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Elaborato Finale

The extrapolation of occluded motion: basic mechanism and application

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Introduzione

Predire la futura posizione di un oggetto in movimento che viene nascosto per un breve periodo di tempo è molto importante per interagire con le numerose variabili dinamiche del nostro mondo circostante. Per predire quando questo oggetto riapparirà alla nostra vista è necessario estrapolarne il movimento (motion extrapolation, ME) durante il periodo in cui non è visibile. Ci sono molte lacune in letteratura riguardo i meccanismi sottostanti a questa apparentemente semplice operazione e questa tesi mira proprio allo studio di questi. Esperimenti comportamentali solitamente utilizzano un compito in cui si chiede ai partecipanti di premere un tasto quando ritengono che un oggetto in movimento, che viene nascosto da un occlusore durante la parte finale del suo percorso, abbia raggiunto una certa posizione spaziale indicata da un indizio. L'istruzione più comune data ai partecipanti è quella di fare una stima del tempo di contatto fra l'oggetto target e l'indizio (time to contact, TTC) (Tresilian, 1999; Rosenbaum, 1972). In questo tipo di esperimento il target non ricompare mai. Un altro paradigma è quello di chiedere ai soggetti di riportare se un target, che viene nascosto per un periodo di tempo più o meno lungo, ricompare in tempo, o in anticipo, o in ritardo rispetto a quanto atteso dai partecipanti nel caso in cui il target mantenesse un moto rettilineo uniforme (Makin, Poliakoff & El-Deredy, 2009; Makin, Poliakoff, Ackerley & El-Deredy, 2012).

Esperimenti

Nella prima parte di questa tesi (Capitolo II), sono andato ad investigare il ruolo che assume il sistema di memoria visiva durante l'estrapolazione di movimento. Inoltre mi sono chiesto se le illusioni che modificano la percezione di velocità interferiscano con l'estrapolazione di movimento andando a modificare la stima del tempo di contatto di due target con differente velocità esperita, ma stessa velocità fisica. La velocità percepita di un oggetto veniva modificata cambiando il contrasto o la dimensione degli oggetti (Thompson, 1972; Epstein 1978). I risultati mostrano come in un compito di stima del tempo di contatto i partecipanti stimino un tempo di contatto più lungo quando la velocità percepita viene diminuita e un tempo di contatto più corto quando la velocità percepita è aumentata nonostante la velocità fisica sia sempre la stessa. Pertanto l'illusione di velocità viene mantenuta nel sistema di memoria visiva influenzando la stima del tempo di contatto.

Il Capitolo III, prende in esame la relazione fra movimento reale e movimento estrapolato. Gilden e colleghi (1995) hanno mostrato come un adattamento visivo abbia un effetto sul giudizio della stima del tempo di contatto. Un ulteriore passo rispetto a questa ricerca è stato indagare se anche effetti di adattamento e priming rapidi possano influire sul giudizio del TTC. Adattamento e priming visivo rapidi avvengono a livelli corticali di elaborazione molto precoci, e se questi hanno un effetto sul TTC è ragionevole pensare per estensione che il movimento estrapolato possa essere elaborato anch'esso (o almeno in parte) a questi livelli. Ai partecipanti che hanno preso parte a questo esperimento veniva mostrato nella stessa regione retinica dove successivamente il target veniva occluso, uno stimolo di adattamento lungo (600ms) o uno stimolo di adattamento breve (80ms) costituito da una tessitura che si muoveva o nella stessa direzione del target o nella direzione opposta. I risultati mostrano come un adattamento lungo nella stessa direzione del target produca una stima maggiore del TTC (similmente ad un motion aftereffect), mentre un adattamento breve produca una sottostima (similmente ad un effetto di priming). Questo indica che l'estrapolazione del movimento possa essere processato (almeno parzialmente) addirittura ai primi livelli dell'elaborazione visiva del movimento dove i meccanismi di priming e adattamento rapidi vengono computati.

Il Capitolo IV della mia tesi esplora non solo i fattori visivi del movimento estrapolato ma anche l'elaborazione temporale. Una prima questione è se l'elaborazione temporale in un compito TTC possa essere descritto da una componente elettrofisiologica come la CNV. Una seconda questione è trovare correlati elettrofisiologici per l'estrapolazione del movimento. I partecipanti che prendevano parte all'esperimento venivano adattati con una tessitura in movimento usando la stessa procedura usata da Gilden e colleghi (1995) mentre l'attività elettrocorticale veniva registrata. L'adattamento produceva un bias nella stima del tempo di contatto e la direzione dell'adattamento modulava l'ampiezza della CNV. Infine una deflessione negativa (N190) è stata trovata negli elettrodi temporo-occipitali come indice dell'estrapolazione del movimento. Questi risultati mostrano come durante un compito di TTC, l'elaborazione temporale sia evidenziata e descritta dalla componente CNV, e come questa componente possa essere modulata da un adattamento visivo di movimento. Inoltre la N190 trovata in questo studio potrebbe essere un marker dell'attivazione dei meccanismi alla base dell'estrapolazione del movimento.

Nel Capitolo V, l'obiettivo è stato quello di distinguere tra "estrapolazione" e "interpolazione" del movimento invisibile. L'estrapolazione è la capacità di estrarre la traiettoria, velocità, direzione e inferire approssimativamente la posizione di un oggetto in movimento non più visibile, perché nascosto da un occlusore, grazie alle informazioni presentate durante il suo percorso visibile. L'interpolazione è concetto molto simile al precedente, quindi anche in questo caso grazie al movimento visibile si può estrarre la traiettoria, velocità e direzione dell'oggetto nascosto da un occlusore. La sostanziale differenza è che per interpolare sono necessari degli indizi visivi posizionati lungo la traiettoria invisibile. Se l'occlusore è invisibile e la traiettoria è simmetrica rispetto a uno di questi indizi spaziali, è possibile unire questi indizi (punti) in una mappa spazio-temporale e inferire dove e quando l'oggetto ricomparirà, cosa non possibile in assenza di indizi spaziali e quindi nella condizione di sola estrapolazione. In un nuovo tipo di compito i partecipanti all'esperimento dovevano premere un tasto il più velocemente possibile, quando vedevano ricomparire un target in movimento rettilineo uniforme che veniva nascosto da un occlusore per un certo periodo di tempo. I risultati mostrano che è possibile addirittura anticipare la ricomparsa del target. Infatti talvolta i partecipanti premevano il tasto di risposta qualche centesimo di secondo prima che il target effettivamente ricomparisse. Questo però era possibile solo in alcune circostanze: 1) l'occlusore non doveva essere messo nella zona in cui è presente la macchia cieca, dove non ci sono proiezioni alla corteccia, 2) doveva esserci il movimento visibile (traiettoria visibile) del target prima della scomparsa e 3) quando l'occlusore era totalmente invisibile un indizio visivo, come la croce di fissazione, doveva essere presentato per indicare la parte centrale della traiettoria invisibile. Quando queste condizioni erano presenti, i partecipanti potevano usare l'informazione spaziale data dal punto di scomparsa e dalla croce di fissazione che indicava il centro della traiettoria invisibile, per inferire per simmetria il punto di ricomparsa dello stimolo. Quindi, avendo a disposizione un set di punti discreti nello spazio sui quali stimare in quale momento il target li avrebbe attraversati, i partecipanti probabilmente interpolavano questi punti in una mappa spazio-temporale per inferire dove e quando il target riappariva. Questo processo di interpolazione di movimento è considerato come un processo di filling-in amodale.

L'ultima parte della mia tesi coinvolge un'applicazione pratica dell'estrapolazione del movimento. Nel capitolo V, viene mostrato come sia impossibile interpolare quando l'occlusore è posto sopra la macchia cieca e quando mancano indizi che nella traiettoria invisibile. In questo caso infatti i partecipanti rispondevano con un vero tempo di reazione e non anticipavano la risposta. Pazienti con maculopatia degenerativa non possono vedere con la loro fovea dal momento che è danneggiata. Pertanto non hanno più proiezioni di questa zona retinica alla corteccia. In un compito in cui viene chiesto di premere un tasto di risposta quando un oggetto scompare nel loro scotoma o riappare dal loro scotoma è quindi improbabile che riescano ad anticipare la risposta usando un meccanismo di interpolazione. È stato condotto un esperimento in cui cinque soggetti con maculopatia degenerativa dovevano appunto rispondere il più velocemente possibile quando un pallino in movimento scompariva dentro il loro scotoma e premere di nuovo lo stesso tasto quando questo ricompariva dal loro scotoma. I partecipanti ripetevano questo tipo di compito per numerose traiettorie (lineari) del pallino. Unendo i punti nello spazio in cui il paziente riportava di non vedere o di vedere nuovamente il target, un programma al computer riproduceva forma e dimensioni dello scotoma. Lo scotoma trovato veniva poi confrontato con quello ottenuto con la microperimetria Nidek-MP1. Una correlazione lineare con un R^2 di circa 0.8 è stata trovata nella misurazione dello scotoma con la Nidek-MP1 e lo scotoma misurato con quest’ultimo esperimento unendo i punti nello spazio in cui i pazienti vedevano ricomparire il pallino. Pertanto questo programma molto semplice potrà nel futuro essere usato per misurare la dimensione di uno scotoma quando apparecchiature costose e complesse come la Nidek-MP1 non sono disponibili.

Abstract

Introduction

Predicting the future states of moving objects that are hidden by an occluder for a brief period is of paramount importance to our ability to interact within a dynamic environment. This phenomenon is known as motion extrapolation (ME). Numerous gaps in the literature can be found disregarding the mechanisms involved in ME of which the current thesis attempts to address. Behavioural experiments usually utilize a prediction-of-motion paradigm, which requires participants to make a direct estimation of the time-to-contact (TTC). In this task, the initial trajectory of a target stimulus is presented, which then becomes occluded, observers are then asked to respond when they believe the target has reached a marked point behind that occluder without it ever actually reappearing (Tresilian, 1999; Rosenbaum, 1972). Alternatively, other experiments have adopted a timing discrimination task in which participants are required to indicate whether a moving target, following occlusion, reappears ‘early’ or ‘late’ (Makin, Poliakoff & El-Deredy, 2009; Makin, Poliakoff, Ackerley & El-Deredy, 2012).

Experiments

In the first part of this thesis, I investigated whether the visual memory system is active during the extrapolation of occluded motion and whether it reflects speed misperception due to the well-known illusion such as the apparent slower speed of low contrast object or large size object (Thompson 1982; Epstein 1978). Results revealed that with a TTC task observers estimate longer time to contact with low contrast and large stimuli compared to high contrast and small stimuli respectively. Note that the stimuli in both conditions are moving at equal speed. Therefore, the illusion of the apparent slower speed with low contrast and large stimuli remains in the visual memory system and influences motion extrapolation.

Chapter III aims to investigate the interaction between real motion and motion extrapolation. Gilden and colleagues (1995) showed that motion adaptation affects TTC judgment showing that real motion detectors are somehow also involved during ME. A step further that I made was to investigate the effect of brief motion priming and adaptation, occurring at the earliest levels of the cortical visual streams, on time-to-contact (TTC) estimation of a target passing behind an occluder. By using different exposure times of directional motion presented in the occluder area prior to the target’s disappearance behind it, my aim was to modulate (prime or adapt) extrapolated motion of the invisible target, thus producing different TTC estimates. Results showed that longer (yet sub-second) exposures to motion in the same direction of the target produced late TTC estimates, whereas shorter exposures produced shorter TTC estimates, indicating that rapid forms of motion adaptation and motion priming affect extrapolated motion. My findings suggest that motion extrapolation might occur at the earliest levels of cortical processing of motion, where these rapid mechanisms of priming and adaptation take place.

In Chapter IV of my thesis, I explore not only the visual factors of motion extrapolation, but also the timing mechanisms involved and their electrophysiological correlates. The first question is whether the temporal processing is required for accurate ME, and whether this is indexed by neural activity of the Contingent Negative Variation (CNV). A second question is, whether there is a specific electrophysiological correlates that highlight the shifting from real motion perception to motion extrapolation. In this electroencephalographic experiment, participants were adapted with a moving texture (Gilden et al., 1995). The adaptation with the moving texture could bias and modify temporal processing. Participants made a direct estimation of Time to Contact, which showed that classic adaptations were able to bias temporal judgments and modulate the amplitude of the CNV, suggesting a complex feedforward-feedback network between low- and high level cortical mechanisms. Finally, a negative defection (N190) was found, for the first time, as a neurophysiological correlate in the temporal-occipital electrodes in the right and left hemisphere for the rightwards and leftwards ME respectively, indicating the involvement of motion mechanisms of intermediate cortical level in ME.

Chapter V aims to show at distinguishing between extrapolation, and interpolation of occluded motion. Extrapolation is the ability to extract the trajectory, speed and direction of a moving target that becomes hidden by an occluder, thanks to the information extracted from the visible trajectory. Interpolation is a similar phenomenon, i.e. from the visible trajectory one can extract speed and direction as in Extrapolation. The main difference is that for interpolate visible cue are needed along the invisible trajectory. If the occluder is invisible and the occluded trajectory is symmetrical respect to a visible cue, one can connect these cues (spatial points) in order to form a spatio-temporal map and infer where and when the target will reappear. This is not possible in absence of visible cues such as in extrapolation condition. In a new task, observers were required to press a button as fast as possible (reaction time) when they saw a moving target reappearing from an invisible occluder. Results showed that observers could even anticipate the reappearance of an object moving behind the occluder. However, only in some circumstances: i) when the occluder was not positioned over the blind spot but in retinal areas that project to the visual cortex; ii) with an entirely invisible occluder the visible motion before occlusion had to be presented and iii) visual-spatial cues had to signal the center of the invisible trajectory. When these conditions are given, observers can use the spatial information given by the point of disappearance, the visible cue that represented the center of the invisible trajectory, then infer the point of reappearance by symmetry. Therefore having a set of discrete spatial positions (and its cortical representation) in which the moving occluded target will be in a certain moment of time, it is convenient to interpolate this point in order to create a spatio-temporal map to infer where and when the object will be (saliency map). I consider this process of motion interpolation as an amodal filling-in process.

The last part of my thesis involved a practical application of ME. Participants cannot interpolate when the moving target passes in a zone over retinal areas that do not project to the visual cortex (blind spot). In this case, observers perform a true reaction time and do not anticipate the response. Patients with Macular Degeneration cannot see with their fovea since it is damaged. Therefore, that part of the retina does not project to the visual cortex anymore. In a task in which they have to press a response button when a moving target disappear into or reappear from their scotoma, we predict that they cannot anticipate the response to the reappearance of the target. Five patients with macular degeneration were therefore instructed to press a button when they see a moving target disappear into and reappear from their scotoma. Patients repeated this task several times with different linear trajectories of the target. Connecting the point in space in which a patient presses the button, it was possible to draw the shape and the size of the scotoma with a software. The size of the scomota found with this experiment was compared with that measured with a Nidek MP-1. A linear correlation of R2 about of 0.8 was found between the Nidek MP-1 and scotoma measured connecting the point in which patients reported to see the target reappear from their scotoma. Therefore, this software which was written by me (considering its limits) may become a useful tool to obtain a reliable perimetry in a given situation in which an expensive machine such as the MP-1 is not available.

Chapter I

Literature Review

1.1 Introduction

In the world we live in, where everything is in constant motion, we find that many objects continuously cross our visual field. At times, their trajectory becomes hidden for a brief period by other objects. In these circumstances, the ability to accurately judge the time of reappearance of the hidden object becomes very important. For example, to avoid an accident while driving, we have to judge, and we often do it quite accurately, the time it takes for a motorbike to pass behind a still bus at a bus stop. This common skill (innate ability) brings up many interesting questions. Firstly, every observer probably is convinced that the biker is continuously in motion. Therefore: - Is this merely a matter of belief or of knowledge based on past experience, or is the continuity of the movement actually "seen" by the observer? (Burke 1952). Do visible and invisible motion similarly depend on spatio-temporal parameters? Finally, how do we perform an estimate of occluded motion on the basis of visible motion and what kind of mechanisms and brain areas are involved? This thesis attempts to answer these fundamental questions.

In the 20th century, the focus was on the perception of continuity (Burke 1952, Michotte 1946, 1950; Michotte, Thinès, Crabbé 1964; Michotte & Burke 1951; Sampaio 1943). Indeed, in Burke's (1952) experiment, one object disappeared behind a screen and another similar object reappeared from it. He studied conditions in which the observers had the impression of one object in continuous and uniform motion that passed behind the screen (tunnel) and he called this phenomenon the "tunnel effect". In this study it was shown that observers "see" the movement in the "hidden" phase despite the fact that they all agree that the "hidden" phase cannot be described in terms of sensory qualities. In fact, they see neither the colour nor the form of the object during its course behind the tunnel. The absence of the direct sensorial stimulation justifies the use of the term "amodal data" to describe the way in which the hidden movement is "seen" by the observer. Burke (1952) concluded that: - these "amodal data" form the bridge between the modal phases and become an integral part of the total sensory experience. He added: – a complex system of excitations elaborate modal and amodal phases in similar ways and one can thus consider this amodal aspect of the combined experience (modal + modal phases) as a truly perceptual phenomenon.

In the last decade of the 20^{th} century and the first of the 21^{st} century, the focus was on the ability to accurately predict when a moving object reappeared from behind an occluder. Previous studies have addressed this issue by using a prediction-of-motion paradigm, in which observers estimate the time to contact (TTC) using the speed information of the object's initial trajectory (prior to occlusion), i.e., the time between the disappearance of a target's leading edge behind the occluder, and when it would make contact with a given point of interception. The difference between the "total response time" (total response time = TTC + duration of the visible trajectory) and the "physical arrival time" results in the "timing error" (Benguigui & Bennett, 2010; Benguigui, Broderick, & Ripoll, 2004; DeLucia & Liddell, 1998; Makin & Poliakoff, 2011; Makin, Poliakoff, Chen, & Stewart, 2008; Makin, Stewart, & Poliakoff, 2009; Peterken, Brown, & Bowman, 1991; Rosenbaum, 1975). This TTC task is often also referred to as the prediction motion task (Benguigui & Bennett, 2010; Benguiguiet al., 2004; DeLucia & Liddell, 1998; Makin & Poliakoff, 2011; Makin et al., 2008; Makin et al., 2009; Peterken et al., 1991; Rosenbaum, 1975) while the action of "estimating" motion behind the occluder is called motion extrapolation (DeLucia & Liddel, 1998). In mathematics, extrapolation means estimated value beyond the original and known set of points. Therefore, in the motion domain, extrapolation is the operation to estimate the future position in time of an occluded moving target using the information of the visible trajectory (known dataset): space, time and speed.

Rosenbaum (1975) found that observers perform a time to contact task accurately at all speeds. However, several studies suggest that the relationship between the physical arrival time (actual TTC) and TTC (estimated) is not linear (Sokolov & Pavlova 2003) and may depend on different parameters such as target's speed, duration of occlusion, presence of distractors (Baures, Baures, Hecht, & Benguigui 2010; Lyon & Waag 1995). Reynolds (1968), for example, has reported that the timing accuracy of extrapolation tends to increase with increasing inhomogeneity of the display background. Peterken and colleagues (1991) reported that, the time over which the prediction was made rather than the interval for which the target was visible, the distance over which the prediction was made, or the velocity of the target, was found to affect performance. Sokolov & Pavlova (2003) found that the timing error was smaller for long than for short visible trajectories, and for small (0.2 degrees of visual angle, abbreviation: deg) than for large targets (0.8 deg) with a speed of 10 deg/s. Surprisingly, with a target speed of 2.5 deg/s these effects were reversed. Sokolov & Pavlova's (2003) findings suggest that: - when extrapolating motion with targets and visible extents of different sizes, the visual system implements different scaling algorithms depending on target speed. A study which seems to be in conflict with the results found by Sokolov & Pavlova (2003) is that conducted by Horswill, Herman, Ardiles & Wann (2005) in which they showed using very ecological stimuli and approaching motion, that a motorbike (small stimulus) is generally judged to arrive later than a van (large stimulus) having the same speed. However the type of motion used here: translational vs. approaching and the different parameters implemented, did not allow direct comparison of the two studies.

A simple variant of TTC task (or prediction motion task) is an absolute identification (AI) task (Oberfield & Hecth 2008; Braida & Durlach 1972). Only two discrete values of target TTC are generally presented during the experiment: an early TTC and late TTC and observers decide whether the TTC of a target is lower or greater than a standard. Using this paradigm Oberfield & Hecth (2008) asked observers to view a directly approaching target in the presence of a distractor object moving in parallel with the target. They found a contrast effect: if the distractor arrived later than the target, it caused a bias toward early responses relative to the condition without a distractor, whereas the early-arriving distractor had no significant effect. They even found this contrast effect using a prediction-motion task (see Oberfield et al., 2008 Experiment 5). On the other hand, Lyon & Waag (1995) investigated the extrapolation of a target with fixed velocity that travelled along a circular 2-D path. The target moved over an arc of 90 deg and then disappeared. Participants were to assume that the motion continued and after a variable temporal interval, a visible and still line appeared along the circular trajectory to mark the end of the "invisible" motion. The task was to indicate if the position of the hidden target have passed or not the line (pass/ no pass response). In a first experiment, they used different speed and time of occlusion. They showed that participants loss in accuracy with increasing duration of invisible motion and the rate of decline is about the same for targets of different velocity (if the temporal window is held constant). More recently, Bennett, Baures, Hecht, & Benguigui (2010) showed an overestimation of TTC during short periods of occlusion (less than 1 s) and an underestimation for long periods (greater than 1s) regardless of the length of the occluder. These results are in agreement with Peterken and colleagues (1991) who claimed that temporal factors are the major determinants of prediction of the future position of a moving target.

