). However, non-coaligned Gabor patches (orthogonal orientation to the trajectory) may also elicit a response from neurons tuned to all orientations, which in turn, might propagate activity in horizontal connections. In fact, we also found a temporal facilitation enhancement for orthogonal orientation. Our results suggest that moving objects enhance onset detection at positions next to the leading edge of motion and that the effect is stronger when moving Gabor patches are coaligned with the trajectory direction. Moreover, when we analysed both Experiments 3 and 5 (coaligned Gabor and non-coaligned Gabor, respectively) we found a main effect regarding the number of trajectories, but not regarding Gabor carrier orientation. Thus, it seems more relevant the number of motion trajectories than Gabor carrier orientation for the anticipatory mechanism.

Although, there is a study that found a perceptual speeded-up effect of coaligned Gabor along the trajectory we did not obtain analogous results. In the study of George et al. (2002) coaligned trajectories were perceived as moving faster compared with non collinear trajectories. These authors propose a faster propagation of information through horizontal connections for those Gabor with carrier orientation according to the direction of the trajectory. Moreover, Gabor patches aligned along the trajectory elicited responses with shorter latency as measured with magnetoencephalography (MEG) (Paradis et al., 2012). Furthermore, RTs also have been documented as able to decrease with perceived velocity (Kuldkepp, Kreegipuu, Raidvee, & Allik, 2011) and given such evidence, we were expecting a related result on perceptual facilitation for those stimuli known to be perceived as moving faster (i.e. co-aligned Gabor). It can be the case that middle temporal area (MT) plays an important role enhancing perception at the leading edge of motion (without regard to stimuli orientation) with strong feedback to V1. MT is known to modulate the facilitatory travelling wave and in this case may prompt perceptual facilitation as well as a reaction for a moving object presented in the visual field (Jancke & Erlhagen, 2010).

Furthermore, increasing the distance between a stimulus location and the RF of a specific neuron decreases the subthreshold activity that such specific neuron would receive by adjacent neurons through horizontal connections. Similarly, we manipulated the *distance* between the target and the leading edge of motion to test if increasing distance would decrease the facilitatory effect. However, we found such facilitatory effect in all the distances tested (Experiment 6) probably because they were not sufficiently long to suppress such effect. It may be the case that motion trajectories induce a strong perceptual bias that affect an area with more than two visual angles ahead of motion. It is well known that motion propagates a peak of activation that spreads further ahead of the trajectory (Jancke et al., 2010, 2004, 2010b) and might be that this peak is ahead of motion for several visual angles. Moreover, the travelling wave caused by motion in our experiment could so accentuated that a longer distance was needed in order to vanish the facilitatory effect. Thus, further research testing longer distances are needed in order to clarify its role on perceptual facilitation.

On the other hand, perceptual facilitation induced by motion has been reported in other experiments, as for instance, using the Flash Lag Effect (FLE). The FLE increased when moving objects converged to the spot where the moving object would be presented in the next future indicating an increased perceptual facilitation for the moving object (Maiche et al., 2007). Additionally, perceptual facilitation by means of a lower threshold to detect objects at the leading edge compared to the trailing edge of motion has been reported as well (Arnold et al., 2007; Roach et al., 2011; Van Doorn & Koenderink, 1984; Verghese et al., 1999). In fact, V1 neurons have a shorter delay at the offset regarding the onset of moving objects (Bair et al., 2003), which may be related to the perceptual improvement at the leading regarding the trailing edge of motion. Possibly related to this perceptual improvement, recent studies using functional magnetic resonance imaging (fMRI) showed less blood oxygenation level dependent (BOLD) signals at the leading edge of motion and the opposite effect for the trailing edge which may be related to a forward predictive mechanism (Alink et al., 2010; Schellekens et al., 2015, 2014). However, as mentioned in the introduction, there is still debate in whether motion facilitates perception at the leading or trailing edge of a moving object (for a discussion see: Arnold et al., 2014). Taking into consideration our results, we cannot disentangle whether facilitation is distinct at leading or at trailing edge of motion, and thus, further research is required for clarification on this matter.

Moreover, our findings do not support motion masking as target detection was not impaired by motion. In fact, we found that a static target located next to the leading edge of motion was perceived earlier and brighter. This could be due to the fact that motion masking is an effect that occurs when the object to be detected within motion trajectories has an irregularity, such as change in contrast, colour, shape or gaps; or if the spatiotemporal property of the moving object is disrupted (Kanai et al., 2009; Polat, Sterkin, & Yehezkel, 2007). On the contrary, in our experiments the target was located where the moving object would be in the next future and thus, the spatiotemporal propriety of the moving object was maintained constant. Moreover, we observed that facilitation increased with the number of motion trajectories which give further evidence against a possible effect of motion masking.