Moreover, numerous studies investigated whether eye movements can increase the accuracy of motion extrapolation. Peterken and colleagues (1991) reported that there were no differences in TTC estimation between fixation and pursuit condition with a target velocity of 5 deg/s or 10 deg/s. However, with a moving target at 2.5 deg/s the TTC estimation was better with eye movements. The authors' conclusion was that pursuit of the occluded object could be the preferred and most effective strategy; however, eye movements are not a prerequisite for accurate estimation of TTC. Bennet et al., (2010) reported that the speed of the target affect the accuracy of TTC estimation but only when fixation is required. They added - the velocity effect exhibited by the fixation group was consistent with participants exhibiting a relatively constant misperception for each level of object velocity. Finally, they conclude there is an advantage in the TTC task with pursuit thanks to the available retinal and extra-retinal input. Makin & Poliakoff (2011) asked participants to discriminate correct reappearance times of a hidden moving object from incorrect (too early or too late) with a two-alternative forced-choice button-press during eye movements recording (discrimination task). They reported that when eye movements were permitted, the accuracy increased. Moreover, they even found that when participants were required to fixate, small changes in eye position around fixation (< 2 deg) were influenced by occluded direction target motion. In other words, when the occluded target was near the left of the screen, mean eye position was nearer the left, and when the target moved rightwards, mean eye position moved rightwards with it. DeSperati & Deubel (2006) asked observer to fixate a central cross and extrapolate (observers were instructed to imagine the invisible target) the motion of a spot that moved along a circular trajectory and then vanished. During this task, a flash was presented with some displacement relative to the direction and position of the imagined spot. The task of the observers was to make a saccade to the flash. Saccades were delayed about 50ms when the flash appeared displaced from the imagined spot, compared to when the flash was presented in its proximity. Jonikatis, Deubel & DeSperati (2009) showed a clear relationship between eye position and invisible target position in a concurrent motion imagery task. They added that from their analyses of eye movements traces, participants tried to “pursue” with a sequence of saccades the invisible motion of the target with their eyes. Note that because smooth pursuit eye movements usually are not elicited in the absence of the direct sensory experience, saccadic – instead of pursuit – eye movements were expected in Jonikatis and colleagues’ (2009) study. To conclude: eye movements are helpful during motion extrapolation, however observers can accurately do the same operation with a fixation point on the screen.

Different theories have been proposed to explain the mechanisms of motion extrapolation. In the nineties, a theoretical approach to understanding time-to-contact estimation in the approaching motion has been dominated by the tau-hypothesis, which has its origins in J.J. Gibson’s ecological approach to perception. The hypothesis proposes that a time quantity (tau), present in the visual stimulus, provides the necessary time-to-contact information. The basic notational device is extremely simple: if X is a time varying quantity and dX is its temporal derivative, the tau function of X, written $T(X)$, is defined to be X/dX and has the dimension of time (Tresilian, 1995). Lee & Young (1985) referred to as tau margin the quantity $–T(X)$ where

-X is the distance of an approaching target from an observer. However, Tau's hypothesis has some critical limitations such as: (1) it neglects accelerations; (2) it provides information about TTC with the eye (but not between for example two objects in the space); (3) it requires that an object be spherically symmetric; (4) it requires that the object's image size and expansion rate be suprathreshold. Moreover, Lacquaniti and colleagues (1993) and Tresilian (1990) have shown the fallacy of the TTC based only on the tau. First Lacquaniti and colleagues (1993) demonstrated that an estimate of the ball's acceleration was contributing to the estimates of TTC used to make the catch. Second, Tresilian (1990) showed that even when the only visual information about TTC available to observers was that provided by tau (or its equivalent) performance in an interceptive task was far too accurate to have been based on tau. Several authors proposed revised version of the *tau* hypothesis, however recent findings suggest that judging time-to-collision is task- and situation-dependent, is of many different origins (of which *tau* is just one) and is influenced by the information-processing constraints of the nervous system (Tresilian, 1999). Another possible and simpler strategy is to count down the time of occlusion after having taken the necessary timing cues from the visible motion (Tresilian 1995, DeLucia & Liddel 1998). DeLucia & Liddel (1998) tested this hypothesis with a double task. The main task was a TTC task. The second and interference one was to judge the relative temporal duration of the presentation of two lines (visual task) or of two tones (auditory task). The rationale of this study was: if the motion extrapolation in a prediction motion task (or TTC task) involves only a clocking process (count down during the invisible trajectory) both interference tasks should decrease the performance by the same amount. On the other hand, if it is involved (somehow) the visual system (for example visual tracking strategy) there should be a worse performance with a concurrent interference visual task than with the concurrent interference auditory task. DeLucia & Liddel (1998) did not find any differences in the main TTC task, however their experiment showed a decrement in the performance of the second interference task, (i.e. the relative duration task) but only when visual stimuli were used. This suggests that motion extrapolation demands visual resources. However, the authors added that is not likely to rule out the possibility that the interference task changes the strategy or process involved in a TTC task. An interesting study made by Gilden, Blake & Hurst (1995) could shed light on the role of the visual system during motion extrapolation. In the latter study, participants had to make a TTC judgment when a moving object disappeared beyond an occluder. However, before each trial, the region corresponding to the occluder was adapted with translational motion. This adaptation lasted 150 s on the first trial, and was followed by top-ups of 10 s on each successive trial. The results showed that when the target object moved in the same direction as the adaptation, TTC estimates were longer, whereas when the target object moved in the opposite direction with respect to that of adaptation, TTC estimates were shorter. The interpretation given by the authors was that adaptation of the occluder area biases the responses of motion detectors (with receptive fields sensitive to that area) toward the direction of motion opposite that of adaptation (similar to what occurs in the classical motion aftereffect [MAE] (for a review see Mather, Pavan, Campana & Casco 2008). This increases the motion signal of the extrapolated motion of the target object when its direction is opposite with respect to the adapted one, and decreases the motion signal of the imagined motion of the target object when its direction is the same with respect to the adapted one. Based on this study it appears that motion detectors are also very important during motion extrapolation. However, there are some "distinguo", the instruction in Gilden et al.,'s (1995) study was to imagine the moving target behind the occluder and the operation of motion extrapolation with imagery could be different from the motion extrapolation without it. In fact, imagery could be: i) the fundamental and most important operation of motion extrapolation; or ii) (most likely) it could be only one of the numerous processes active during this operation or iii) not necessary at all (Makin & Poliakoff 2011). Therefore, although we cannot conclude that motion detectors for real motion are necessarily involved during motion extrapolation, yet they may come into play when observers were required to imagine the target behind the occluder. Recently, Makin & Poliakoff (2011) proposed that observers extrapolate using a "tracking strategy". They reported some evidences indicating that lateral motion extrapolation involves tracking the moving target, updating its spatial position thanks to the continuously shift of the visuospatial attention. Other studies are in line with this hypothesis, for instance, Lyon & Waag (1995) showed that visual moving distractors that take away resources from the visuo-spatial attention system reduce motion extrapolation performance and DeSperati & Deubel (2006) found that the detection of briefly flashed probes was enhanced when they were presented in the current position of the occluded target. In addition, Makin & Poliakoff (2011) stressed and carefully investigated the role of eye movements. Indeed, in a discrimination task (discriminate correct reappearance times of a hidden moving object from incorrect, too early or too late, they found that eye movements during occlusion were related to participants' judgment, with better performance with good pursuit than bad pursuit in judging when the target reappeared early. Furthermore, observers reported more often early reappearance as "correct" in the fixation condition. The authors conclude that an overlapping system controls for eye movements and judgments on motion extrapolation tasks. This view is compatible with the premotor theory of attention, in which sensorimotor networks that guide responses to external locations produce shifts of spatial attention. According to this theory, attention and motor planning are not distinct cognitive modules; it is possible to shift attention to a spatial location by planning an action aimed at that location, even if the planned action is never executed (Eimer, Van Velzen, Gherri, & Press, 2007). To summarize Makin & Poliakoff's (2011) hypothesis was that motion extrapolation is guided by a shifting of visuospatial attention to external target location.

Recently, motion extrapolation has been investigated intensively with neuro/electrophysiological technique (Assad & Maunsell, 1995; Barborica & Ferrera, 2002; Ilg & Thier, 2003; Makin, Poliakoff & El-Deredy, 2009; Makin, Poliakoff, Ackerley & El-Deredy, 2012). Assad & Maunsell (1995) trained two rhesus monkey in a task in which a moving target disappear and then depending on experimental context, they could infer the target to be moving or stationary. These authors recorded the activity of the neurons in the posterior parietal cortex and they found that half of these neurons are significantly more active when the monkey inferred the object to be in motion rather than stationary. Barborica & Ferrera (2002) instead recorded the activity of the frontal eye field (FEF) in monkeys during an estimation of the position of an invisible target moving at different speeds. They found that the activity of the FEF was modulated according to the speed of target motion and therefore, they conclude that FEF may be involved in updating the internal representation of target trajectory for predictive saccades. Ilg & Their (2003) found that some neurons recorded in medial superior temporal area (MST) of three rhesus monkeys did not respond differently during pursuit of real and imaginary target. Makin et al., (2009) recorded in human observers the electroencephalography activity during motion extrapolation. They found similar positive event related components over the right temporo-occipital region in tracking a visible and occluded (extrapolation condition) moving target. For the authors this provided further evidence that the same neural systems are involved in tracking both visible and occluded targets. However, in the visible condition, the positive deflection began immediately with the peak that came early with faster stimuli, whereas in the occluded condition the positive deflection began around 200ms following the onset of occlusion and was not modulated by target velocity or location. In a successive study Makin et al., (2012) investigated whether the activation in the temporo-occipital cortex depended on the direction of the target: from left to right or vice versa or if the right occipital cortex was fundamental regardless the direction of motion during the tracking in motion extrapolation and to update the shift of the visuo-spatial attention. Note that neuropsychological studies showed the dominance of the right cortex for the attentional systems (Heilman, Watson & Valenstein, 2002). Makin et al., (2012) found that tracking was not invariantly right-sided. During tracking of occluded motion the positive component at posterior electrodes shift across the scalp depending on the direction of the moving target. In other words, the positivity was ipsilateral to the direction of the moving target. From their findings, they simply conclude that the attentional system that guide the update of the shift of the visuo-spatial attention in ME is symmetrical.

Numerous fMRI studies investigated the neural correlates of a moving occluded target (Jiang, Ding, Gold, & Powell, 2008; Lencer, Nagel, Sprenger, Zapf, Erdmann, Heide, & Binkofski, 2004; Nagel, Sprenger, Zapf, Erdmann, Kömpf, Heide, Binkofski, Lencer, 2006; Shuwairi, Curtis, & Johnson, 2007; Kaas Weigelt, Roebroeck, Kohler, & Muckli, 2010). Jiang et al., (2009) recorded eye movements and measures the blood-oxygen-level dependent (BOLD) response during smooth pursuit task. Observers had to track a target moving in a sinusoidal way before its occlusion. These authors reported that during occlusion there are a significant activity of the right early visual cortex, but not in motion-processing area MT/V5 and they conclude that the right early visual cortex can be the mind’s eye that receives input from higher level memory regions to produce simulated vision during occlusion. On the other hand Kaas and colleagues (2010) with the direct instruction of ‘imagine the occluded target’ found out a significant activation of the left mediotemporal area (hMT/V5+). Moreover they analyzed fMRI data using the Granger causality maps (Roebroeck, Formisano & Goebel, 2005). Granger causality maps (GCMs) are statistical maps of the influence from a designated reference region to all other regions in the brain and from all other brain regions to the reference region. Taking the individually localized left hMT/V5+ ROIs as reference regions, they mapped both outgoing influence to other targets in the brain, and incoming influence from other source regions. Conceptually, source activations represent regions whose activation consistently predicts the future activation (i.e. next time-point) of hMT/V5+. Hence, these source regions are hypothesized to have exerted a task-related causal influence on the cortical activation of hMT/V5+. With this statistical analysis, they found that left parietal lobule induced a modulation of hMT/V5+ during motion extrapolation. Moreover, a down-regulation was found in lower visual areas. Kaas and colleagues (2010) proposed that this down regulation could be reflecting inhibition to avoid visual input from interfering with the imagery construction. Nagel and colleagues (2006) reported a correlation between the smooth pursuit velocity (in this condition the target was visible) and BOLD response in the right hMT/V5+. Instead, in a condition with occluded target a negative correlation were found with the FEF, left parieto insular vestibular cortex (PIVC) and the left angular gyrus. Nagel and colleagues concluded that V5 is directly related to the maintenance of an optimal smooth pursuit velocity (SPV) during visual feedback, whereas the FEF, prefrontal cortex (PFC), angular gyrus and PIVC are involved in reconstitution and prediction whenever SPV decrease, especially during maintenance of smooth pursuit in the absence of a visual target. However, note that the interval of investigation for smooth pursuit in the absence of visual target was very small, indeed Nagel et al., (2006) reported that participants were able to pursuit the target only 200ms after disappearance, and then saccades replaced SPEM (smooth pursuit eye movement) (Their & Ilg, 2005). Lencer et al., (2004) tried to investigate the cortical network in a smooth pursuit task in the absence of the visual stimuli (a visible moving target became invisible along some part of its trajectory). They reported many important brain areas active during the occluded motion such as FEF, superior parietal lobe, anterior and posterior intraparietal sulcus, premotor cortex and supplementary and presupplementary eye field, supramarginal gyrus, dorsolateral prefrontal cortex, cerebellar areas and basal ganglia. Shuwairi and colleagues (2007) tried to isolate the specific areas active during occluded motion. They found a significant activation in the precentral sulcus, inferior parietal lobule, temporal cortex and prefrontal cortical regions along the dorsal medial wall compared to an unoccluded condition.

The literature reviewed so far clearly showed that motion extrapolation is not a simple sensorial-cognitive process and different mechanisms may be active during extrapolation such as visual memory, timing, prediction, shift of the visuospatial attention and imagery. In particular, when imagery is involved the activity in the brain areas seems to be a little bit different. However, the role of the visual areas is not very clear at the current state of the literature. It has been shown that the cortical network of the motion extrapolation is very complex and depend on the task instruction and experimental condition (e.g. imagery vs. prediction; pursuit vs. fixation) and required many cortical areas, and according to Lencer et al., (2004)'s study even cerebellar areas and basal ganglia. In summary previous studies showed how complex is this apparently simple operation of motion extrapolation and the probable cortical networks behind it. This thesis aim to shed light on the role of the sensorial and cognitive mechanism of the extrapolation of the occluded motion and to bring new relevant findings in this topic.

1.2 Purpose of the thesis

As pointed out in the previous session, motion extrapolation has received a considerable amount of interest in the past and in recent years. The experiment outlined in the following thesis aimed to further investigate the elaboration of occluded motion trying to find out the underlying processes and mechanisms involved.

In the first part of this thesis (Chapter II), I describe a study investigating whether the visual memory system can retain visual illusion of speed misperception during invisible (or occluded) motion. It is well known that observers can perceive one of two objects with equal physical speed as faster. For instance, observers usually see low contrast objects as slower compared to high contrast objects (Thompson, 1982) or large objects as slower than the smaller ones (Epstein 1978). Sokolov & Pavlova (2003) showed in a time to contact task (TTC) an effect of larger size target: at low speed, the error rate was lower whereas at high speed was higher. However, the large target of Sokolov & Pavlova was made by a horizontally oriented pair of light dots (0.15 in diameter) separated by 0.8 deg (centre-to-centre). Therefore, this type of target was not actually a large target and the authors did not check if this stimulus elicit speed misperception according to the transposition principle (large object perceived slower in speed) (Epstein, 1978). Therefore, from this study is not possible to conclude that the memory system can retain the size-dependent speed illusion during occluded motion. In the study reported in Chapter II, I used high or low contrast and small or large moving targets. Firstly, I checked if these stimuli could elicit speed misperception according to the literature. Secondly, observers were asked to do a prediction motion task (TTC task) to see whether low contrast and large moving target lead actually to a longer TTC than high contrast and small target respectively. Thirdly, I used these stimuli in a discrimination task where any counting or timing strategy is strongly discouraged (Makin et al., 2008). To summarize in Chapter II, I explore whether the early visual memory system can retain in memory the speed illusion due to the contrast and size during invisible motion, as revealed by both TTC estimation and discrimination task.

The purpose of the study reported in Chapter III is to investigate the interaction between real motion and motion extrapolation. Gilden and colleagues (1995) showed that motion adaptation affects TTC judgment showing that real motion detectors are somehow also involved during ME. I went a step further and I investigated the effect of brief motion priming and adaptation, occurring at the earliest levels of the cortical visual stream, on time-to-contact (TTC) estimation of a target passing behind an occluder. By using different exposure times of directional motion presented in the occluder area prior to the target’s disappearance behind it, our aim was to modulate (either prime or adapt) the extrapolated motion of the invisible target, thus producing different TTC estimates. The rationale behind this study is that, if motion extrapolation of the (invisible) moving object is indeed biased by rapid forms of adaptation of the same sorts that produce rMAE and rVMP, and since such adaptation occurs at early levels of visual motion processing (Campana, Maniglia, & Pavan, 2013; Campana, Pavan, Maniglia, & Casco, 2011; Théoret, Kobayashi, Ganis, Di Capua, & Pascual-Leone, 2002; Campana, Cowey, & Walsh, 2002; 2006), then motion extrapolation must also rely somehow on these early levels of processing.

In Chapter IV, the aim is to investigate the timing processes and the electrophysiological correlates of ME, and how they can be modulated by visual factors. The first issue addressed is whether motion adaptation can actually bias the TTC estimation (Gilden et al., 1995) even without the instruction to imagine the invisible target. A second purpose is to investigate whether the electrophysiological correlate of the TTC task is a frontal component called Contingent Negative Variation (CNV), that has been suggested to index temporal processing and expectation (Tecce, 1972) and most importantly, to explore whether the effect of motion adaptation on TTC results into a modulation of the negativity of the CNV. A third purpose of Chapter IV is to investigate whether there are other electrophysiological correlates that indicates the shift from visible to invisible motion besides the temporo-occipital activity (Makin et al., 2008; Makin et al., 2012). In Chapter V, this thesis aims at studying a mechanism that has been neglected so far and that can operate in synergy with invisible motion. Undoubtedly, a moving object appears to move (we know that it moves) continuously even though it is no longer projected on the retina (Burke 1952, Michotte 1946, 1950, Michotte, Thinès, Crabbé 1964; Michotte & Burke 1951; Sampaio 1943). When the occluder is invisible observers have to extrapolate the future position of the moving target using the information of the visible trajectory (speed, space and time). In other words, extrapolation is the process to estimate value beyond the original and known set of value. In motion extrapolation the original and known set of values are the points (in space and time) of the visible trajectory and the values that must be extrapolated are the points of the invisible trajectory. An example of everyday life is a driver that extrapolates road conditions (for example a road trajectory after a curve) beyond his sight while driving. A different but similar phenomenon is interpolation: constructing new data points within the range of a discrete set of known data points. During the elaboration of invisible motion, interpolation mechanism would "fill-in" the object trajectory once it is known where the object is headed and where it will reappear. In other words, having a set of discrete spatial positions in which the moving occluded target will be in a certain moment of time, an internal model of this moving target is constructed in order to allow the interpolation of the intermediate spatial positions in time so as to infer where and when the object will be. To summarize the two processes are very similar, but for interpolation to occur it is necessary to know or infer, for example thanks to visible cue along the invisible trajectory, where the moving occluded target will reappear whereas for extrapolation this inference is not necessary. In this part of the thesis (Chapter V) I investigated whether interpolation is possible during the elaboration of invisible motion and whether the cortical representation of the space is needed in order to “fill-in” amodally the object trajectory. When observers interpolate, they could create a spatio-temporal map of the invisible trajectory from the information of the visible one and therefore they could determine precisely when and where the object will reappear. From a cognitive point of view, interpolation leads to the formation of an internal representation of the moving target that should be more accurate (more information available) than the visuo-spatial representation formed using only extrapolation.

In the final Chapter (VI) I show a practical application of motion extrapolation. People with macular degeneration (MD) cannot see with their fovea since it is damaged, hence the condition in which a moving dot that passes through their scotoma is very similar to the situation in which one have to predict when a moving object reappear from behind an occluder. I asked MD patients to track a moving dot along a linear trajectory maintaining their eye tested fixed (they have to hide a large stimulus in the blind spot), and to press a button when the dot disappeared inside and reappeared from their scotoma. Then a software measured the length of the scotoma along that axes. Having many trajectories and interpolating the spatial point in which the target disappeared and reappeared, the software drew the size of the scotoma. I refer to this perimetry as “interpolation” perimetry since it interpolates the spatial point in which the target disappeared and reappeared. To study the accuracy of this low cost device a comparison was made with the Nidek-MP1 that is a very accurate and expensive device with a gaze tracker incorporated to measure the size of the scotoma. Moreover, connecting only the point in which the target reappears and comparing the size of the scotoma obtained in this way with that given by the Nidek-MP1, I can investigate whether MD patients infer when the occluded target is going to reappear by pressing the button before the reappearance of the target or whether they actually wait to see it again. In the first case, the size of the scotoma should be underestimated or very similar to that measured with the Nidek-MP1, in the second, the obtained scotoma size should be larger.