4.2. Predictive coding

Lateral connections mediated by long range horizontal connections could be the mechanism that leads to subthreshold activation of neighbouring neurons when a stimulus starts to move (Chavane et al., 2011; Paradis et al., 2012; Seriès et al., 2003). This subthreshold activity may improve the sensory representation of neurons preparing them to the forthcoming moving stimulus. It is also very likely that neurons compute sensory information by a predictive coding.

Our findings support the hypothesis for a predictive anticipation of future positions of a moving object. However, results about trajectory length were contradictory to our expectations as we expected that longer trajectories would induce facilitatory effects in a higher degree than short trajectories. Firstly, longer trajectories when compared to short ones, would elicit the transmission of more motion signals to adjacent neurons through horizontal connections creating a travelling wave that should spread further along the trajectory. Secondly, taking into account a predictive coding perspective, we expected that longer trajectories would minimize neurons error coding further along the trajectory regarding shorter trajectories. It is worth of note that we ran a control experiment presenting one static Gabor during 17 ms to be sure that motion was a necessary condition (Experiment 10). Due to the reason that the object did not move it was impossible to predict its new position, and, in fact, results revealed no facilitatory effects. However, Gabor patches that moved in two close locations presented for 33 ms (16.7 ms + 16.7 ms) were sufficient to induce facilitatory effects. Thus, it seems that two locations are enough in order to predict the future third position (in our case the third position was the position where the target was subsequently displayed). The facilitatory effect observed in that future position may be prompted by a mechanism that take into account the very recent past (Palmer et al., 2015). Besides, predictive filtering models suggest that the system only needs three consecutive movements along the same direction to signal the presence of a trajectory (Burgi, Yuille, & Grzywacz, 2000). In our study, two positions were enough to prompt earlier onset detection because it can be the case that information is enough to establish prior probabilities and predict posterior probabilities regarding a probable third position.

A possible explanation for our length outcomes is the proposed predictive coding by Eriksson and colleagues (2012). They suggest that a neuron is able of combining stimulus and error coding, which in turn, permit that a single neuron computes an object free of assumptions (direct stimulus recognition) as well as the error of prediction that depends on experience (Eriksson et al., 2012). In their model, neurons would first signal error coding and afterwards they would code the stimulus information (stimulus coding). The proposed model predicts that a high contrast moving object would elicit a lower error coding and a sooner and stronger stimulus coding. On the contrary, low contrast moving objects neurons would trigger a higher error coding and a later and weaker stimulus coding regarding the high contrast stimuli (model represented in Figure 41, page 106). This model can explain our findings for high contrast and low contrast motion trajectories, as higher facilitation was found when the target was preceded by high contrast motion. On the other hand, the model can also account for our length results. We hypothesized that an object with higher contrast that moves along two close positions would elicit lower prediction error and a sooner and stronger stimulus coding similarly as higher contrast motion with longer trajectories would. Following this assumption, independently of the trajectory length the system will rapidly enhance stimulus coding for any high contrast motion (see Figure 41, page 106). In sum, trajectory contrast would modulate neurons response in a higher degree regarding trajectory lengths.

Another possibility is an heuristic suppression from the leading to the trailing edge of motion as proposed by Schellekens and others (Schellekens et al., 2015). These authors suggest that predictive coding of motion follows a heuristic algorithm, rather than literally predicting the trajectories of motion. The authors reported no significant differences in BOLD activation for different trajectories durations. However, such study manipulated longer durations (1500 – 4000 ms) compared to our study and for that reason we cannot directly compare both results. However, heuristics solutions are implemented in several models, as for example, to solve the aperture problem, time to collision (TTC), rotatory motion perception, Hering illusion, among others (Agaoglu, Herzog, & Öğmen, 2015; DeLucia, 2004; Hubbard, 2013; Kozhevnikov & Hegarty, 2001; Perrinet & Masson, 2012; Vaughn & Eagleman, 2013). Heuristics strategies may be used as an ongoing strategy in perceptual judgments to overcome processing speed (Braunstein, 1976; DeLucia, 2004). Therefore, it may be possible that to perceive motion trajectories the system applies heuristic strategies to process future positions fast and effortless without large demands of cortical activation. Hence, when an object moved in a short trajectory produced a facilitated effect on targets detection, which could reflect heuristic strategies aimed at favouring the efficiency of motion processing, independently of trajectories length.

In conclusion, we found that there is a perceptual facilitation for a static target if it is located next to the leading edge of coaligned moving objects depending on trajectory’s contrast, number of trajectories and distance from the target. Therefore, when several objects move with higher contrast (independently of trajectory length and Gabor orientation) and the target is located closer to the leading edge of the moving object a facilitatory effect occurs.