Chapter II

Illusory speed is retained in memory during invisible motion

2.1 Introduction

In this study, I wanted to investigate how the memory of the speed of a moving object is maintained during the extrapolation of occluded or invisible motion. In a prediction motion task the "timing error" of TTC is often found to depend on speed (Lyon & Waag, 1995; Peterken et al., 1991; Sokolov, Ehrenstein, Pavlova, & Cavonius, 1997; Sokolov & Pavlova, 2003). Rosenbaum (1975) reported that participants perform a prediction motion task accurately at all speeds if the target keep constant speed during its trajectory (no acceleration and no deceleration). However, several studies suggest a nonlinear relationship between visual speed and time to contact. Lyon and Waag (1995) found that observers made many errors in a task in which they had to detect when a slow moving target passes a given cue during the invisible motion compared to when they had to detect a fast moving target. Sokolov & Pavlova (2003) found that the accuracy in a TTC task depends on the interaction among size of the target, the speed and the extent of the invisible trajectory. In sum, depending on the visible velocity (either too low or too fast), on the time of occlusion, and on the length of the visible trajectory, the memory of speed during occluded motion may not always be isomorphic to the input received from the visible trajectory. The most likely explanation is that the underlying neural mechanisms for coding velocity in part corresponds to those involved in memory of speed (Pasternak & Greenlee, 2005) and in part do not. Indeed as already stated in the introduction (Chapter I) there is evidence from both fMRI (Jiang, Ding, Gold & Powell, 2008; Lencer et al., 2004; Nagel et al., 2006; Shuwairi, Curtis & Johnson, 2007) and primate neurophysiological data (Assad & Maunsell, 1931; Barborica & Ferrera, 2003; Ilg & Thier, 2003) of distinct regions of the cortex that increased activity during periods of occlusion relative to full visibility. The activation of these brain areas during occlusion could indicate that visible and occluded motion evokes different speeds processing. However, this seems odd. Indeed, previous psychophysical studies show that speed information that must be used during ME is stored in an extremely precise manner in short-term memory. Speed discrimination thresholds are not impaired within a retention interval of 30 s (Greenlee, Lang, Mergner & Seeger, 1995; Magnussen & Greenlee, 1992; 1999). Magnussen and Greenlee (1992) tested two velocities: 2.5 and 5 deg/s for a 2 c/deg drifting grating. Although discrimination thresholds increased at higher speeds, reference velocity did not interact with the retention interval: i.e. the Weber fraction was almost constant across retention intervals. These results suggest that observers can use speed information stored in short-term memory precisely. Therefore, I would expect that the time to contact reflect the memory of target speed. Furthermore, if this memory of the target speed is altered by a visual illusion, this misperception should be reflected on the TTC. To sum up, my study questions whether speed information, as/when modulated by target contrast and size, is stored in the early visual perceptual memory system and whether it remains active during occluded motion. In this case, we predict that differences in perceived speed will be reflected during occluded motion, independent of the range of visible speed, of the length of the visible trajectory, the length of the occluder, and of the type of task. I manipulated parameters that are known to produce an illusory perceived speed of a moving target. It is well known that perceived speed is affected by contrast (Thompson, 1982, 2003; Thompson, Brooks, & Hammett, 2006). Furthermore, the perceived speed of an object is modulated by its size and by the width of the visible window where the object moves (Epstein, 1978). I measured, as in previous works, the TTC to a visible cue (a bar). I did not compute a simple (absolute) “timing error” (Peterken et al., 1991), but rather analyzed the remembered speed: a ratio between the length of the invisible trajectory and the TTC measured only during invisible motion. I believe that this ratio reflects a true pattern of underestimation and overestimation errors. For instance, let us assume that a high contrast target is perceived about 12 deg/s fast whereas a low contrast target is perceived about 10 deg/s. When they travel behind an occluder 12 deg long an observer will estimate (if the memory of speed is retained during invisible motion) 1 second of occlusion for the high contrast target and 1.2 second of occlusion for the low contrast one, hence the difference in the TTC estimation will be of 0.2 second. Let us assume also that the illusion of slower speed with low contrast target remain constant regardless the value of speeds used (in this example - 2 deg/s). When an observer see the high contrast target moving about 6 deg/s, the speed of the low contrast one will be about 4 deg/s. In this case, the difference in the TTC estimation, when they travel an occluder 12 deg long, will be about 1s. One could conclude wrongly that at low speed the “timing error” is greater for low contrast target when actually the difference in the perceived speed is about 2 deg/s for both high and low speed targets. For this reason, I choose to analyze the differences in speed (remembered speed) and not the differences in time.

2.2 Experiment 1.1

It has been shown that high contrast stimuli appear to move faster than low-contrast stimuli (Gegenfurtner, Mayser, & Sharpe, 1999; Stone & Thompson, 1992; Thompson, 1982, 2003; Thompson et al., 2006). For example, Thompson et al., (2006) found that underestimation of speed at low contrast occurred with grating targets of low (2 cpd) and high (8 cpd) spatial frequency. Experiment 1.1 was carried out to check whether the effect of contrast on perceived speed also occurred when using small circles in a continuous translational motion. In this experiment participants were asked in a two interval forced choice (2IFC) to indicate which of two stimuli, one with high contrast and one with low contrast, was moving faster. The stimuli were presented in two different intervals.

2.2.1 Method

Participants

Six volunteers, 4 males and 2 females, aged between 23 and 25, all right handed, took part in this experiment. They all had normal or corrected-to-normal vision. I obtained informed consent from each subject at the beginning of each experiment.

Stimuli and apparatus

Participants sat in a dark room, 57 cm away from the display screen. Viewing was binocular. Stimuli were generated with Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997) and displayed on a 19-inch CTX CRT Trinitron monitor with a refresh rate of 100 Hz. The screen resolution was 1024 × 768 pixels. Each pixel subtended ~1.9 arcmin. The luminance of the background was 0.8 cd/m^2. Stimuli were presented as small circles of 0.5 deg in diameter. The luminance of the standard stimulus (SS) was 144 cd/m^2 and that of the comparison stimulus (CS) was 1.1 cd/m^2. Both were presented approximately at eye level. Luminance was measured using a Minolta LS-100 photometer. Each target appeared abruptly and traveled horizontally, either leftward or rightward, with equal probability. The motion trajectory was produced by presenting the target in a new position in each frame. The visible trajectory started 9 deg from the center and ended after 12 deg. The speed of high-contrast SS was fixed at 2.5, 5, or 10 deg/s; the speed of the low-contrast CS varied on nine levels: SS speed of 2.5 deg/s: 1.3, 1.6, 1.9, 2.2, 2.5, 2.8, 3.1, 3.4, 3.7 deg/s; SS speed of 5 deg/s: 3.8, 4.1, 4.4, 4.7, 5, 5.3, 5.6, 5.9. 6.1; SS speed of 10 deg/s: 8, 8.5, 9, 9.5, 10, 10.5, 11, 11.5, 12 deg/s. Stimulus duration depended on speed; it ranged from 3243–9230ms, 1967–3157, and 1200–1500ms in the low-, medium-, and high-speed conditions of the SS, respectively.

Experimental procedure

The experiment consisted of three blocks, each devoted to one speed, preceded by 18 trials of practice (2 repetitions x 9 speed levels). Each block consisted of a random presentation of 180 trials comprising 20 repetitions of the 9 speed levels. After 90 trials, a resting pause of 5 minutes was given. In each trial, SS and CS trajectories were randomly presented in sequence, interleaved by an interval of 500ms. I used a 2IFC task in which the participant had to report whether the stimulus perceived was faster in the first or in the second presentation. All participants were instructed to track the moving targets and to press the appropriate key (counterbalanced between subjects) to indicate the interval with the faster target. The next trial started 1000ms after the subject pressed the appropriate button. No feedback was given.

2.2.2 Results

Psychometric functions (Figure 1) were fitted to the probabilities of perceiving the low-contrast target faster than the higher contrast one, as a function of the physical speed levels (Finney, 1971). I then conducted a two-tailed *t*-test to compare individual PSEs, i.e. the point of subjective equality to the point of physical equality of speed (PE). Results revealed that the PSEs were larger than PE at every speed of the SS: low ($t_{(5)} = 2.76$; $p = 0.04$; $d = 1.15$, power = 0.62); medium ($t_{(5)} = 3.37$; $p = 0.02$; $d = 1.38$, power = 0.77); and high ($t_{(5)} = 3$; $p = 0.03$; $d = 1.22$, power = 0.67). This indicates that when the circles moved at the same speed, the low-contrast ones were perceived as slower. Interestingly, the ratio between PSE and PE was constant at all speeds (1.04 ± 0.01), suggesting that the effect of contrast on perceived speed increased linearly with speed.

Figure 1

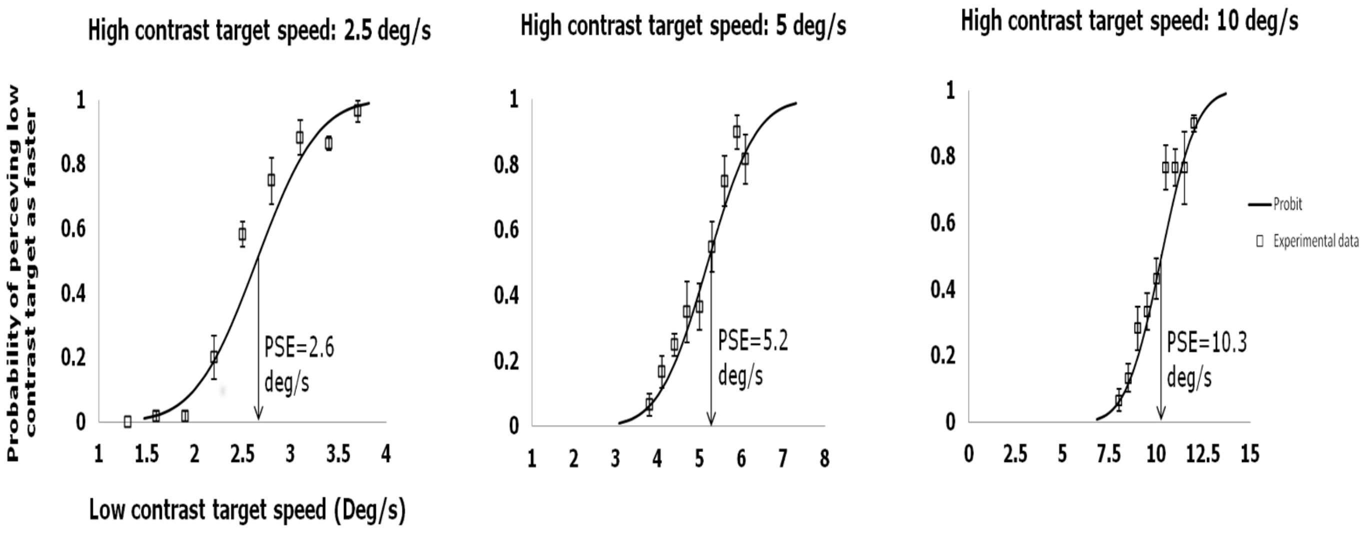


Figure 1. *The probability of perceiving a low-contrast target faster than a high-contrast target. PSE, point of subjective equality, indicates the speed that low-contrast stimuli should have to be perceived as fast moving as the high-contrast stimuli.*

2.3 Experiment 1.2

Experiment 1.1 showed that the speed of the lowest contrast target was underestimated. The PSE–PE ratio was constant, indicating that the underestimation increased linearly with speed. Experiment 1.2 investigated whether the illusory speed was retained during occluded motion. If speed was retained, we predicted the low-contrast target to be "perceived" as moving slower behind the occluder with the result of an overestimation of TTC. Furthermore, we predicted a constant ratio between this stored signal and the one obtained at high contrast across visible speeds. This would be indicative of similarities between the perception of speed during visible motion and the memory of speed active during occluded motion.

2.3.1 Method

Participants

The same volunteers of Experiment 1.1 took part in this experiment.

Stimuli and apparatus

The apparatus, shape, and contrast of the stimuli were the same as in Experiment 1.1. The target appeared abruptly 7 deg to the left or to the right of the screen with equal probability, and the extent of the linear visible motion trajectory was always 12 deg. The speed of the stimulus was 2.5, 5, or 10 deg/s. The length of the invisible trajectory was either 4 or 12 deg. A cue, a gray bar (luminance 1.89 cd/m^2, width 0.17 deg, height 1.7 deg) represented the end of the invisible trajectory (Figure 2). Stimulus duration varied from 1.6 and 9.6 s, depending on the speed and the length of the invisible trajectory.

Experimental procedure

I used the psychophysical method of constant stimuli. The experiment consisted of six blocks, three with a low-contrast target and three with a high-contrast target. A block consisted of 120 trials randomly presented: 3 speed levels x 2 occluder lengths x 20 repetitions, preceded by 12 practice trials (3 speed levels x 2 occluder lengths x 2 repetitions). The observers were instructed to follow the target with their eyes until it reached the cue. They were also invited to "follow" the target with their eyes while it moved behind the occluder, and instructed to press the space bar when it reached the bar cue. The next trial started 1000ms after the key press. No feedback was given.

Figure 2

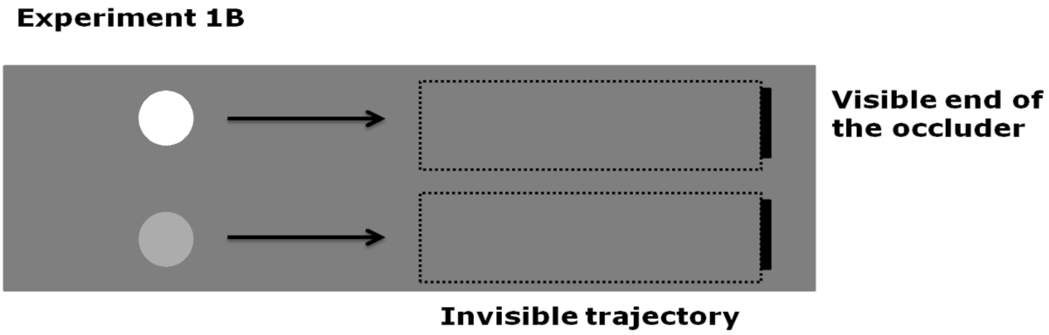


Figure 2. *Diagrammatical representation of the events in a single trial for the high- and low-contrast conditions. The participant pressed a button at the time they thought the target should contact the visible cue (black line).*

2.3.2 Results

From the $TTC_{invisible}$ (i.e. the time of key press minus the time of target disappearance at the beginning of the invisible trajectory - $TTC_{invisible}$) and the length of the invisible trajectory itself, we estimated the remembered speed: Remembered speed = length of the invisible trajectory / $TTC_{invisible}$. In Figure 3, the oriented lines in a time–space plot reflect remembered speed (Adelson & Bergen, 1985). For each speed level, we compared remembered speed data with a two-way repeated-measures ANOVA having contrast (low vs. high) and invisible trajectory (short vs. long) as main factors. Results reveal an effect of contrast on TTC for the high ($F_{(1, 5)} = 28.02$, $p = 0.003$), medium ($F_{(1, 5)} = 27.27$, $p = 0.003$), and low speed of SS ($F_{(1, 5)} = 16.01$, $p = 0.01$). Neither the effect of the occluder length (high: $F_{(1, 5)} = 0.09$, $p = 0.78$; medium: $F_{(1, 5)} = 0.007$, $p = 0.94$; low: $F_{(1, 5)} = 4.13$, $p = 0.01$) nor the interaction contrast x occluder length (high: $F_{(1, 5)} = 0.2$, $p = 0.67$; medium: $F_{(1, 5)} = 0.63$, $p = 0.46$; low: $F_{(1, 5)} = 1.13$, $p = 0.34$) was significant. These results indicate that target contrast modulates not only perceived speed but also remembered speed.

The ratio between the remembered speeds obtained in the high- and low-contrast conditions is very similar at all speeds (low: 1.10, medium: 1.12, high: 1.12), suggesting that the effect of contrast on remembered speed increases linearly with speed. This suggests the involvement of a visual perceptual memory system that precisely retains the illusory speed during occluded motion. Interestingly, the remembered speed ratio is higher than the PSE–PE ratio obtained during visible trajectory (medium: $t_{(5)} = 2.93$, $p = 0.03$; high: $t_{(5)} = 3.89$, $p = 0.01$) in Experiment 1.1, suggesting that an additional phenomenon may contribute to render the remembered speed illusory. In addition, we conducted single-sample two-tailed *t*-tests to compare estimated TTC with actual values. The difference was significant only for the low-contrast target for both occluder lengths at the medium- (short: $t_{(5)} = 2.65$; $p = 0.045$, $d = 1.08$, power = 0.73; long: $t_{(5)} = 2.51$; $p = 0.05$, $d = 1.03$, power = 0.69) and high-speed conditions (short: $t_{(5)} = 2.78$; $p = 0.04$, $d = 1.14$, power = 0.77; long: $t_{(5)} = 2.96$; $p = 0.03$, $d = 1.59$, power = 0.76). These data indicate a true underestimation of the remembered speed with a low-contrast target.

Figure 3

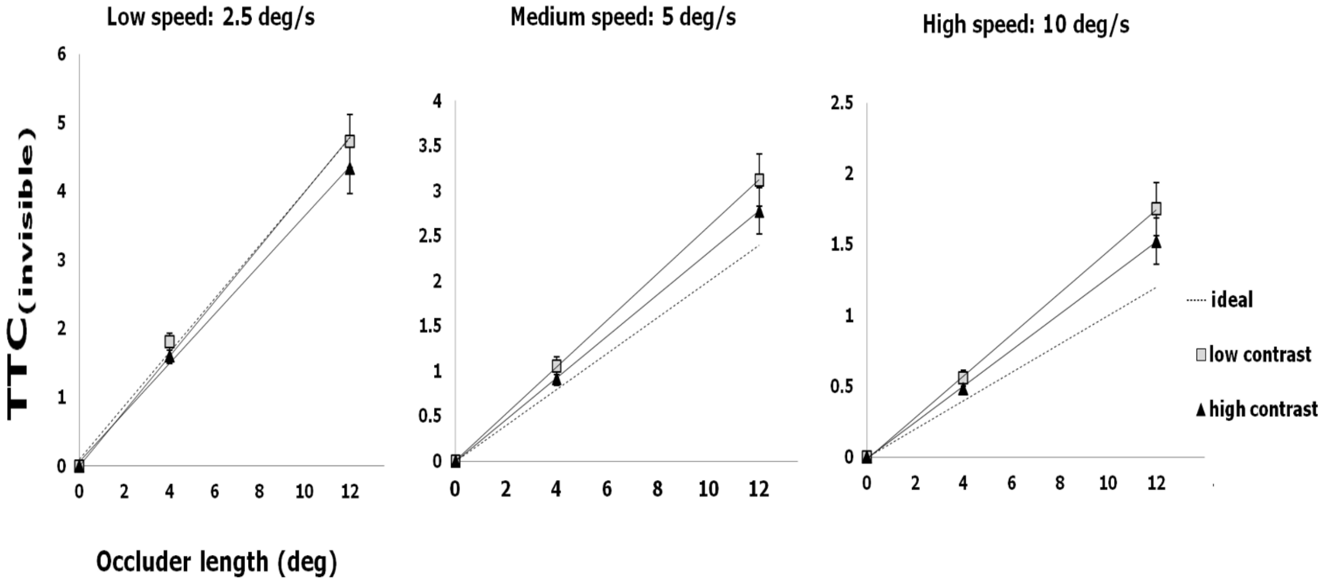


Figure 3. *The slopes of the oriented continuous lines on a time (TTCinvisible) space (occluder length) plot reflect remembered speed in the low- and high-contrast conditions. The dotted line represents the ideal slope that would be obtained if remembered speed perfectly reflected physical speed.*

2.4 Experiment 2.1

Results of Experiment 1 show that remembered speed, which according to the "tracking model" (Makin & Poliakoff, 2011) is needed for judging TTC, retains the illusory effect of contrast on perceived speed. To further investigate whether the illusion of speed is retained in memory, we applied the “transposition principle” (Brown, 1931). According to this principle, the perceived speed of one object is modulated by its size and by the width of the visible window within which the object moves. The bigger the target size and the frame that delimits its motion, the slower is the perceived speed (Wallach, 1939). Other studies followed this seminal work (Epstein, 1978; Rock, Hill, & Fineman, 1968; Zohary & Sittig, 1993). Epstein & Cody (1980) pointed out that the crucial factor producing the illusion was the size of the target, whereas the presence of the frame was irrelevant. In Experiment 2.1, we varied the shape and size of the target, i.e. a flat and long rectangle versus a square 10 times taller, in order to allow targets of different sizes to reach the end of the invisible trajectory at the same time. To our knowledge, there are no studies that report the “transposition principle” when shape and size co-vary and it is worthwhile to inquire whether the transposition principle holds in these conditions. With size and shape co-varying in Experiment 2.1, we evaluated the extent of the transposition principle during visible motion.

2.4.1 Method

Participants

A different group of nine participants, 2 males and 7 females, aged between 22 and 30, took part in this experiment. All participants had normal or corrected-to-normal vision.

Stimuli and apparatus

The apparatus was the same as in previous experiments. The SS (small shape) was a rectangle of 0.25 deg in height and 2.5 deg in width, and the CS was a square of 2.5 deg. Both were presented approximately at eye level, with a luminance of 144 cd/m^2 on a dark background (luminance 0.8 cd/m^2). Each target appeared abruptly and traveled horizontally, either leftward or rightward. Frame rate and visible trajectory were as defined in Experiment 1A. The speed of the small SS was fixed at either 2.5 or 7.5 deg/s; the speed of the large CS varied according to nine levels: SS speed of 2.5 deg/s: 1.3, 1.6, 1.9, 2.2, 2.5, 2.8, 3.1, 3.4, 3.7; SS speed of 7.5 deg/s: 5.5, 6, 6.5, 7, 7.5, 8, 8.5, 9, 9.5. Stimulus duration ranged from 3243 to 9230ms and from 1263 to 2181ms in the low- and high-speed conditions, respectively.

Experimental procedure

The experiment consisted of two blocks, each devoted to one speed preceded by 18 trials of practice (2 repetitions x 9 speed levels). For the rest I used the same experimental procedure of Experiment 1.1.

Results

Psychometric functions (Figure 4) were fitted to the probabilities of perceiving the large shape as faster, as a function of the physical speed levels. We then conducted a two-tailed *t*-test to compare individual PSEs with PE. Results showed that the PSEs were larger than PE at high speed ($t_{(8)} = 6.03$; $p < 0.001$; $d = 2$, power = 0.93) but not at low speed ($t_{(8)} = 0.28$; $p = 0.79$; $d = 0.09$, power = 0.06). This indicates that at a speed of 7.5 deg/s, the larger shape was perceived as slower. Different from Experiment 1.1, a PSE–PE ratio larger than 1 was found only at the highest speed (1.08).

Figure 4

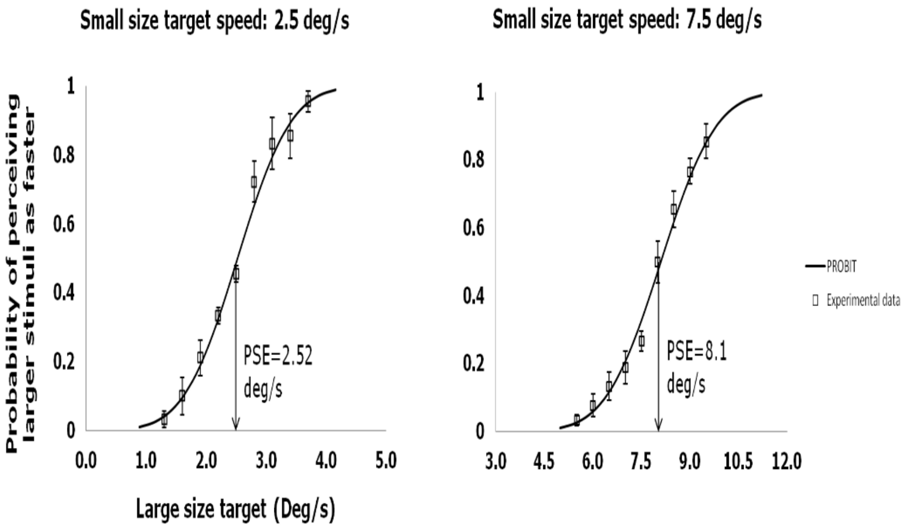


Figure 4. *Probability of perceiving the large shape as faster than a small shape. The PSE indicates the speed that the large shape should have to be perceived as faster as the small shape.*

2.5 Experiment 2.2

Experiment 2.1 shows that at faster and equal speeds, a larger target is perceived as slower than a target of smaller size. Experiment 2.2 investigated whether the illusory speed, as inferred from TTC, is retained during occluded motion. Both targets had the same width and speed, then reached the end of the occluder at the same time. However, we predicted the largest target to be “perceived” as moving slower behind the occluder, resulting in an overestimation of TTC. As in Experiment 2.1, we predicted a remembered speed ratio > 1 at highest speed. This would be indicative that a visual perceptual memory system is active during occluded motion, which precisely retains subjective visible speed.

Figure 5

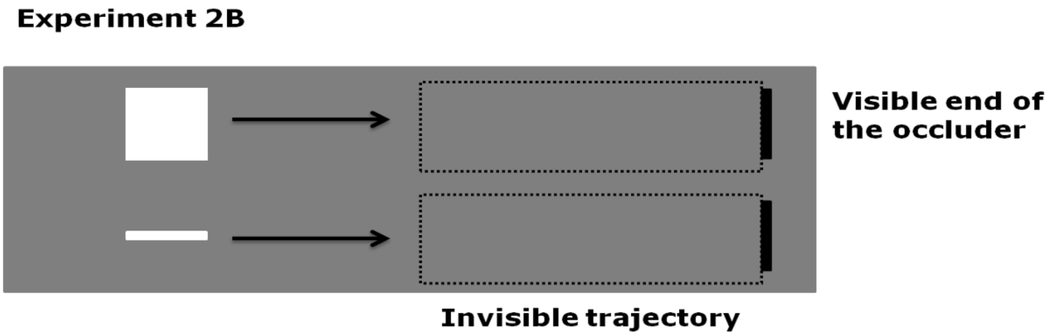


Figure 5. *Diagrammatical representation of the events in a single trial for the larger and smaller size conditions. The participant pressed a button at the time they thought that the target should contact the visible cue (black line).*

2.5.1 Method

Participants

The same nine volunteers took part in this experiment.

Stimuli and apparatus

The apparatus, stimulus shapes, and luminance were identical as in the previous experiment (2.1). The target appeared abruptly 7 deg to the left or to the right of the screen with equal probability, and the extent of the visible motion trajectory was always maintained at 12 deg (Figure 5). The speeds of the stimuli were either 2.5 or 7.5 deg/s. Stimulus duration was 1.6 or 4.8 s, depending on the speed and the length of the invisible trajectory: 4 or 12 deg.

Experimental procedure

I used the psychophysical method of constant stimuli. This experiment consisted of one block of 160 trials randomly presented: 2 speed levels x 2 occluder lengths x 2 size of the target x 20 repetitions, preceded by 16 practice trials (2 speed levels x 2 occluder lengths x 2 size x 2 repetitions). After 80 trials, a 2-minute pause was given. The observers were instructed to follow the target with their eyes during its visible and invisible trajectory, and to press the space bar when it reached the bar cue. The succeeding trial started 1000ms after the subject pressed the appropriate button. No feedback was given.

2.5.2 Results

Remembered speed is represented on a time–space plot (Figure 6). Although size did not affect the PSE at low speed, results of this experiment revealed an effect of size on remembered speed for both low ($F_{(1, 8)} = 10.93$, $p = 0.01$) and high speed ($F_{(1, 8)} = 18.14$, $p = 0.003$) during occluded motion. Neither the effect of the occluder length ($F_{(1, 8)} = 1.29$, $p = 0.29$; $F_{(1, 8)} = 1.99$, $p = 0.19$ for low and high speed, respectively) nor that of the interaction size x occluder was significant (low: $F_{(1, 8)} = 1.82$, $p = 0.21$; high: $F_{(1, 8)} = 1.61$, $p = 0.24$). This indicates that the subjective illusory speed during visible trajectory is retained during the occluded motion. The one-sample t-test revealed that with a large target, the TTC is significantly greater than the actual one at high speed for both occluder lengths (short: $t_{(8)} = 2.31$, $p = 0.05$, $d = 0.70$, power = 0.59; long: $t_{(8)} = 2.74$, $p = 0.02$, $d = 0.80$, power = 0.72). At high speed, where the transposition principle works, the remembered speed ratio (1.12) does not significantly differ from the PSE–PE ratio (1.08) obtained during visible trajectory ($t_{(8)} = 1.61$, $p = 0.15$).

Figure 6

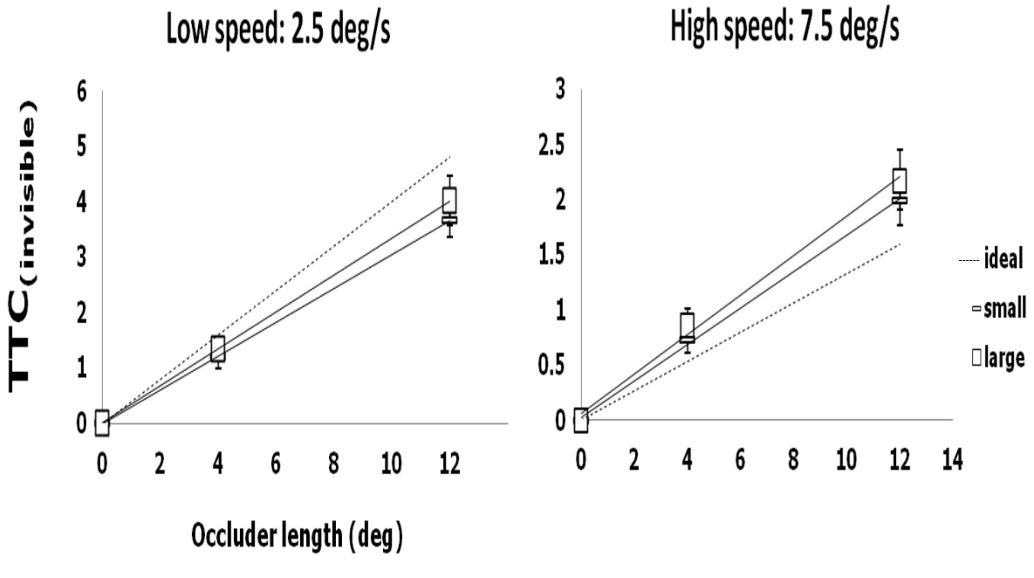


Figure 6. *The slopes of the oriented continuous lines on a time (TTCinvisible) space (occluder length) plot reflect remembered speed in the small and large size conditions. Dotted lines represent the ideal slope that would be obtained if remembered speed perfectly reflected physical speed.*

2.6 Experiment 3

Our data show an underestimation of remembered speed for the low contrast (Experiment 2.1) and for the large targets (Experiment 2.2), indicating that remembered speed is involved during occluded motion and reflects the perception of visible speed. It is possible that changing contrast and size/shape influences subjective perception of speed and time during the initial visible part of the presentation, which combined with amplitude of the visible and occluded part of the trajectory could then influence the estimation of time to contact based on a counting strategy. That is, participants could establish an estimation of TTC prior to target occlusion, and then countdown to contact without any need to memorize speed during occlusion. To check this possibility, we ran a third experiment in which the occlusion duration and the position of reappearance were always unpredictable, preventing any *a priori* knowledge of when or where reappearance would occur (DeLucia & Liddell, 1998; Makin & Poliakoff, 2011; Makin et al., 2008). A persistence of an effect of contrast with this paradigm would favor the hypothesis that participants can precisely use speed information stored in short-term memory during the extrapolation of occluded motion.

2.6.1 Method

Participants

Six volunteers, 3 males and 3 females, aged between 23 and 28, all right handed, took part in this experiment. They all had normal or corrected-to-normal vision. I obtained informed consent from each subject at the beginning of each experiment.

Stimuli and apparatus

The apparatus was the same as in Experiment 1.1. The stimuli, luminance, and diameter were the same as in Experiment 1.1. The length of the invisible trajectory was 4, 8, or 12 deg. The velocity of the stimuli was always 7.5 deg/s. The visible trajectory (12 deg) started 11 deg from the center. Without altering the length of the invisible trajectory, a reappearance error of ±0, 150, and 300ms was added (Figure 7). After the reappearance, the target ran 6 deg and then disappeared. At 300ms after target offset, a 300-Hz pure tone alerted observers to press the response button.

Figure 7

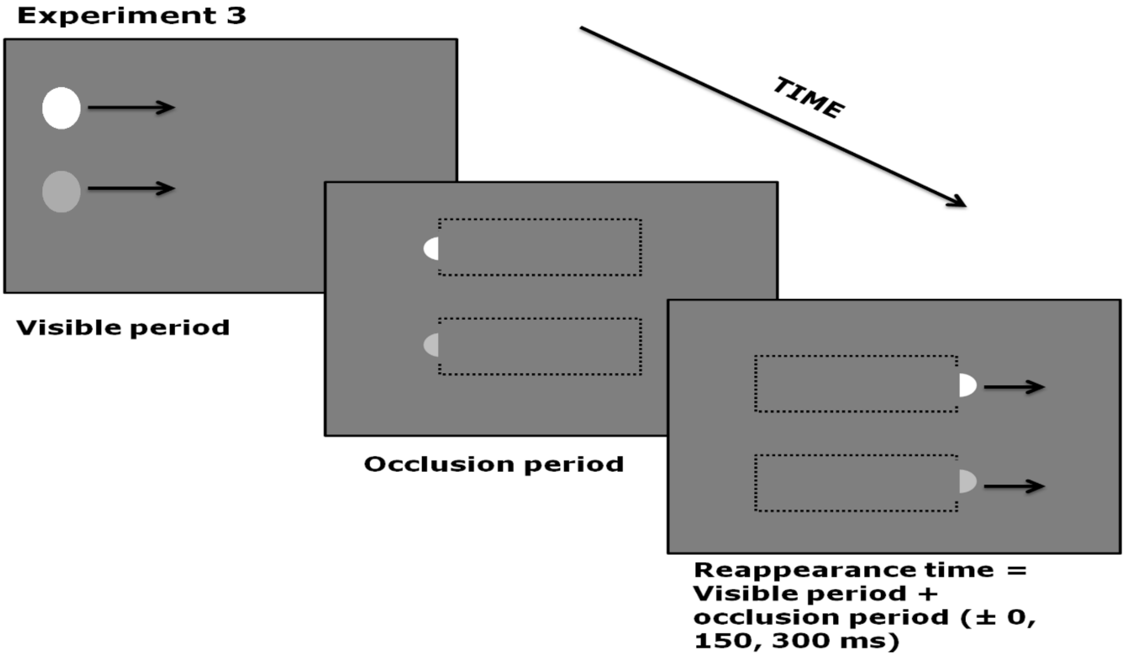


Figure 7. *Diagrammatical representation of the events in a single trial for the high- and low-contrast conditions. The target reappeared either at the correct time or with an error of ±150 or 300ms, assuming a constant velocity during occlusion. Participants discriminated between early and late reappearances.*

Procedure

I used the psychophysical method of constant stimuli. The experiment consisted of 300 trials randomly presented: 2 contrast x 3 occluder lengths x 5 levels of reappearance errors x 10 repetitions, preceded by 30 practice trials (2 contrast x 3 occluder lengths x 5 levels of reappearance error x 1 repetition). After 150 trials, a 2-minute pause was given. The observers were instructed to press an appropriate button to indicate whether the target reappeared earlier or later, even when the target reappeared in time. Eye movements were allowed. The next trial started 500ms after the subject pressed the appropriate button. No feedback was given.

2.6.2 Results

We conducted a 2 x 3 x 5 repeated-measures ANOVA with contrast (low vs. high), occluder length (short, medium, and long), and reappearance errors (-300, -150, 0, 150, 300ms) as main factors. Results (Figure 8) revealed a significant main effect of the contrast ($F_{(1,5)}$ = 16.87, p = 0.009) and reappearance errors ($F_{(1,5)}$ = 9.96, p = 0.003), indicating higher accuracy with low-contrast targets. This effect confirms (Magnussen & Greenlee, 1992) that remembered speed follows Weber's law. Indeed, according to Weber's law is easier to discriminate tiny difference if the value of the variable under investigation is small (in this case the value is the illusory speed of the low contrast target that is smaller than the value of the speed of the high contrast target). In other words, remembered speed at low contrast is underestimated and this would explain why subjects are more accurate in discriminating very small reappearance errors in the low-contrast condition.

Figure 8

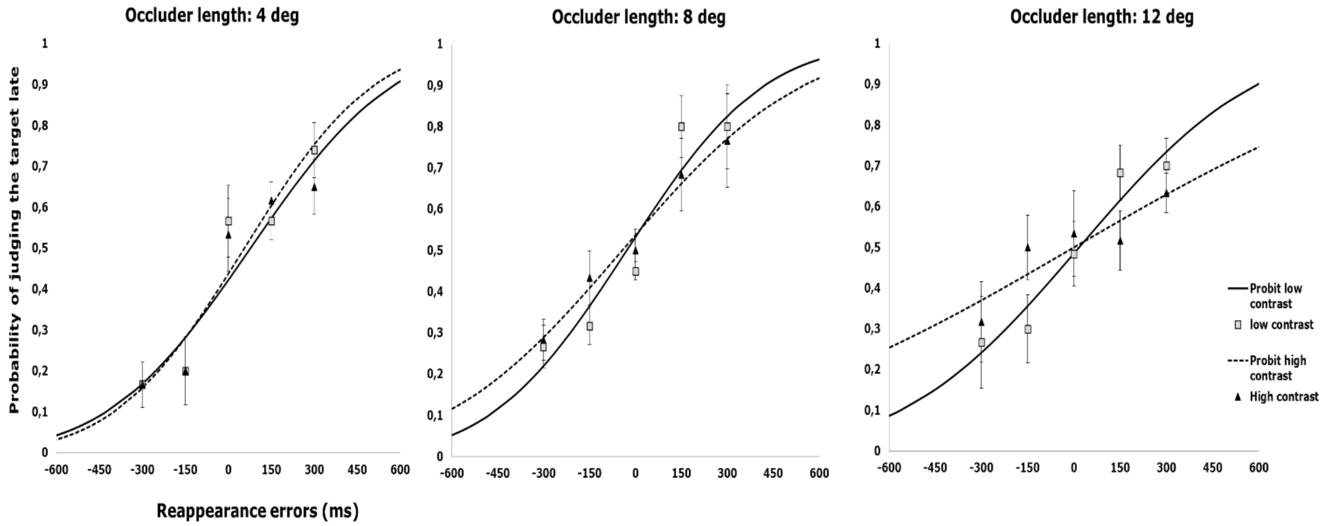


Figure 8. *Psychometric functions of probability of judging the target late on reappearance error, for the low- and high-contrast conditions.*

2.7 Discussion

In agreement with the literature, Experiments 1.1 and 2.1 show that speed is underestimated when the size of the target is increased or when its contrast is lowered. We did not replicate the finding (Thompson et al., 2006) that the effect of contrast inverts when the target speed is larger than either 4 deg/s (with 2-cpd target) or 2 deg/s (with a 8-cpd target). Alternatively, I found a linear relationship between the effect of contrast and speed. This may be due to the different stimulus analyzers involved: high-level shape analyzers in our stimulus conditions versus low-level spatiotemporal tuned filters in the conditions of Thompson et al. (2006). In Experiment 2.1, I found an effect of large target size despite the absence of the reference frame. However, it is smaller (8%) with respect to that reported in previous studies. Epstein (1978) reported an increment of 45% in perceived velocity when the size was halved. The absence of the reference frame could explain the difference. However, Epstein and Cody (1980) showed that the frame of reference is not necessary. Compared with previous studies, I used a fixed trajectory length. This factor, together with the different shapes used (the smaller size target was a rectangle and the larger one a square), could explain the smaller illusion. Most importantly, Experiments 1.2, 2.2, and 3 showed that the misperception of speed due to either contrast or size influenced remembered speed, as inferred from TTC during occluded motion. Interestingly, results of Experiment 2.2 are in line with previous findings (Sokolov & Pavlova, 2003; Sokolov et al., 1997), but not with studies made in an ecological environment (Horswill, Helman, Ardiles, & Wann, 2005) where the effect of the size on the TTC is reversed. In Experiment 3, by using a paradigm that prevents or at least discourages counting (DeLucia & Liddell, 1998; Makin & Poliakoff, 2011; Makin et al., 2008), we confirmed that contrast affects remembered speed. Results suggest that remembered speed follows Weber’s Law: given that remembered speed$_{\text{(low contrast)}}$ < remembered speed$_{\text{(high contrast)}}$, a smaller Δ remembered speed needs to be added (or subtracted) to discriminate it. Indeed, as Figure 8 shows, the effect of the contrast seems greater with the longer occluder length. This may account for higher accuracy in discriminating very small reappearance errors with a low-contrast target. The results provide support for the involvement of an early visual perceptual memory system during occluded motion. I believe that the modulation of remembered speed by contrast and size is an effect that cannot be assimilated to any of the speed effects previously described. Apart from other studies that find a dependency of TTC on the length of the occluder (Bennett et al., 2010; Sokolov & Pavlova, 2003), I found no effect of occluder length on remembered speed, neither in Experiment 1.2 nor in Experiment 2.2. In other words, given a fixed visible speed, the remembered speed gathered from TTC is similar, regardless of occluder length. I believe that these results are reliable because they are free from bias. Instead, previous studies used the “timing error” which is not a bias-free parameter: since speed is space over time, the same variation in remembered speed leads to a smaller “timing error” at high speed. Thus, the lower error at high speed previously found (Peterken et al., 1991; Sokolov & Pavlova, 2003) could only be an artifact.

Second, the illusory remembered speed cannot be confounded with the effect of speed on TTC (Bennett et al., 2010; Lyon & Waag, 1995; Peterken et al., 1991; Sokolov & Pavlova, 2003). Figures 3 and 6 disentangle these two effects. They show, as expected, that remembered speed is underestimated in both experiments at high speed, whereas at low speed, remembered speed either reflects perceived speed in a precise manner (Experiment 1.2) or is overestimated (Experiment 2.2). Yet, we found that the remembered speed ratio is isomorphic with the PSE–PE ratio. In Experiment 1, the two ratios are constant across speeds. In Experiment 2, the illusion is present in both perceived and remembered speeds only at high speed. Third, the illusory remembered speed cannot result from an interaction between speed and visible trajectory (Sokolov & Pavlova, 2003) since the visible trajectory is fixed in all conditions. One apparent contradiction in the results of Experiment 1 is that the value of remembered speed ratio (~1.12, Experiment 1.2) is larger than that of the PSE–PE ratio (~1.04, Experiment 1.1). One possible explanation is that size constancy by depth cues fails during occlusion (Dresp, Durand, & Grossberg, 2002; Gregory, 1963; Ward, Porac, Coren, & Girgus, 1977). Therefore, observers judge the target as smaller than it is, and according to Thompson et al. (2006), this gives rise to a larger effect of contrast. Results demonstrate that visible illusory speed affects either the absolute judgment (Experiments 1.2 and 2.2) or the discrimination (Experiment 3) of remembered speed. This suggests the involvement of an early visual memory system by either a mental imagery or a higher level velocity representation (more likely during pursuit) that retains the sensory characteristics of visible speed. Based on these findings, we are tempted to speculate that remembered speed might share processing with visual memory processes occurring at low cortical levels (Huber & Krist, 2004; Borst, Ganis, Thompson, & Kosslyn, 2012). Indeed, Makin et al. (2009) showed a positive event-related component over occipitoparietal areas both with visible and invisible moving targets; although in the occluded condition, the peak occurs 200ms after the onset of occlusion and is not related to a target velocity. Kaas et al. (2010) showed that imagery of a motion trajectory produced a bold signal in MT/V5. In conclusion, our results agree that TTC estimation during occluded motion is mediated by memory and suggest that an early visual perceptual memory system closely linked to mechanisms of visual discrimination is involved (Huber & Krist, 2004; Jonikaitis et al., 2009). This memory may share the proprieties of either visual imagery or mental representation and produce an internal simulation of the continuous motion of the invisible target.