4.3. Spatial attention

Spatial exogenous attention (stimulus-driven) should be recruited as well when moving objects are displayed, as motion per se can direct attention (Predebon, 1996). It may be possible as well that exogenous attention is related to the preactivation of adjacent neurons when processing a predictable moving object, i.e. a type of sensory facilitation (Schneider & Bavelier, 2003). Accordingly, when attention is recruited for a specific attribute as shape, speed or colour, the corresponding cortical area responsible to process that attribute, exhibit higher activity (Corbetta et al., 2008).

Exogenous attention is automatic, involuntary, fast and responsible for the detection of unexpected or relevant stimuli reaching its peak at 100 ms after stimulus onset (Corbetta, Patel, & Shulman, 2008; Nakayama & Mackeben, 1989). Hence, it is unlikely that spatial attention would explain our results for a number of reasons. Firstly, neither motion nor static Gabor attracted exogenous attention due to their short duration on the screen. Secondly, all experiments were conducted while participants fixed at the centre of the screen and targets appeared above and below the fixation point. If participants pursuited motion trajectory they would not be able to decide if the target moved up or down and data would reflect that difficulty. Moreover, subjective reports of participants revealed that they were only aware of (the last) four-three motion signals. Trajectories were so fast that if they looked at trajectories, thereafter, they would need to redirect attention again by a saccadic eye movement and this would not able them to correctly answer the experimental question; this was reinforced in practical trials.

4.4. Limitations of the present research and further work

We were able to show a perceptual facilitatory effect of moving objects at the area next to the leading edge of motion. Notwithstanding, our study has a number of limitations that we would like to acknowledge. The main limitation of Experiments 1 and 2 was the fact that targets were not located in the same horizontal axis as the moving object. So, we decided to design a new paradigm for the following experiments; we created an illusionary effect induced by moving objects in the surrounding. However, we did not directly assessed detection signal theory or reaction times to analyse spatial facilitation. Instead, we generated a different research question to assess whether the participants had seen the target (located nearby motion) before than the distant target as we believed this could be an elegant manner to access temporal facilitation. Another limitation concerns the distance used in Experiment 4 that was not enough to vanish the facilitatory effect and for that reason long distances should have been tested.

Taking the outcomes from this doctoral dissertation several experiments would be needed in order to shed light in spatial facilitation by the manipulation of key factors as, motion speed, target's orientation and stimulus onset asynchrony (SOA) between motion and the target. In addition, perceived brightness remained unexplored as we only assessed it in one experiment (Experiment 4) and it will be of relevance to study as well whether brightness perception also depends on orientation, trajectory contrast, distance or on trajectory length. Moreover, considering the same paradigm investigated here we could also assess reaction times to observe if it correlates with the present results (Experiments 3 - 10). Additionally, it will be pertinent to test the same experiments with slower motion that may be more sensible to horizontal connections dynamics. Furthermore, it would be opportune to study effects at the trailing edge of motion as well as at the middle of the trajectory to further elucidate the role of motion on spatial facilitation.

We tried to link psychophysical and physiological findings in order to provide an effortful debate on how the facilitatory effect would be implemented for a better understanding of visual motion processing. Our studies revealed that variables known to mediate latency of neural information spread through horizontal connections influence perception as well. Following these outcomes, perceptual latency may be strongly connected to neural latency and such evidence is pertinent for moving objects and its influence in human motion perception. However, as mentioned former many relevant aspects remain unexplored at the end of this doctoral dissertation. Future research will further characterize this spatial facilitation and its implications for the human visual systems that compute motion and anticipates positions further ahead of motion trajectories.

5. Conclusions

Chapter 5

5. Conclusions

In conclusion, our psychophysical results show that perceptual facilitation of a static stimulus can be enhanced when located in close spatial proximity from the leading edge of motion. The facilitatory effect reported here could result from a preactivation of those visual cortex neurons coding for the region of the space next to the predicted trajectory, as a preparation of the system for processing subsequent input (Jancke et al., 2004; Maiche et al., 2007; Paradis et al., 2012; Yilmaz et al., 2007). The preactivation of neurons along the trajectory may be the mechanism responsible of a faster and perceptual facilitation processing for moving objects as reported here. However, a possible role of modulatory signals from feedback connections is also probable.

In summary, we provide evidence that motion induces spatial facilitation by means of a perceptual facilitatory influence at the area next to the leading edge of motion. Specifically, this facilitatory effect depended on the number, on the contrast of motion trajectories and on predictability of the trajectory, whether orientation of moving objects and trajectory length had a less deterministic role. More research is warranted to ascertain these hypotheses and to provide more insight about the role of motion dynamics in human visual perception.

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