Chapter III

Probing the involvement of the earliest levels of cortical processing in motion extrapolation with rapid forms of visual motion priming and adaptation

3.1 Introduction

In this part of the thesis, the purpose is to investigate the interaction between real motion and motion extrapolation (ME). Moreover, I will try to show psychophysically the role of the early visual areas during ME. In Gilden et al.'s (1995) study, participants had to make a TTC judgment when a moving object disappeared beyond an occluder with a further instruction to imagine the target in motion behind the occluder. However, before each TTC judgment, the region corresponding to the occluder was adapted with translational motion. This adaptation lasted 150 s on the first trial, and was followed by top-ups of 10 s on each successive trial. The results showed that when the target object moved in the same direction as the adaptation, TTC estimates were longer, whereas when the target object moved in the opposite direction with respect to that of adaptation, TTC estimates were shorter. The interpretation given by the authors was that adaptation of the occluder area biases the responses of motion detectors (with receptive fields sensitive to that area) toward the direction of motion opposite that of adaptation (similar to what occurs in the classical motion aftereffect [MAE]). This increases the motion signal of the imagined or extrapolated motion of the target object when its direction is opposite with respect to the adapted one, and decreases the motion signal of the imagined motion of the target object when its direction is the same with respect to the adapted one. The influence that prior adaptation had on TTC estimations suggests that the underlying mechanism is perceptual and engages the same neural structures involved in both motion imagery and motion perception—that is, intermediate-level extrastriate areas ranging from V2 to V5/MT, to the parietal cortex (Goebel, Khorram-Sefat, Muckli, Hacker & Singer, 1998; Kaas,Weigelt, Roebroeck, Kohler & Muckli, 2010). The question that I posed in this study was the following: Which are the earliest cortical stages involved in TTC estimation and motion extrapolation? In order to answer this question, I took advantage of recently investigated phenomena involving rapid forms of motion adaptation. Indeed, even exposures to directional stimuli much shorter than those used to elicit the classical MAE can bias the perceived motion direction of a subsequently presented ambiguous test pattern. Kanai and Verstraten (2005) showed that adaptation durations of 80ms and interstimulus intervals around 120ms are able to produce a bias in perception of a subsequent flickering stimulus in the same direction as the adaptation (rapid visual motion priming [rVMP]), whereas increasing the adaptation duration up to 320–

640ms had the opposite effect, producing a rapid form of MAE (rMAE; Kanai & Verstraten, 2005). Converging evidence from various psychophysical studies has suggested that these rapid forms of motion adaptation occur at an early stage of motion processing. For example, adaptation to a counterphase flickering pattern (ambiguous motion) has been used to probe the level of processing of motion adaptation. Despite simultaneously activating early motion detectors in opposite directions, ambiguous usually leads to the perception of directionality, which is determined at higher levels of cortical processing (Williams, Elfar, Eskandar, Toth, & Assad, 2003). Adaptation to ambiguous motion produces neither rVMP nor rMAE, suggesting that these two effects rely upon low-level sites of motion processing (Kanai & Verstraten, 2005). In fact, ambiguous motion did produce a facilitation effect similar to that of priming, but with a slower time course than rVMP, suggesting that "a different kind of plasticity exists at a later stage" (Kanai & Verstraten, 2005). Given the relative independence of first- and second-order motion at early stages of processing, transfer of adaptation (adapting with one and testing with the other) from first- to second-order motion (or vice versa) could also be used to investigate the level of processing of rapid forms of adaptation. Corroborating the low-level-processing hypothesis arising from the findings with ambiguous motion, it has been found that transfer between the two types of motion was small or absent: rVMP and rMAE can be elicited by both first- and second-order motion, but only if both the adapting and test stimuli are of the same motion type (first- or second-order; Pavan, Campana, Guerreschi, Manassi, & Casco, 2009). Finally, by using components of the optic flow (complex motion) typically processed at intermediate and high levels of motion processing (Morrone, Tosetti, Montanaro, Fiorentini, Cioni, & Burr, 2000; Wall, Lingnau, Ashida, & Smith, 2008) to investigate the level of processing of rapid forms of adaptation, it was shown that, whereas rMAE can be elicited by both simple translational motion and complex motion, rVMP can only be produced with simple translational motion (Pavan, Campana, Maniglia, & Casco, 2010). This finding proposes the notion that the faster the adaptation (and interstimulus interval; rVMP), the earlier the level of processing. All of these findings suggest an early locus of processing of these rapid effects, and this is particularly true for rVMP, which cannot be elicited by complex motion. Neuro-interference studies have confirmed the idea that rMAE can be processed at intermediate and low levels of processing: Indeed, both the classical MAE and rMAE are more strongly reduced when either areas V2/V3 or V5/MT are disrupted with transcranial magnetic stimulation (TMS) during the interstimulus interval (Campana, Maniglia, & Pavan, 2013; Campana, Pavan, Maniglia, & Casco, 2011; Théoret, Kobayashi, Ganis, Di Capua, & Pascual-Leone, 2002). With regard to motion priming, TMS studies implicate area V5/MT (but not area V1) in this form of implicit memory (Campana, Cowey, & Walsh, 2002; 2006), whereas at present no neurointerference studies are available that have investigated the neural circuitries involved in the generation of rVMP. The rationale behind this study is that, if motion extrapolation of the (invisible) moving object is indeed biased by rapid forms of adaptation of the same sorts that produce rMAE and rVMP, and since such adaptation occurs at early levels of visual motion processing, then motion extrapolation must also rely on these early levels of processing. The present study is in some ways similar to that of Gilden and colleagues (1995). The difference between these studies is that the present one goes a step further, by using not just the classical timing for generating the MAE, but implementing brief subsecond adaptation that might tap even earlier stages of motion processing, thereby producing either priming or aftereffect. The results will show that both brief and longer (but still subsecond) adaptation durations are able to influence motion extrapolation, but with opposite results: when the direction of the adapting pattern was the same as that of the target (congruent), longer adaptation durations (600 ms) on the occluder area produced an increase in response times (late TTC estimation), whereas briefer adaptation durations (80 ms) on the occluder area produced a decrease in response times (early TTC estimation). These data suggest that the adaptation mechanisms that produce rMAE and rVMP, respectively, are able to influence motion extrapolation, and thus that early levels of visual processing are involved in motion extrapolation. In this study I analyzed the TTC of the invisible trajectory instead of the “remembered speed” as in Chapter II, since the focus is not on the accuracy in judging the TTC with different levels of speed (see final part paragraph 2.1).

3.2 Experiment 1

3.2.1 Method

Participants

Seventeen participants (ten female, seven male) participated in this experiment (they were between 21 and 35 years of age). All participants were naive to the purpose of the experiment and gave written informed consent according to the Declaration of Helsinki prior to their inclusion in the experiment. They all had normal or corrected-to-normal visual acuity.

Apparatus

Participants were seated in a dark room 57 cm from the display screen. Viewing was binocular; stimuli were generated with MATLAB and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and were displayed on a 19-in. CTX CRT Trinitron monitor with a refresh rate of 100 Hz. The screen resolution was 1024 × 768 pixels. Each pixel subtended ~1.9 arcmin. The maximum luminance was 125 cd/m2, and the minimum luminance was 0.9 cd/m2. Luminance was measured using a Minolta LS-100 photometer.

Stimuli

The target stimulus was a small circle (0.5 deg in diameter, 125 cd/m^2), appearing 13 deg to the left or the right from the center of the screen with equal probabilities (in order to avoid the buildup of directional aftereffects), and travelling with a horizontal trajectory toward the opposite side of the screen at a constant speed of either 3 or 6 deg/s. The extent of the linear visible motion trajectory was 6.3 deg. After that, the target disappeared under an invisible occluder (same luminance as the background), which was 7.5 deg in length and 2 deg in height. A gray bar (0.3 deg in width × 4 deg in height, 24 cd/m^2) represented the end of the invisible trajectory, whereas a red dot (0.1 in diameter, 24 cd/m^2) placed 0.2 deg above the center of the invisible tunnel was the fixation spot. Figure 9 shows a schematic representation of the stimuli. An adapting random-pixel array texture was employed before the disappearance of the target. The texture had the same size and position as the invisible occluder (with no overlap with the gray bar) and was made by assigning a random value between 0 and 255 RGB to each pixel, with a mean luminance of 28 cd/m^2. The texture could have three types of motion: (i) in the same direction as the target's motion (congruent condition), (ii) in the opposite direction with respect to the target's motion (incongruent condition), and (iii) no net motion direction (random noise, control condition). The speed of the texture with a specific direction was 16 deg/s. A high speed was chosen in order to avoid any kind of plausible cue of speed (or time) that could allow inference of the TTC of the target, whose motion was much slower, and also in order to increase the strength of the aftereffect on the (imagined) motion of a target with lower speed (Bex, Verstraten & Mareschal, 1996; Campana et al., 2013). In the random noise condition, each pixel changed its RGB value randomly every 40ms, producing the effect of a detuned TV. The adapting texture could last either 600ms (long adaptation) or 80ms (brief adaptation). These are the stimulus durations capable of producing, respectively, rMAE and rVMP (Kanai & Verstraten, 2005; Pavan et al., 2009; Pavan et al., 2010). The texture was always removed 120ms before the target reached the end of the visible trajectory (before disappearing behind the occluder). As soon as the texture disappeared, the visible gray bar was displayed.

Experimental procedure

Participants were instructed to maintain fixation on the central red spot and to press the spacebar when they thought the leading edge of the moving target (imagining that it maintained the same constant speed and direction behind the occluder) reached a gray bar indicating the end of the invisible trajectory (TTC estimation). The intertrial interval was 1 s, and no performance feedback was given. Moreover, participants were instructed to ignore a texture patch, which was briefly displayed before the disappearance of the target. The two texture durations (long adaptation [600ms] vs. brief adaptation [80ms]) were displayed separately in two different blocks. Each block consisted of 20 repetitions for each combination of speed (low speed [3 deg/s] vs. high speed [6 deg/s]) by texture motion (congruent, incongruent, or random noise), for a total of 120 trials, randomly presented.

Figure 9

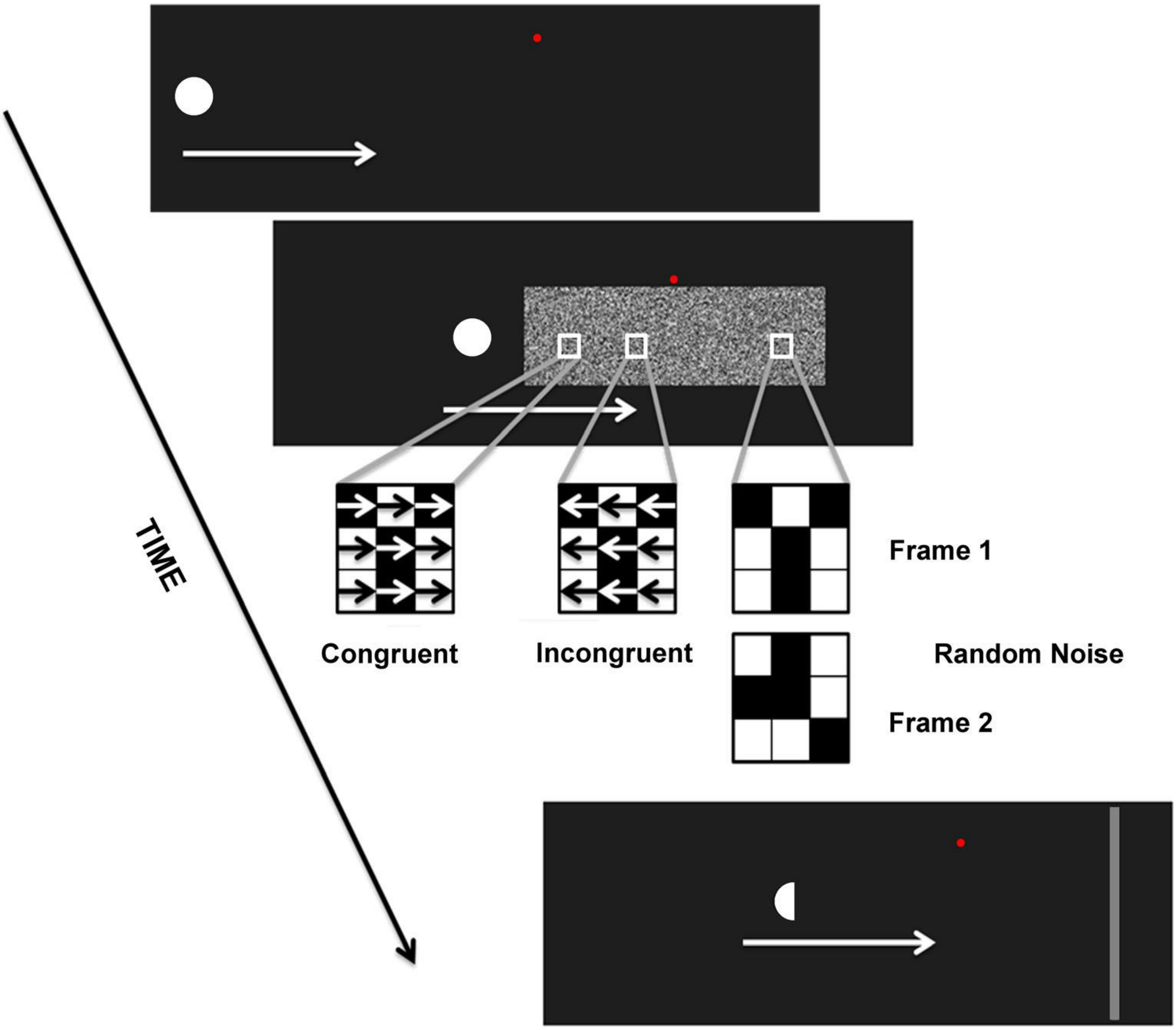


Figure 9. Illustration of a trial in Experiment 1. *A moving target traveled along a linear path at a constant speed. Then, a texture appeared for either 600ms (long adaptation) or 80ms (short adaptation). The texture could move congruently (same direction with respect to the target's motion) or incongruently (opposite direction with respect to the target's motion), or it could contain dynamic random noise (no directional energy). The texture was removed 120ms before the end of the visible trajectory of the target. Finally, the participants had to press a button when they thought that the moving target (imagining that it maintained the same constant speed and direction behind the occluder) reached the gray bar, indicating the end of the invisible trajectory.*

3.2.2 Results

We analyzed the mean TTC of the invisible trajectory estimates with a three-way repeated measures analysis of variance (ANOVA), with Adaptation Duration (long vs. brief), Speed (low vs. high), and Texture Motion (congruent, incongruent, random noise) as the factors. Since for Texture Motion the sphericity of the data was violated, as indicated by a significant Mauchly's test ($W_2 = 0.58$, $p < .05$), the Greenhouse–Geisser correction for the degrees of freedom was used for this factor. The ANOVA showed a significant effect of speed ($F_{(1,16)} = 792.16$, $p < 0.0001$, $\eta^2_p = 0.98$) and a significant interaction of texture motion with adaptation duration ($F_{(2,32)} = 8.21$, $p < 0.005$, $\eta^2_p = 0.34$). The effect of speed was as expected, since faster targets indeed produced lower TTC estimates. Bonferroni-corrected post-hoc t-tests indicated that, for both long and brief adaptations (able to produce, respectively, rMAE and rVMP), a significant difference (of opposite signs for the two adaptation durations) was apparent between congruent and incongruent texture motion. In other words, long adaptation produced longer ($t_{(16)} = –3.92$, $p < 0.005$) TTC estimates for congruent motion (2.1 s) with respect to the incongruent motion condition (2.02 s). With long adaptation, I also found significantly longer TTC estimates ($t_{(16)} = –3.17$, $p < 0.05$) for congruent motion (2.1 s) with respect to random noise (2.03 s) (Figure 10). These results suggest that the invisible motion of the target was slowed when the occluder area was adapted in the same direction as the target, with respect to the condition in which the occluder area was adapted in the opposite motion direction (or even with random noise) from that of the target. Overall, these results suggest that the same mechanism implied in rMAE is able to modulate invisible motion of the target behind an occluder. On the other hand, brief adaptation produced shorter ($t_{(16)} = 3.57$, $p < 0.01$) TTC estimates for congruent motion (1.98

s) with respect to the incongruent motion condition (2.06 s; Figure 11), paralleling the results obtained with rVMP (Kanai & Verstraten, 2005). The absence of differences between either the congruent or the incongruent condition and random noise (with the exception of a significant difference between congruent motion and random noise with long adaptation and high speed) may be due to the small size of the effect (~100 ms) on a judgment on the order of seconds, in conjunction with the high variability between participants (there was a twofold difference in TTC estimates between the fastest and slowest participants), yielding a significant between subjects effect ($F_{(1, 16)} = 688$, $p < 0.0001$, $\eta^2_p = 0.34$), reflected in the large error bars reported in the Figures 10 and 11. This is probably due to the fact that the TTC estimation task is a subjective judgment, and thus highly variable. It is still possible, though, that the present results reflect changes in the perceived speed of the visible target, rather than in its imagined speed once occluded. Indeed, in Chapter II I showed that TTC judgments are highly dependent on the perceived speed of the target stimulus prior to occlusion. However, since here the presentation of the adapting stimulus occurred during the late portions of the target motion trajectory, this hypothesis is quite unlikely. However, in order to test this, I ran a control experiment in which I measured the perceived target speeds with the different experimental configurations (short- vs. long-duration adapting texture, congruent vs. incongruent direction of the adapting texture with respect to the target motion).

Figure 10

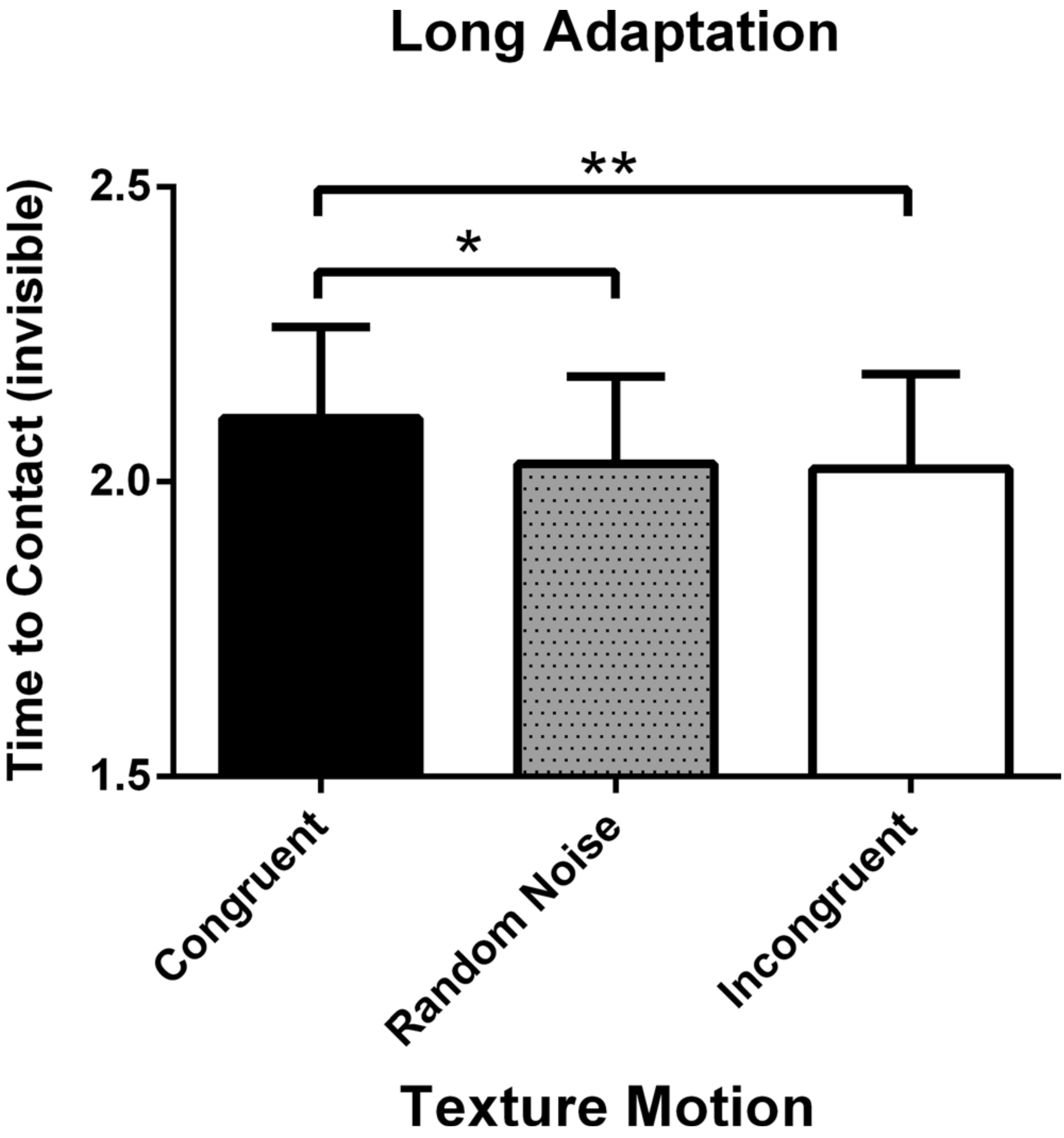


Figure 10. Long adaptation: *Results of the block with a long-duration adapting texture (n = 17). Motion adaptation (600ms) with a congruent moving texture (black column) produced late response times (TTC estimation) relative to incongruent (white column) and random-noise (gray column) textures. Error bars indicate 1 SEM. *p < .05. **p < .01.*

Figure 11.

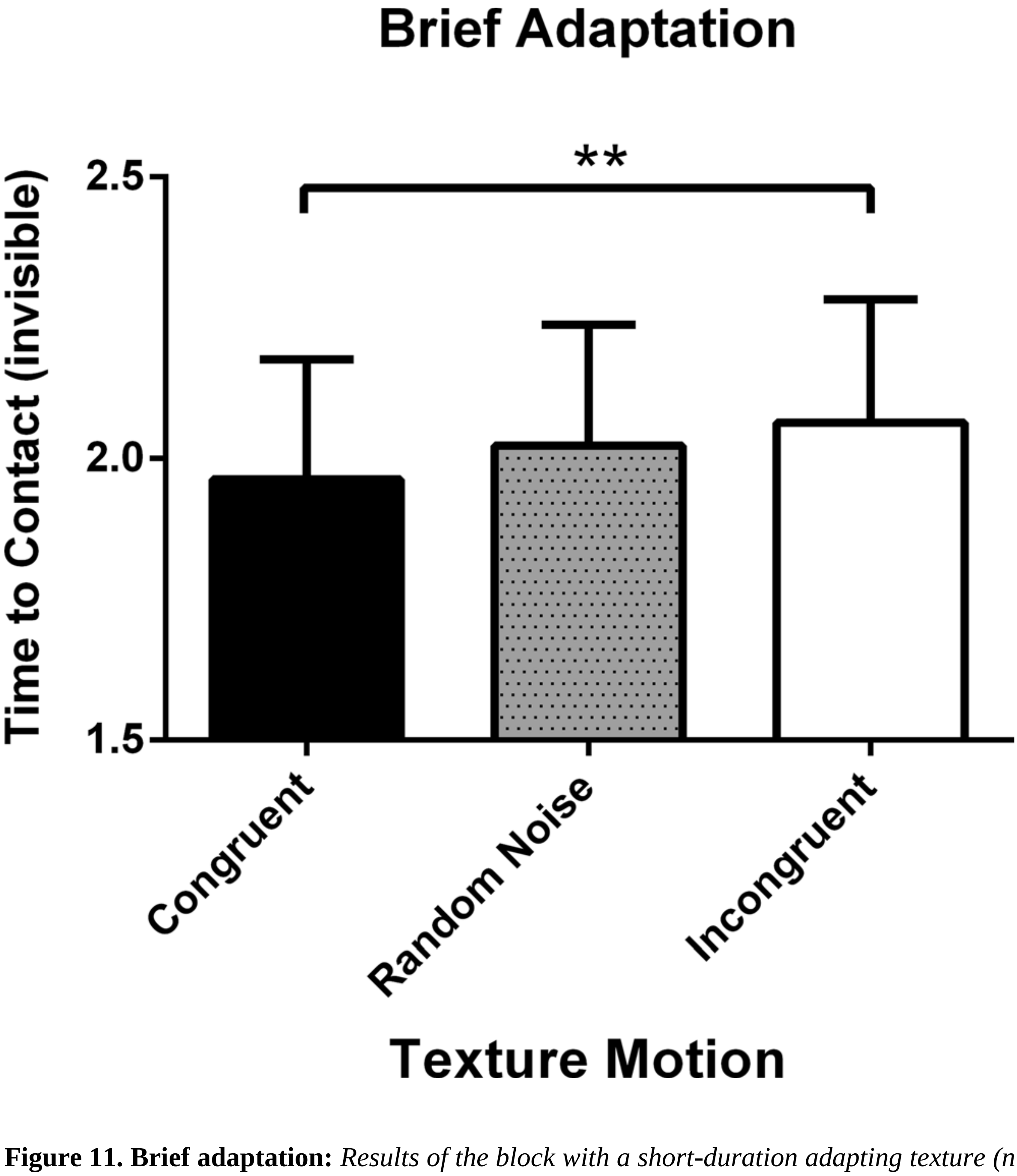


Figure 11. Brief adaptation: *Results of the block with a short-duration adapting texture (n = 17). Motion adaptation (80ms) with a congruent moving texture (black column) sped up response times (TTC estimation) relative to the incongruent moving texture (white column). Error bars indicate 1 SEM. **p < .01.*

3.3 Experiment 2

To test whether the adapting texture could modify the perceived speed of the visible target before occlusion, I measured the point of subjective equality (PSE) with a two interval forced choice using two simple one up–one down staircases interleaved in the same block. Stimuli from the descending and ascending staircase conditions were presented randomly within the same block.

3.3.1 Method

Participants

Eighteen students from the University of Padova (nine female, nine male; ages 19–22 years) took part voluntarily in this experiment. The participants had normal or corrected-to-normal vision and were required to give written informed consent according to the Declaration of Helsinki.

Stimuli and apparatus

The apparatus was the same as in the previous experiment, as well as the target and texture features. Two different moving targets with the same behavior were presented in two different temporal windows. The target that kept the same speed throughout the experiment (3 or 6 deg/s) was referred to as a standard stimulus (SS), whereas the comparison stimulus (CS) was the target that changed its speed according the participant’s response. The starting position, direction, and end of the visible trajectory were the same as in Experiment 1. After 1 s from the disappearance of the target, the first temporal window ended, and the second moving target appeared. The congruent moving texture was always presented with the SS, whereas the incongruent texture was always presented with the CS. I contrasted the congruent and incongruent moving textures instead of using a random-noise texture as the SS because our aim was to maximize the possibility of finding possible biases due to the texture motion direction. The onset and duration of the texture were exactly the same as in the previous experiment according to the different block conditions (brief vs. long adaptation).

Experimental procedure

Participants were asked to keep their fixation on the central red dot and to indicate by pressing one of the two response buttons (vertically aligned) which of the two intervals contained the faster target. The next trial then started 1.5 s after the participant’s response. Participants performed four blocks: (1) SS with low speed (3 deg/s) and brief adaptation (80 ms), (2) SS with high speed (6 deg/s) and brief adaptation (80 ms), (3)SS with low speed (3 deg/s) and long adaptation (600 ms), and (4) SS with high speed (6 deg/s) and long adaptation (600 ms). The starting speed of the CS was half of and double the SS speed for the ascending and descending staircases, respectively. The initial step of the staircase was set at 10 % of the SS speed. After each reversal, the step size was halved until 0.1 % of the SS speed was attained. The adaptive procedure could stop either after a total of 64 trials or after 12 reversals, whichever came first. The mean speed of the CS across the last eight reversals of the ascending and descending staircases was averaged and taken as a PSE threshold estimate (Campana et al., 2011; McKee, Klein, & Teller, 1985).

3.3.2 Results

I compared the speed of the SS with the PSE of the CS resulting from each of the four blocks/experimental conditions with a one-sample t-test. The results indicated that, in none of the conditions the perceived speed of the CS (target with the incongruent moving texture) was different from the speed (either slow, 3 deg/s, or fast, 6 deg/s) of the SS (target with the congruent moving texture): slow speed, brief adaptation: 3.06 deg/s ($t_{(17)} = 1.3$, $p > 0.05$); slow speed, long adaptation: 3.01 deg/s ($t_{(17)} = 0.23$, $p > 0.05$); high speed, brief adaptation: 6.12 deg/s ($t_{(17)} = 0.71$, $p > 0.05$); high speed, long adaptation: 6.2 deg/s ($t_{(17)} = 1.5$, $p > 0.05$). This result rules out the possibility that the effects found in Experiment 1 were due to a modification of the perceived speed of the visible target trajectory by the moving texture presented just before target's disappearance.

3.4 Experiment 3

Another plausible possibility is that the effect of rapid adaptation on motion extrapolation could have been caused by a change in the perceived position of the invisible start of the occluder (the end of the occluder was marked by a gray bar, and may thus have been less susceptible to apparent position shifts). In fact, besides causing the MAE, motion adaptation is also able to produce a shift of position in the direction opposite the adapted one (position aftereffect [PA]; McGraw, Whitaker, Skillen, & Chung, 2002), independently from the MAE (Whitney & Cavanagh, 2003), and even when motion was just "implied" from static pictures (Pavan, Cuturi, Maniglia, Casco, & Campana, 2011). Although PA has only been found with prolonged adaptations and with test stimuli overlapping the adapted region (McGraw et al., 2002; Pavan et al., 2011; Pavan & Mather, 2008), it is possible that it can also be induced by brief adaptations and with test stimuli located at the edge of the adapted region. If so, this could also explain the results of our first experiment: After adaptation to the same direction as the target motion, the PA might increase the apparent width of the occluder by extending its invisible edge back in the direction of the PA, leading to longer TTC estimates. The opposite could occur for adaptation in the opposite direction to the target (shortening the occluder and therefore TTC). To test this hypothesis, I used a modified PA procedure with adapting textures and timing similar to Experiment 1, coupled with a Vernier task. Two vertically displaced adapting textures moving in opposite directions were displayed, and the lines of the Vernier task were subsequently presented at the edges of the adapted regions. Note that, by using two adapting textures and a Vernier, I increased (in fact, doubled) any PA, if present, with respect to the amount that could have been in Experiment 1, in which only one moving texture was presented.

Figure 12

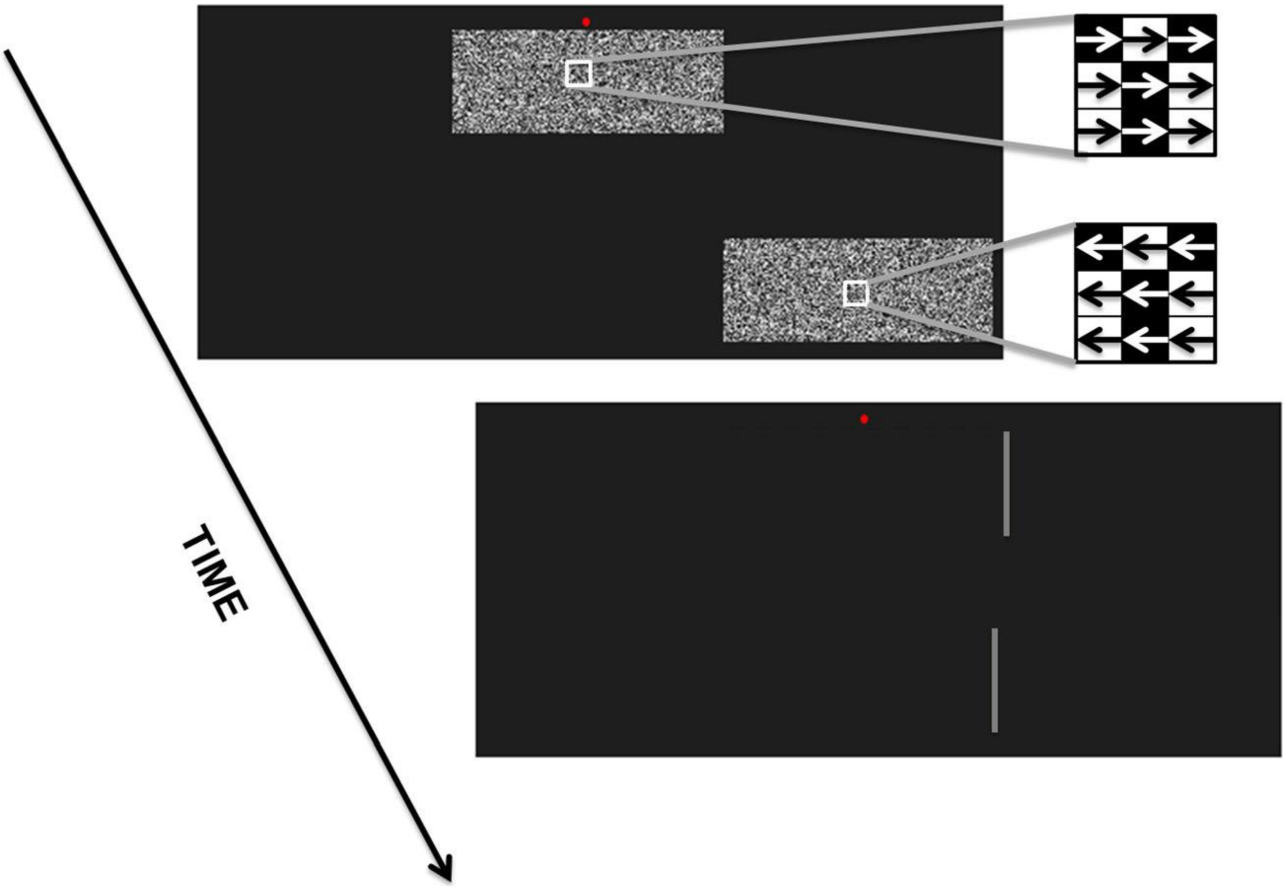


Figure 12. ***Illustration of a trial in Experiment 3***. *Two moving textures appeared for either 600ms (long adaptation) or 80ms (short adaptation). One texture was presented just below the fixation point, and the other texture could be presented either on the right (like the one shown*

here) or on the left. The two textures could move inward, as illustrated above, or outward. The textures were removed 120ms before the onset of the Vernier stimulus, which lasted for 100ms. Finally, the participants had to indicate whether the upper line of the Vernier stimulus was displaced to the left or the right of the lower line.

3.4.1 Method

Participants

Seventeen students from the University of Padova (nine female, eight male; ages 19–29 years) took part voluntarily in this experiment. The participants had normal or corrected-to-normal vision and were required to give written informed consent according to the Declaration of Helsinki.

Stimuli

The apparatus was the same as in the previous experiments. Two adapting random-pixel array textures with the same characteristics as the previous experiments were employed and displayed before the appearance of the thin lines target (3.8-arcmin width) used to measure Vernier acuity. One of the textures had the same size and position as in the previous experiment, with respect to the fixation spot. The second texture had the same size but was placed 3 deg under the first and was displaced to either the left or the right of the first texture, so that an edge of the first texture was aligned with an edge of the second texture: When the second texture (lower in position) was presented on the left, its right edge was aligned with the left edge of the upper texture; when the second texture was presented on the right, its left edge was aligned with the right edge of the upper texture (Figure 12). As in the previous experiments, the adapting texture could last either 600ms (long adaptation) or 80ms (brief adaptation). The Vernier stimulus (luminance = 24 cd/m^2) was always displayed 120ms after the disappearance of the two textures and lasted for 100ms.

Experimental procedure

Participants were instructed to maintain fixation on the central red spot, and the task of the experiment was, in all blocks, to indicate the position of the upper as compared to the lower line by means of a buttonpress. The two textures always moved in opposite directions: that is, inward or outward direction. Participants performed four blocks: (1) inward motion with brief texture durations (80ms: brief adaptation condition); (2) outward motion with brief texture durations; (3) inward motion with long texture durations (600ms: long adaptation condition);

and (4) outward motion with long texture durations. The lower texture was presented at the left or the right part of the visual field with equal probabilities within each block. A trial started with the presentation of the brief or long adaptation texture, and after 120ms, a Vernier stimulus appeared at the same location as the aligned edges of the two textures, with a starting spatial offset along the y-axis of 2 deg. Within each block, four simple staircases (one up–one down; Levitt, 1971), one for each position of the lower texture (left and right) and one for each starting offset displacement (left and right), were used to calculate the PSE for perceiving the two Vernier lines as aligned. The initial step of each staircase was set at 0.2 deg. After each reversal, the step size was halved until it reached 1.9 arcmin (one pixel). Each staircase could stop either after a total of 64 trials or after 12 reversals, whichever came first. If rapid adaptation, the effect of adaptation on the motion extrapolation found in Experiment 1, was caused by a change in the perceived position of the invisible start of the occluder, then I should also find a PA (apparent displacement of the two Vernier lines produced by the adapting textures) modulated by the type of motion (inward vs. outward) and by the adaptation duration (brief vs. long). In particular, I should find different PSEs (of opposite signs) with brief and long adaptations within each type of motion direction (inward or outward), and different PSEs (of opposite signs) with inward and outward motion within each adaptation duration (brief or long).

3.4.2 Results

I analyzed the mean PSEs of the Vernier lines with a two way repeated measures ANOVA, with Adaptation Duration (long vs. brief) and Texture Motion Direction (inward vs. outward) as factors. The ANOVA did not show any significant effects of adaptation duration ($F_{(1, 16)} = 3.17$, $p > 0.5$, $\eta^2_p = 0.16$), nor of motion direction ($F_{(1, 16)} = 0.65$, $p > 0.5$, $\eta^2_p = 0.04$), nor of their interaction ($F_{(1, 16)} = 0.002$, $p > 0.5$, $\eta^2_p = 0.0001$). Paired t-tests on the inward versus outward moving textures, performed separately for the brief (position shift = 0.3 arcmin; $t_{(16)} = -0.53$, $p > 0.05$) and long (position shift = 0.3 arcmin; $t_{(16)} = -0.46$, $p > 0.05$) adaptations, and on brief versus long adaptations, performed separately for the inward [position shift = 1.1 arcmin; $t_{(16)} = 1.2$, $p > 0.05$) and outward (position shift = 1.1 arcmin; $t_{(16)} = 1.9$, $p > 0.05$) moving textures, confirmed the null result of the interaction found with the ANOVA. In fact, the magnitude of the position shift found here was much smaller than that found with the classical PA (6 to 7 arcmin; McGraw et al., 2002), or than that found with implied motion with static photographs (~3 arcmin; Pavan et al., 2011). It appears similar to the magnitude of the position shifts obtained with second-order motion (0.9 arcmin; Pavan & Mather, 2008), although here the effect was not significant, despite the fact that I used a larger sample of participants (N = 17) than did Pavan and Mather (2008) (N = 7). I am aware that with a null result I cannot conclude that no PA takes place with rapid adaptation, but even if it did, its extent was so minuscule (the high-speed target can cover 1 arcmin in less than 3ms, a tiny fraction of the ~100ms difference found in Exp. 1) that it could not influence the TTC estimates in our first experiment.

3.5 Discussion

I have shown that even a very brief exposure to directional motion is able to modulate TTC estimation. When the occluder area was adapted to congruent (same direction as the target's motion) directional motion just before the target disappeared behind it, longer (although subsecond) adaptation produced later TTC estimates with respect to adaptation to incongruent motion (opposite direction with respect to the target's motion). Briefer adaptation to congruent motion, on the other hand, produced earlier TTC estimates. These results demonstrate that motion extrapolation, on which TTC estimates are based, depends upon the activity of the same low level motion detectors that are responsible for rMAE and rVMP. In fact, longer adaptation produces an imbalance between detectors tuned to opposite motion directions, lowering the activity of the adapted detectors and favoring the activity of non-adapted detectors, thus signaling the opposite motion direction with respect to the adapted one and producing rMAE. If the target's motion is congruent with the motion adaptation, the extrapolated motion of the target passing behind the adapted occluder will be hampered, due to lower activity of the detectors tuned to that motion direction. On the other hand, the mechanism underlying briefer adaptation may consist of temporal integration between the adapting and the subsequent test stimulus (Pinkus & Pantle, 1997), so that, if the test stimulus does not have a net motion direction, the motion direction signaled by the motion detectors will be that of the adapting stimulus, thus producing rVMP. In our experiments, if the target's motion was congruent to the motion prime (briefer adaptation), the extrapolated motion of the target passing behind the adapted occluder was facilitated. The exact mechanism by which adaptation might produce an increasing or a lowering of the motion signal, thus increasing or decreasing the TTC, is still a matter of debate. It has been shown that prolonged adaptation modulates the perceived speed of a visible moving pattern (Hietanen, Crowder, & Ibbotson, 2008). Although an effect of brief adaptation on perceived (or extrapolated) speed has never been demonstrated, I can speculate that the mechanism underlying the changes in TTCs due to brief adaptation resides in a modulation of the extrapolated speed of the target: motion detectors responding to the target would sum the speed of the extrapolated motion with (or subtract from it) the speed resulting from brief adaptation. It had already been shown that classical (long) motion adaptation of the occluder area could shift response times by producing late TTC estimates with adaptation in the same direction of the target, or by producing early TTC estimates with adaptation in the opposite direction from the target (Gilden et al., 1995). Those results imply that (a) TTC is performed via imagined or extrapolated motion, and (b) extrapolated motion relies on the activity of those neurons whose responsiveness is altered by adaptation, thus pointing to shared neural processes between extrapolated and real motion, located between areas V1 and MST (Gilden et al., 1995). In fact, numerous studies have already established the involvement of sensory and perceptual visual cortical areas in both mental imagery and working memory functions (see, e.g., Borst, Ganis, Thompson, & Kosslyn, 2012; Kosslyn et al., 1999), on which motion extrapolation is likely to be based. The primary aim of this study was to challenge the earliest levels of visual motion processing, in order to investigate whether or not they are involved in TTC estimation. In order to do so, I exploited perceptual effects arising from rapid exposure to motion, which are able to briefly modulate the responsiveness of motion detectors either in the direction opposite the adapted one (rMAE) or in the same direction (rVMP), depending on the adaptation time and interstimulus interval. Indeed, it has been shown that these rapid effects cannot be generated by high-level adaptation to counterphase flickering (Kanai & Verstraten, 2005), and show little or no transfer between different types of motion that at low levels are processed independently (Pavan et al., 2009). Moreover, rMAE has been shown to depend upon the functional integrity of intermediate and low-level areas (Campana et al., 2011), and psychophysical experiments have shown that rVMP cannot be elicited by types of complex motion (Pavan et al., 2010) that are processed at intermediate and high levels of processing (i.e., from area V3a, thus excluding the involvement of the earlier areas V1 and V2; Wall et al., 2008). Finally, rapid forms of adaptation have been found to depend on both cortical and thalamic short-term depression (Carandini, Heeger, & Senn, 2002; Chance, Nelson, & Abbott, 1998; Chung, Li, & Nelson, 2002). So, although rMAE can occur at both low and intermediate levels of processing (Campana et al., 2011), making the level at which 600ms of adaptation modulates TTC estimation questionable, rVMP has been shown to display characteristics compatible only with the earliest levels of processing (Pavan et al., 2010); therefore, an effect of very brief adaptation (the same that causes rVMP) on TTC estimation clearly points to the earliest levels of motion processing. The results of the present study demonstrate that rapid forms of motion adaptation and motion priming affect motion extrapolation, suggesting that the mechanism underlying motion extrapolation can occur at even earlier levels of processing than those postulated by Gilden in 1995, possibly beginning at the level of primary visual cortex (V1).

Chapter IV

Electrophysiological Correlates of Motion Extrapolation: An Investigation on the Time Related Component CNV and on the Occipitoparietal Activity.

4.1 Introduction

A method used to delineate stages of visual processing, and perceptual contributions of visual motion processing is to induce a phenomenon known as the Motion After Effect (MAE) (Tootel, Reppas, Dale, Look, Sereno, Malach, Brady, & Rosen, 1995, see also Chapter III). MAE is caused by the viewing constant motion in one direction which causes a static object to appear to move in the opposite direction (Nishida & Sato, 1995). MAE can also produce a dynamic effect, were a target moving in the same direction as the MAE inducing stimulus will subsequently appear to move in the opposite direction or appear to move slower than it actually is (Mather, Pavan, Campana & Casco, 2008). MAE is also used to investigate the cortical specialization of motion direction and tests the spatiotemporal tuning of direction selective mechanisms (Biber & Iig, 2011). According to the opponent processing view, MAE adaptations modulate neuronal activity whereby direction selective neurons consistently stimulated by (e.g.) downward motion will subsequently reduce their activity when the visual stimuli changes to a static object, which causes a tilt of balance in favour of (e.g.) upward motion, occurring because downward selective neurons lose sensitivity to their tuned direction (Anstis, Verstraten & Mather, 1998). Gilden, Blake & Hurst (1995) were the first to report that MAE adaptations could modulate ME, shifting late or early the response time in a time to contact task according to the direction (same vs. opposite) of the adaptor and the moving target. They argued that when “imagined motion”, i.e., the speed of the target inferred behind the occluder, was in the same direction as that experienced during adaptation, it was slowed; oppositely imagined motion in the opposite direction than the adapting motion it was increased. Moreover, I showed in Chapter III that also priming and rMAE was able to bias the processing of ME. These evidences suggest that visual areas play a fundamental role and that (at least a part of) the same neural network of visible motion is involved also in ME.

In Gilden’s and my study, the effect of adaptation on ME is reflected in the TTC estimation, i.e. in a temporal judgment. Therefore, it is possible that MAE affects neural mechanism involved in time estimation. I have addressed this issue in an electrophysiological study using ERPs. ERP paradigms that involve an interval estimation usually elicit a late electrophysiological component known as the Contingent Negative Variation (CNV) event related potential (ERP) (Tecce, 1972), in the frontal electrodes. The CNV is typically found using a chronometric paradigm in which the interval between the presentation of two stimuli: the first stimulus is called warning stimulus, the second one that directs the observer to make a behavioral response is called imperative stimulus. The CNV is seen in the foreperiod, i.e. the temporal interval between the warning and the imperative. For example, in prediction motion (TTC task) paradigm the stimulus warning is the disappearance of the moving target behind the occluder, while the imperative stimulus is an endogenous stimulus corresponding at the moment in which one decide to press the response button to indicate the TTC. I asked whether TTC is expressed by the CNV and whether the CNV is modulated by the way in which the TTC is affected by MAE. If motion adaptation modulates the TTC estimation and if TTC estimation elicit a CNV, then different TTC estimations because of motion adaptation should elicit different negativity amplitude of the CNV. Therefore, I would expect a greater negativity of the CNV after adaptation in the same direction of the occluded target that should lead to a longer TTC estimation (Macar, Vidal & Casini, 1999).

Only two studies investigated so far the electrophysiological correlates of motion extrapolation. However, none of them takes into examination the CNV. Makin et al 2009 and Makin et al., 2012 conducted an electroencephalogram (EEG) experiment using a time discrimination task. In the experimental condition, the moving target became occluded near the center of the screen, while in another condition the moving target was visible for the full length of the trajectory. They reported that both conditions produced positive potentials over posterior electrode sites, suggesting that the tracking of visible (actual perception of motion) and occluded targets (motion extrapolation) rely on similar neural systems. More specifically, they showed that the posterior positivity (temporal-occipital electrodes) elicited during visible motion shifted from central to lateralized electrodes at around 200ms after the target crossed fixation. They described this ERP as Hemifield Swith Positivity (HSP). In the occluded condition, the positivity in the temporo-occipital electrodes was found in the central electrodes 200ms post occlusion and was followed by a lateralized positive component that they called occlusion related deflection (ORD) that occurred 260ms post occlusion. This was thought to reflect cortical registration of occlusion, sudden top down predictive maintenance and transference to memory guided tracking. The paradigm used in the present study also allows to investigate whether the after effect of motion adaptation on ME is reflected in the occlusion related deflection as registered in the temporo-occipital electrodes during ME. I predict that a modulation of ORD by congruent adaptation would increase the latency of this component and and change its amplitude. Moreover, looking at Makin et al.,'s (2012) data, a small negative deflection (~180ms) is present before the ORD. This deflection looks like a negative component even thought is in the positive semi-axis. The final step of this work is to investigate if this component could be an index that indicates the shift from actual perception to ME and if it can be modulated by motion adaptation.

To summarize the study reported in this chapter has a number of aims. Firstly, to replicate the effect of the real motion adaptation on ME reported by Gilden et al., (1995) by using a different task: TTC without the instruction to imagine the invisible target. Secondly, to investigate the electrophysiological components/correlates of ME. More specifically: i) to investigate whether the CNV component is evident during motion extrapolation and if this component can be modulated biasing the TTC estimation thanks to motion adaptation; ii) to replicate the same occlusion related deflection (ORD) reported by Makin and colleagues (2012) and see the effect of adaptation on its amplitude and latency, iii) and clarify whether there are other electrophysiological correlates of ME.

The paradigm that used in this study is a prediction motion task (Time to contact task, Benguigui & Bennett, 2010; Benguigui et al., 2004; DeLucia & Liddell, 1998; Makin & Poliakoff, 2011; Makin, et al., 2008; Makin et al., 2009; Peterken et al., 1991; Rosenbaum, 1975). In addition, participants were adapted in the zone where the occluder were placed, with either all leftward or all rightward moving texture made by random greyscale pixel, which elicited classic MAE (confirmed by a pilot study). Simultaneously with the TTC task, I measure the developmental of ERPs during the invisible phase (occluded motion).

4.2 Method

Participants

Eighteen participants took part in the experiment; ranging in ages from 18 to 27; 10 male and 10 female; 1 left handed and 17 right handed. All participants reported normal or corrected-to-normal visual abilities. If their vision was corrected they were required to wear glasses not contact lenses. Participants were Psychology undergraduates; having completed at least 16 years in education recruited from the University of Plymouth. They took part voluntarily as part of the course requirement in return for course credits via an online participation pool. Two participants were paid to take part; all of which were also third year students studying a different subject. The electrophysiological data of two participants were excluded from the analysis due to excessive muscle tension and eye movement artifacts.

Apparatus and Stimuli

The screen monitor was a ViewSonic FuHzion 22” VX2268wm model with widescreen LCD. The refresh rate was set to 100 Hz frame rate with a display resolution of 1680 x 1050 pixels. The contrast was set to default and the luminance was set to maximum and brightness set to 300 cd/m2. Participants were required to sit 1.5 meters away from the screen and respond using an RB Cedrus Response Pad. MatLab Psychtoolbox was used to create and present the experiment (Brainard 1997, Pelli 1997).

Target stimulus (TTC Task)

The target stimulus for the TTC task consisted of a white circle (0.5deg). The motion trajectory was produced by presenting the target in a new position in successive frames. The visible trajectory started from 6.5 deg (from left or right side) from the center of the screen, travelling 3 deg/s. After 3 degrees, the target becomes occluded (smoothly) by an invisible dark rectangle or occluder (8 x 3 deg, w x h) of the same colour and luminance of the background (Michelson contrast of the target: 0.99). The end of the occluder was marked by a grey bar (4.5 deg from the center of the screen) at the opposite side of the screen to target initiation (0.3 x 2.5 deg, w x h). The gray bar appeared after the adaptation period. The target travelled behind the invisible occluder at 3 deg/s so the value between the point of occlusion and the correct TTC was 2.666s.

Adaptations:

Dynamic texture adaptations were made up of a continuous stream of moving pixels which could have rightwards or leftwards trajectory. In the control condition the texture was static. The speed of the moving texture was of 8 deg/s. A different value respect to the target’ speed was used in order to avoid any cue of speed or time that could allow inference of the TTC. The texture was 7 deg long and 6 deg in height placed at the center of the screen with a mean luminance of 90 cd/m². The texture was made of 350 x 350 pixels and ends 1 deg before the end of the invisible occluder in order to avoid a MAE effect on the grey bar. Note that the region adapted was only the region in which the target became occluded.

Fixation Dot

Participants were required to fixate (binocularly) on a specified dot at all times throughout the experiment. This was to minimize eye movements, produce a stronger aftereffect and to ensure participants were not utilizing overt tracking mechanisms. A grey ring of 0.3 deg was presented around the fixation dot in order to avoid MAE effect on it. The fixation spot was 0.1 deg placed with luminance of 100 cd/m². The spatial position of the fixation dot was 3 deg below the center of the screen. The fixation dot was green during the adaptation and at 1.5s (+ / - 300ms) before the start of the TTC trials, the dot changes to red to indicate that during the TTC task that participants were not allowed to blink or move their eyes. The fixation dot turned green once participants had made their TTC response.

Design

For each participant the moving texture was always unidirectional (always rightwards or always leftwards). Eight participants were assigned to left adaptation and the other half to right adaptation in a random way. In the control condition they all were adapted with a static texture. Participants were required to give informed consent and given anther brief and debriefed fully on competition. The experiment was a repeated measures within subject 2 x 2 design. The first factor was the adaptation conditions (static texture or moving texture). The second factor was the congruency, i.e., direction of the moving target: congruent or incongruent respect to the adaptation direction. Despite the fact the texture in the control condition was always static, for simplicity, trials were labeled as congruent or incongruent according to the experimental block. For example if a participant were adapted with the leftwards texture in the experimental block, trials were labeled as congruent also in the control block (static adaptation) when the starting position of the target was in the right part of the screen and the direction was leftwards. In both conditions was measured the response time of a direct estimation of the Time to Contact (TTC).

The Electroencephalogram

Electrophysiological data was collected continuously and simultaneously using the electroencephalogram (EEG) BioSemi Active Two system (Figure 13). The experiment was conducted in an electrically isolated, dark and noise attenuating chamber. ActiView 605-Hires.vi was used to collect and save the recordings from electrode channels. EEG signals were collected from participants with an electrode cap, 10/20 geodesic high-density system using 64 second generation active Ag/AgCl electrodes, referenced online to the mastoids. Electrodes were applied with electro-conductive gel to increase conductivity between electrodes and the scalp. Common mode voltage across scalp electrodes was included to decrease impedances and five loose lead flat electrodes placed on left and right mastoid locations, electro-oculographic electrodes placed under the right eye, and two on outer canthus to monitor and reduce trials containing ocular artifacts. Signals were amplified with a low pass of 4 KHz and direct current (DC) as high pass; signals were sampled at 4096 Hz; speed mode 6. Impedances were kept below 40 ampere for every sensor.

Figure 13

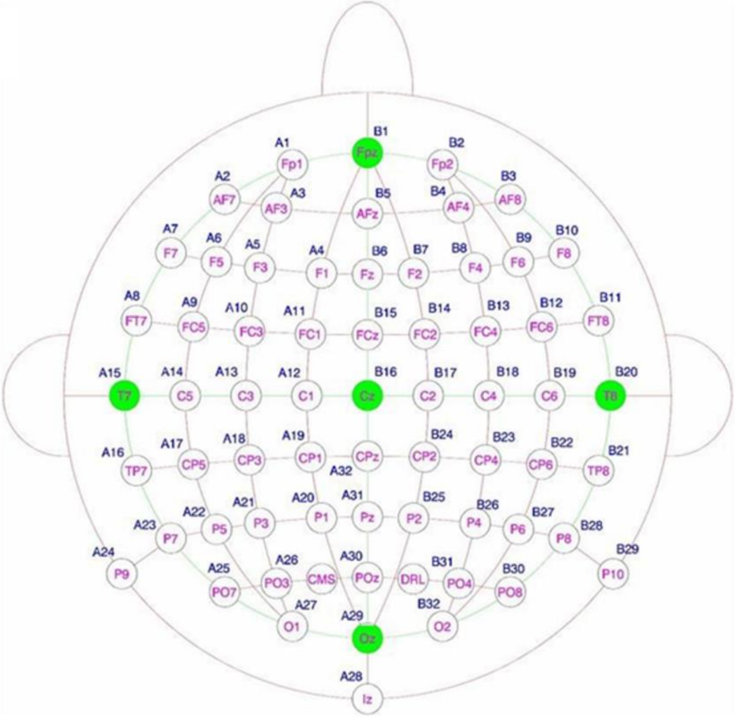


Figure 13. ***BioSemi 10/20 Dense Array* .** *This is the BioSemi montage of electrodes and indicates where the electrodes were placed on the scalp.*

Procedure

Participants were seated in a separate room and placed 150 cm away from the screen. They were instructed to remain as still as possible and maintain fixation on the fixation dot at all times and instructed not to track the target during the TTC task. Participants were informed that when the fixation dot was red they were not to blink; but when it turned green they could. The experiment was divided in 6 blocks: 3 per adaptation conditions (moving texture vs. static texture). Each block consisted of 40 trials for a total of 120 trials per adaptation conditions and 240 trials in total. After each block there was a small break till the participants felt ready to start again. Independently of the type of adaptation in each block the adaptation for the first trial was 60s and 10s for the other (top-up adaptation, Gilden et al., 1995). The adaptation was always in the same direction and the congruency (congruent vs. incongruent) depend on the direction of the moving target. In half of the trials the target moved from left to right, and in the other half trials, the target moved from right to left. Each TTC trial was initiated by a target appearing 10ms after adaptations; from either the left or right side of the screen with equal probability and travelled horizontally across the screen. Participants were instructed to press an assigned response button when they believed the moving target would reach the grey bar that was presented at the opposite side of screen following its occlusion and assume that the target maintained the same direction and speed (Figure 14; 15). After the participants response, the following trial started with the adaptation texture after a random time between 1250 to 1750 ms. The TTC estimates were calculated as the time of visible (1 second) + invisible trajectory until key press for the behavioral data.

Figure 14

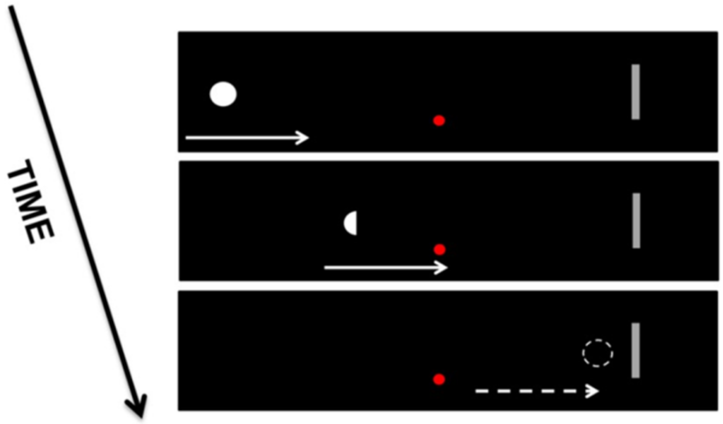


Figure 14. ***An illustration of a Time to Contact (TTC) trial***. *The moving target travelled along a linear path at a constant speed then fell behind an invisible occluder. The task of the participant is to assume the target maintained a constant speed and trajectory behind the occluder and to respond when they believe that the leading edge of the white circle reached the closest edge of the grey bar, marking the edge of the occluder.*

Figure 15: Linear Explanation of the Experiment

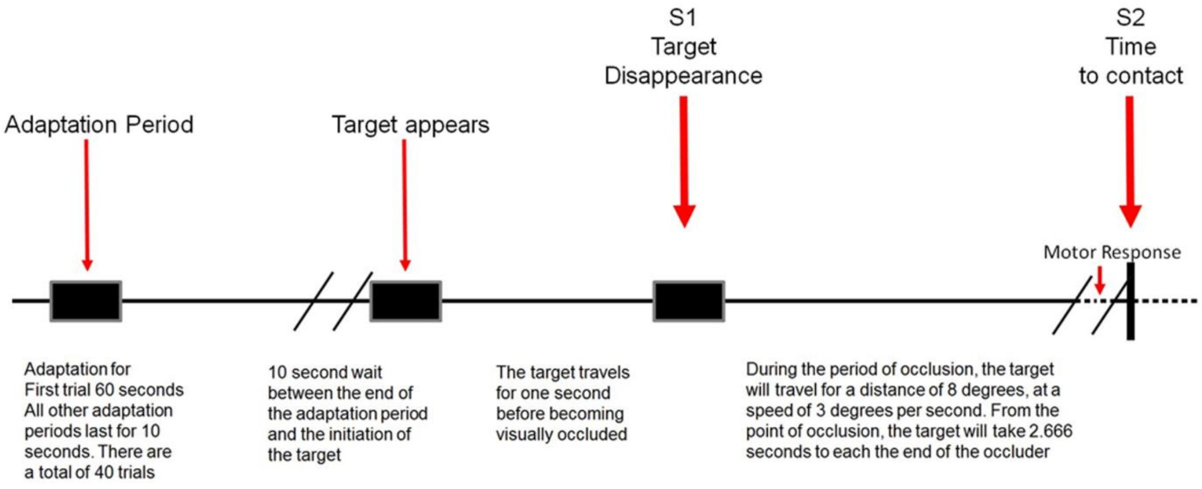


Figure 15. *This figure is representative of how the experimental paradigm aims to investigate activity of the CNV. CNV activity will be measured from 'stimulus 1' which is the point at which the target becomes occluded, up to 'stimulus 2' which is the TTC estimate.*

4.3 RESULTS SECTION

4.3.1 Behavioural Results

Texture Adaptation

A 2 x 2 mixed between-within ANOVA on the TTC was conducted with congruency (congruent vs. incongruent) and condition (moving adapting texture vs. static texture) as a within factors, while the direction of the adaptation (left vs. right) was the between factors. The ANOVA revealed a significant main effect for condition ($F_{(1,17)} = 11.709$, $p = 0.003$, $\eta^2_p = 0.42$) and congruency ($F_{(1, 17)} = 7.533$, $p = 0.014$, $\eta^2_p = 0.32$. This suggest that the TTC is shorter after the adaptation with a moving texture, regardless the congruency. Moreover, the TTC is longer with trials labeled as "congruent" than with those labeled as incongruent. The interaction between condition and congruency is also significant ($F_{(1, 17)} = 6.07$, $p = 0.025$, $\eta^2_p = 0.26$). Planned pairwise comparisons were computed using the Bonferroni adjustment. This further analysis revealed that the TTC measured after the adaptation with a static adapting texture is longer compared to the moving texture either when the trials were congruent ($p < 0.035$) or incongruent ($p < 0.001$) (Figure 16). Moreover, in the adapting moving texture condition the

TTC is significantly longer in the congruent trials compared to the TTC measured in the incongruent trials ($p < 0.01$). This agrees with my hypothesis that, in the moving adaptation condition, the TTC measured in the incongruent trials should have been shorter than the TTC measured in the congruent trials as in previous works (Gilden et al., 1995). However contrary to the expectation, the TTC measured after a static adaptation was significantly longer than the TTC measured in the congruent trials of the moving adapting condition. I speculate an interaction between the direction of motion adaptation that can make longer or shorter the TTC estimation and a general effect of dynamic adapting stimuli that might increase the responsiveness of ME detectors, shortening the TTC. Another hypothesis could be that dynamic stimuli can accelerate the temporal perception (Kanai, Paffen, Hogendoorn, & Verstraten, 2006; Burr, Tozzi, Morrone, 2007). Further investigation is however needed to address this issue.

Figure 16.

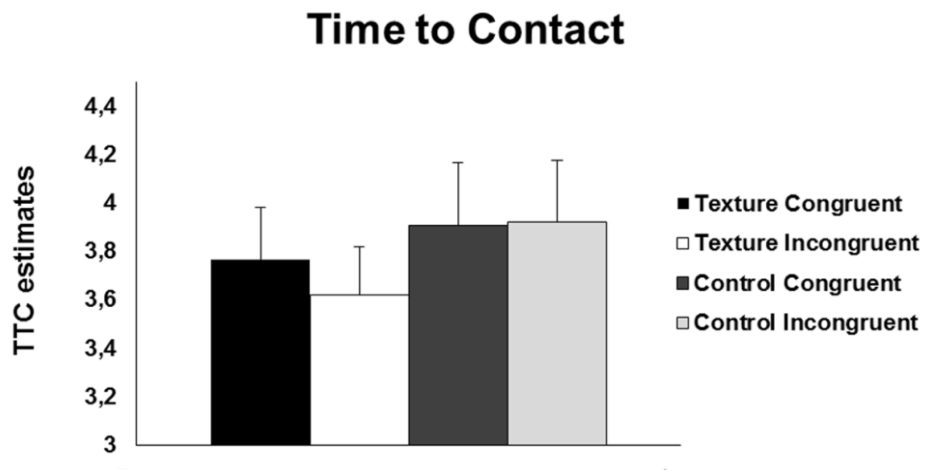


Figure 16. ***Estimated Marginal Means****: showing TTC estimates increased after adapting with the static texture. Moreover, TTC estimates increased with the moving congruent adapting texture compared to the moving incongruent adapting texture, and that there was no difference between congruent and incongruent in the control conditions.*

4.3.2 ERP analyses

Electrical brain activity was recorded from 64 electrode sites. Raw EEG data was filtered at a lowpass of 30Hz prior to any analysis being performed. EEG recordings were inspected for artifacts manually using the Matlab plugin ERPLAB (Lopez-Calderon & Luck, 2014). An average of 2 trials (SD = 2, minimum = 0) were rejected. Two participants were excluded from the analysis due to excessive muscle tension and eye movements.

CNV

A mixed ANOVAs were conducted on the mean amplitude of the average ERPs from each participant. The within factors were the condition (moving adapting texture vs. static texture), the congruency (congruent vs. incongruent) and a cluster of 9 electrodes. These electrode sites were chosen based on the visual differences in the neural activity occurring during congruent and incongruent conditions, relative to other electrodes across the scalp also based on previous literature (Coull & Nobre, 2008, Macar et al., 1999; Mento 2013; Kononowicz & Van Rijn 2011; Coull, 2004; Rao, Mayer, & Harrington, 2001; Wearden, 1999; Macar, Coull & Vidal 2006; Mento, 2013). The electrode sites included for analysis were 5 midline electrodes; Fpz, AFz, Fz, FCz and Fz, and two lateral frontal pairs; F1, FC1, F2 and FC2. The direction of the adaptation texture (left vs. right) was the between-subject factor. The window of interest was from the point in which the target became occluded along the trajectory to the mean Time to Contact response: -200 to 1500ms. Epochs were baseline corrected to 200ms prior to the occlusion of the target. Participants could blink after the response so I had to take, as upper limit of the temporal window, the shortest mean TTC among the participants, then the final part of the CNV is not available in this study. Re-referenced were made offline for visual and statistical analysis to the left and right mastoid.

Posterior electrodes

In order to investigate the occipital activity and compare it with previous findings (Makin et al., 2009; 2012) we average re-referenced offline our data. Unfortunately, the ORD was previously observed only in two studies (Makin and colleagues 2009; 2012). Moreover, I used a slightly different paradigm and target's parameters from them. Therefore, I did not used only an ANOVA on a cluster of electrodes taken by visual inspection as Makin et al., (2012) did, but I used a different approach in the analysis. A first explorative analysis was conducted using the mass univariate analysis (Groppe, Urbak, & Kutas, 2009). This analysis has different advantages such as to reduce the need for a priori defined hypothesis and to reveal unexpected event. A disadvantage is some loss of statistical power due to a multiple comparison adjusted with Bonferroni correction. This disadvantage is even greater with a large number of active electrodes. After the explorative analysis an Anova on the peak amplitude of the average ERPs was conducted in order to increase the power of the analysis and enlighten the differences between leftwards and rightwards ME.

4.3.3 Electrophysiological Results

CNV

Data showed clearly a CNV after the disappearance of the target. A one sample t-test showed that in the electrodes and in the window under investigation the mean amplitude value of the CNV was significantly lower than zero ($p < 0.0001$). The between factor of the adaptation direction (left vs. right) was not significant. The CNV measured was significantly greater in amplitude (more negative) in the condition with a moving adapting texture than the condition with the static texture ($F_{(1, 15)} = 6.66$; $p = 0.022$, $\eta^2_p = 0.32$). The main effect of the electrodes is also significant ($F_{(3.595, 50.336)} = 2.675$; $p = 0.048$, $\eta^2_p = 0.16$). Post hoc pairwise comparison with Bonferroni correction revealed a lower amplitude in the electrodes labeled FpZ ($p = 0.03$). Most interesting is the significant interaction between the condition and congruency ($F_{(1,15)}=8.72$ $p=0.011$, $\eta p^2 = 0.38$). Pairwise comparison Bonferroni corrected showed that in the congruent trials the amplitude of the CNV is greater with the moving adapting texture compared to the static texture ($p<0.01$). Moreover in the experimental condition, i.e., with the moving adapting texture, the amplitude is greater in the congruent trials than the incongruent trials ($p<0.04$). None of other interaction were significant. These results (Figure 17) revealed that the CNV is much more negative after having adapted with a moving texture in the same direction of the target than after having adapted in the opposite direction of the target or having adapted with the static texture. According to the pacemaker-accumulator framework (Buhusi & Meck, 2005) longer TTC estimation should produce more “clock ticks” in the brain and therefore larger and steeper CNV amplitude relative to shorter TTC estimates. Indeed longer interval estimation lead to a greater CNV in amplitude in Macar et al.,’s (1999) work. However, this was not true in my experiment, in fact static adaptation lead to a longer TTC but not to a larger and steeper CNV amplitude. Recent findings (Kononowicz & Van Rijn 2011; Van Rijn, Kononowicz, Meck, Ng, & Penney, 2011) with a stronger methodology (statistical power) failed to show the positive correlation between the reproduced duration and the CNV. TTC estimation is longer by adapting with a real motion stimulus moving in the same direction as the target and positioned in the retinal region where the target trajectory will be invisible (Gilden et al., 1995, see Chapter III). My suggestion is that real motion adaptation not only tire motion detectors stimulated by the adapting stimulus, but also the motion response to ME. Indeed, the TTC estimation is biased. Therefore, the motion response to ME is weakened and ME must relies most on temporal mechanism, with a greater activation of the frontal areas reflected by a greater CNV in amplitude. On the other hand, when adapting in the opposite direction or with a static texture this would not affect the motion response to ME (since the direction of motion is opposite) so that the visual motion areas will show activation.

Figure 17

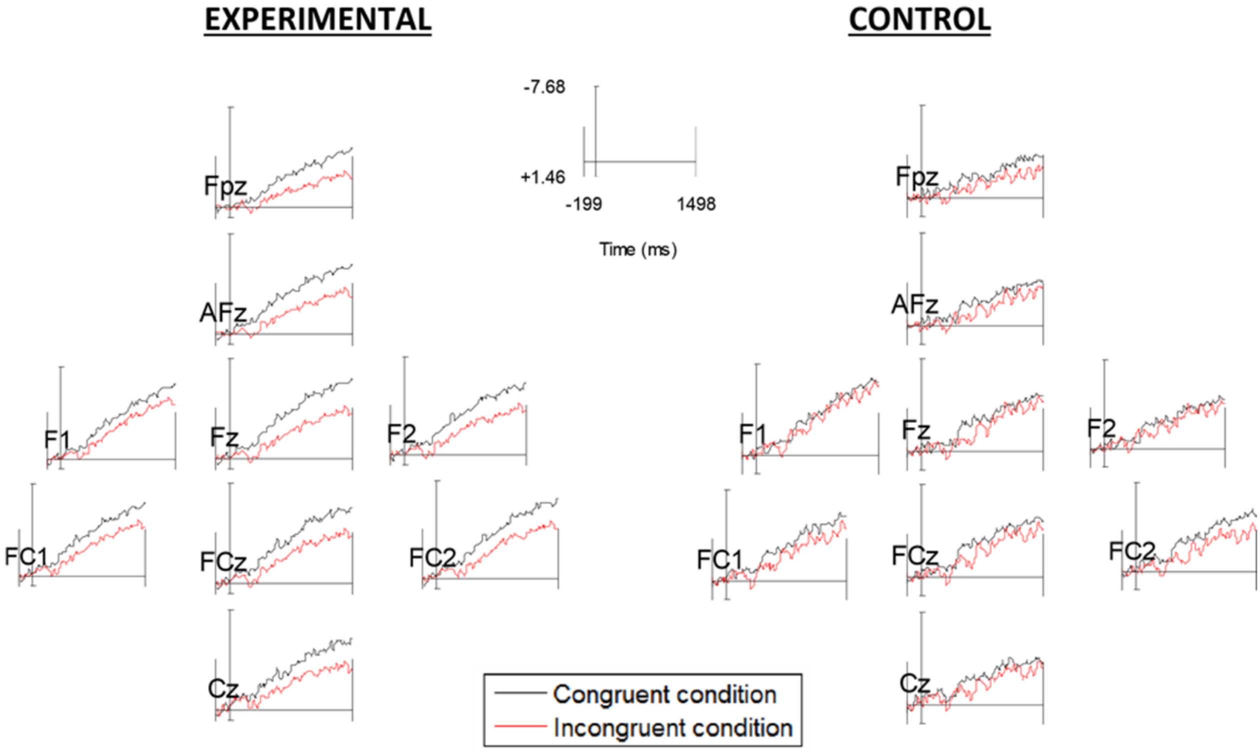


Figure 17. ***Electrode Sites of Interest:*** *CNV in the Texture Adaptation Experiment.*

Posterior Electrodes

One sample t-test showed that in the temporo-occipital electrodes (O1, PO3, PO7, P1, P3, P5, P7 and their right side homologues) and in the window under investigation (-200, 1500ms) the mean amplitude value is significantly greater (positive) than zero ($p < 0.0001$). Furthermore, I performed a series of statistical analysis (Mass univariate analysis and Anova) in order to discover any difference due to the factors under investigation: adaptation direction (left vs. right adaptation), condition (static vs. moving adaptation), congruency (congruent vs. incongruent) and hemisphere amplitude (left vs. right). Differently from my expectations, none of them showed significant differences. These results indicates that the ORD was not lateralized and that it was not affected by adaptation. In this study the absence of the lateralization of the positivity in the posterior electrodes could be due to the slow target used (3 deg/s) compared to that used by Makin and colleagues (2012) (12 deg/s and 20 deg/s). Then I collapsed the data from experimental and control condition (moving adapting texture and static texture) and I re-analyzed the data in order to investigate the brain activity during leftwards ME and rightwards ME regardless the congruency. Mass univariate analysis on 64 channels (*tmax* permutation test, Groppe et al., 2009) and within a temporal window of 150 and 250ms revealed a significant difference in the activity in the electrode labeled P3 (Figure 18) after 183ms from the disappearance of the target ($p < 0.05$). This result showed a negative component in the left hemisphere with a leftwards ME. A cluster of other 4 electrodes in the temporo-occipital areas: P7, PO7, P5, PO3, showed the same behavior of the electrode P3. Moreover, the contralateral electrodes showed the opposite behavior, i.e., a negative component with rightwards ME. This preliminary result which, as Figure 18 shows, is very clear even by simple visual inspection of VEPs lead me to conduct a repeated measured ANOVA on the peak amplitude with a direction of the ME (leftwards vs. rightwards), hemisphere amplitude and electrodes (P7, PO7, P5, PO3, P3 for the left hemisphere and P8, PO8, P6, PO4, P4 for the right hemisphere) as a factors. The interactions ME direction x hemisphere is significant ($F_{(1,15)} = 14.06$, $p = 0.002$, $\eta^2_p = 0.48$). Post hoc pairwaise comparison with Bonferroni correction revealed that in the left hemisphere the component under investigation is more negative with leftwards ME ($p < 0.004$) and in the right hemisphere is more negative with rightwards ME ($p < 0.027$) (Figure 18). Moreover during the leftwards ME the left hemisphere is more negative than the right hemisphere ($p < 0.008$) and there is a trend ($p = 0.065$) that indicate that the right hemisphere is more negative with rightwards ME. Moreover also the interaction hemisphere x electrodes F (1, 15) = 3.54, $p=0.012$, $\eta p^2 =.2$ is significant. Although there is no significant value in the pairwise comparison this interaction suggest that in the right hemisphere the negativity in the electrodes P8 is less evident.

Figure 18

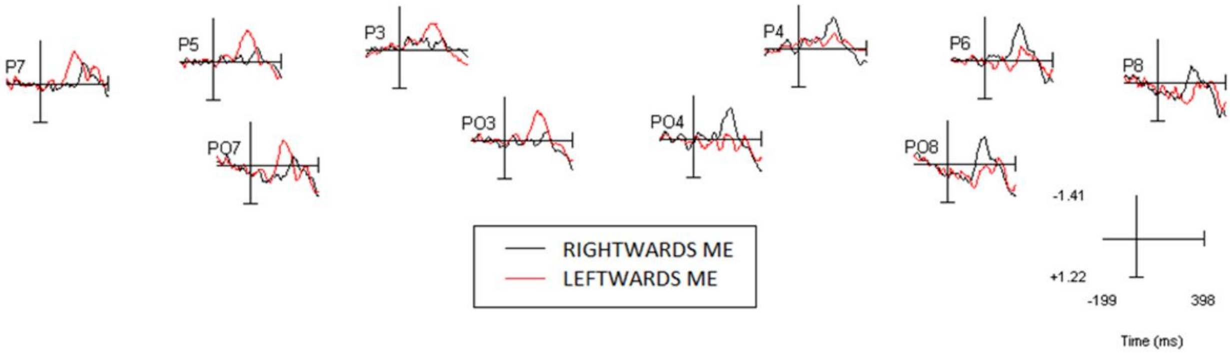


Figure 18. ***Electrode Sites of Interest:*** *Negative deflection (N190) during ME.*

4.4 Discussion

This study showed a series of very interesting results. First, behavioral data show that regardless the congruency of the moving target motion adaptation modulates the TTC response reducing it compared to a static adaptation. However, the TTC is shorter when the motion adaptation is in the opposite direction of the moving target compared to when the motion adaptation is in the same direction of the moving target suggesting that the motion adaptation interferes/modulates with ME. Second, electrophysiological results showed that the paradigm that I used elicits a strong CNV and this deflection is modulated by the congruency between the motion adaptation and the moving target. Finally, my data revealed that there was occipital positivity which starts around 200ms post occlusion as reported in Makin et al., (2012) .Differently from Makin et al.'s findings (2009:2012), we found that this component was not lateralized ~260ms post occlusion. In addition, our data do not indicate a modulation of the amplitude of this component by adaptation. However, I found a negative component with a peak about 190ms post occlusion in the ipsilateral hemisphere to the direction of the moving target. In other word ME in the left direction elicit this negative component in the left hemisphere and ME in the right direction elicit the negative component in the right hemisphere. This result is new because Makin et al.,'s

(2012) also found this negative deflection peaking around 180ms, but they did not report its laterality.

The behavioral result are very surprising. According to our hypothesis in the moving adaptation condition the TTC measured in the incongruent trials was shorter than the TTC measured in the congruent trials as in previous works (Gilden et al., 1995). However, contrary to the expectation the TTC measured after a static adaptation was significantly longer than the TTC measured in the congruent trials of the moving adapting condition. I speculate a complex interaction between real motion detectors and ME detectors. When real motion detectors activated by the adapting stimulus and tuned for a certain direction are tired this has a repercussion on the ME detectors that elaborate invisibile motion in the same direction, probably because they involved similar neural network, leading to a longer TTC. However a dynamic stimulus presented before the ME, regardless its duration and direction, could make the ME detectors more responsive pre-activating the network of ME, shortening the TTC. Another hypothesis could be that a dynamic adapting stimulus can change the temporal perception (Kanai, Paffen, Hogendoorn, & Verstraten, 2006; Burr, Tozzi, Morrone, 2007) speeding-up the passage of time. To our knowledge there is no study that investigates the temporal perception after long motion adaptation therefore further experiment are necessary to shed light on this point.

The electrophysiological data showed as expected a large CNV elicited during a TTC task. Surprisingly, longer TTC estimation because of motion adapatation increase the amplitude of this negative deflection, whereas the opposite is true with shorter TTC estimation because of the adaptation in the opposite direction. At first sight the interpretation of this datum is that in motion adaptation condition the TTC in the congruent trial is longer than the incongruent, therefore according to pacemaker-accumulator framework (Buhusi & Meck, 2005) ME in this condition should produce more “clock ticks” leading to a much more negative CNV. There are however two problems with this explanation. First recent works (Kononowicz & Van Rijn 2011; Van Rijn et al., 2011) with a strong methodology and statistical power failed to show a positive correlation between the duration and the CNV amplitude. Second, in the static adaptation condition the TTC is even longer but the CNV is not more negative than in adaptation condition, actually is significantly more positive. My interpretation is that motion adaptation in the congruent trials disrupt the balance in the network between the visual and frontal areas. Therefore, the visual areas during ME are less active and then the judgment must rely mostly on the frontal areas (involved in temporal processing). I believe that the larger amplitude of the CNV is the result of this unbalance in the network. An fMRI study may be clarify this interpretation.

Surprisingly, motion adaptation does not seem to modify the amplitude of the posterior (temporo-occipital) electrodes during ME. I do not have a clear explanation about this. I speculate that since 1 s elapses between the end of the adaptation and the disappearance of the target, this amount of time is sufficient to recover partially the activity of the visual areas. One could argue that if the visual areas are fundamental for ME and if they recover, then the TTC should not be different between congruent and incongruent trials. However it has been shown (Kohn & Movshon, 2003) that MT neurons of macaque need more than 14s to recover the normal firing rate after 40s of motion adaptation (top-up 5s). Therefore is probable that in human 1 s could be enough to cancel temporo-occipital EEG differences, but it does not mean that all the neurons in those areas are recovered. Indeed, for measuring EEG signal is necessary an amplifier that amplify the voltage up to 100,000 times and pyramidal neurons of the cortex produce the most EEG signal (Klein & Thorne 2006), therefore, EEG cannot reveal the entire brain activity (only macro-difference in voltage) and the effect of the adaptation during ME on the posterior areas might be hidden. Moreover, usually the effect of motion adaptation are observed by means the reduction in amplitude of the N2 elicited by a subsequent stimulus, (Hoffman, Unsold and Bach, 2001; Heinrich, 2007), but after the adaptation for 1 s there are no physical or endogenous (ME) stimuli in the region adapted. Finally, I believe, that the balance of the activity between the visual and frontal areas are not restored after 1 s from the end of the motion adaptation as shown by frontal activity (CNV). Basing on these evidences, I am still convinced of the fundamental role of the visual areas during ME even though there was no difference in the EEG recording.

The data were also collapsed in a way to confront leftwards and rightwards ME for comparing our result with previous work. Makin et al., (2012) stressed that during leftwards ME the left hemisphere is more positive and the right hemisphere is more positive during rightwards ME with a moving target fast 12 deg/s. They showed a positivity activity in the occipital areas that arise ~200ms after occlusion and a lateralized component ~260ms post occlusion labeled ORD. Finally, they barely touched on a negative deflection ~180ms post occlusion. The task used by Makin and colleagues (2012) was to indicate if the target reappeared from the occlusion in time or not (discrimination task) and used a very fast target (12 deg/s and 20 deg/s). These differences could explain why I did not find the lateralized ORD. However our result are in way similar: I found the occipital positivity that start ~200ms post occlusion and a negative deflection before the positivity suggesting common mechanism underlying ME and visible motion even in different paradigm (TTC vs. discrimination). A very surprising datum is the negative component that peak around 190ms post occlusion. This N190 was lateralized according to the ME direction and it is evident in the temporo-occipital electrodes. This component could be an index of the ME starting point and the attentional covert (feature) tracking during the absence of the visual stimulus (Makin & Poliakoff, 2011, Shiori Cavanagh, Miyamoto, Yaguchi, 2000). Is interesting the fact that this component arise about 200ms and not immediately after occlusion. Previous studies (Jonikatis et al., 2009, Bennet & Barnes 2004, Nagel et al., 2006, Their & Ilg, 2005) showed that ocular pursuit are possible after the initial period of occlusion (up to 200). Probably within 200ms is very unlikely that a moving object can significantly change in direction, speed and velocity (Schlag & Schlag-Rey, 2002), therefore ME during the first period of occlusion can rely on the “stored” retinal input, regardless the task involve ocular pursuit or fixation. After this period the ME must rely on different processes and the N190 that I found can be an electrophysiological correlate of this shift. Makin & Poliakoff (2011) stressed the fact that the shift of the visuospatial attention to an external location is basically the base of ME and this process alone is sufficient to explain ME. Although the visuospatial tracking is fundamental for ME (Makin & Poliakoff, 2011; Makin et al., 2012), our study showed how different activity in the frontal areas that are involved in timing mechanism can modify/interfere with ME. Moreover, I showed how this timing mechanism could be modulated by the low level cortical activity. To summarize the computation of ME required numerous areas and different sensorial-cognitive mechanism. In this study, the focus was on the visual and timing mechanism and on the possible index of the starting point of ME suggesting a complex neural network for computing ME. However, is very probable that this study have investigated only a small part of the neural network that compute ME. In fact primate neurophysiological data and fMRI studies (Barborica & Ferrera, 2003; Shuwairi et al., 2007; Nagel et al., 2006; Lencer et al., 2004; Ding et al., 2009) showed many other areas active during ME such as DLPFC, FEF, SEF, cerebellum, insula, inferior parietal lobe, cuneus, IPS and ACC. Further studies are needed in order to fully understand the contribution of each brain areas to this apparent simple process known as Motion Extrapolation.

Chapter V

“Seeing” invisible motion thanks to mechanisms of interpolation

5.1 Introduction

In this chapter, I aim to study the interpolation of invisible motion. This mechanism has been neglected so far and could operate in synergy with motion extrapolation. Extrapolation means estimate value beyond the original and known set of point. Interpolation instead means to construct new data points within the range of a discrete set of known data points. Therefore, in motion domain, extrapolation is the operation to estimate the future position in time of an occluded moving target using the information of the visible trajectory (known dataset): space, time and speed. Indeed, in some tasks observers do not know where and when (and if) the object will reappear, therefore the only data set available is that given by the visible motion and they can only extrapolate the future position in time of the occluded moving target. In some other conditions instead, participants know or can infer where the object is going to reappear, for example, when the occluder is visible or when there are some visible cue(s) to mark the centre or the end of the invisible trajectory. In this case, not only the dataset from the visible motion is available but also (some) spatial data of the occluded trajectory. Therefore, interpolating the point available of the occluded trajectory could be possible to construct an internal model or spatio-temporal map of the moving target for inferring in a better way when and where the target will be along the occluded trajectory.

Previous literature suggested that basing on the information about the visible trajectory stored in the brain, the visual system might be capable of evoking a pattern of activity during occlusion, thus accounting for the “perception” of invisible motion when the object moves behind the occluder (Assad & Maunsell, 1995; Barborica & Ferrera, 2003; Ilg & Their 2003). Based on this information, an interpolation mechanism would “fill-in” the object trajectory once it is known where the object is headed and where it will reappear. In other words, having a set of discrete spatial positions in which the moving occluded target will be in a certain moment of time, an internal model of this moving target is constructed in order to allow the interpolation of the intermediate spatial positions in time so as to infer where and when the object will be (Figure 19).Within this acceptation, interpolation of invisible motion would be another example of motion phenomena that involves the subjective impression of an object following a path even in the absence of any physical stimulus, such as apparent motion (Wertheimer, 1912), attentive tracking (Shioiri, Cavanagh, Miyamoto & Yaguchi 2000; Wertheimer, 1912; Cavanagh,1992;

Verstraten, Cavanagh & Labianca, 2000) and path-guided motion (Shepard & Zare, 1983). Within this theoretical framework, our hypothesis is that invisible motion is equivalent to an amodal filling-in (Michotte, Thinès & Crabbé, 1964; Komatsu, 2006; Pessoa & Neumann 1998).

Figure 19

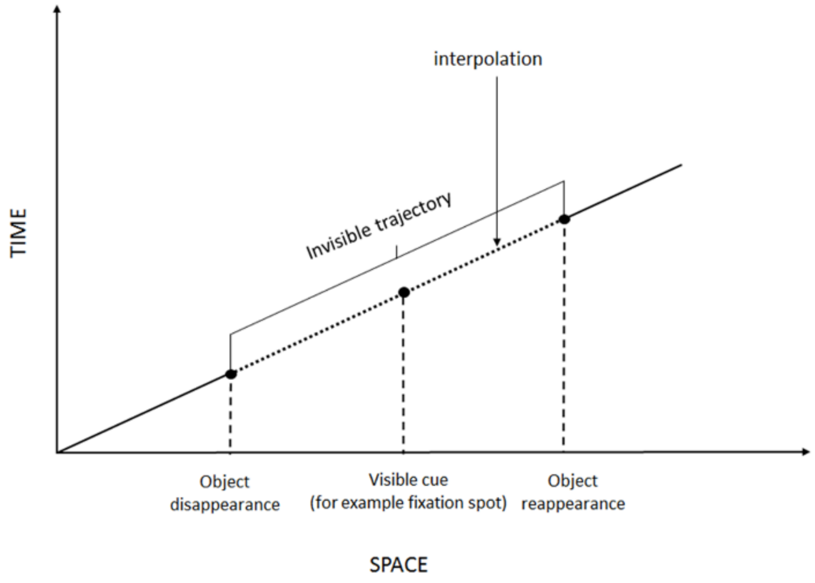


Figure 19. ***Illustration of interpolation.*** *Black dots represent a set of discrete spatial position. The black line represents visible speed, the dotted black line represents interpolated motion. From a continuous data set -: the visible motion - specific information, such as the speed, is extracted to construct a new data set, i.e. the intermediate value in space and in time (dotted line).*

In the present study, I wanted to use a method that would directly demonstrate in human participants that invisible motion is filled-in by interpolation. My first assumption is that interpolation by "motion filling-in" requires a cortical representation of the retinal region behind the occluder. Previous studies that have investigated filling-in in the blind spot (Ramachandran, 1993; Durgin, Tripathy & Levi 1995; Ramachandran & Gregory 1991; Tripathy & Levi 1994; Maertens & Pollmann 2007) did not provide any evidence that it can actually occur. Those who claim the contrary also cannot rule out the possibility that, instead of being filled-in, the area of the blind spot is simply ignored or unattended to. Based on this assumption I predicted that, if the occluder is placed over the blind-spot, where a cortical representation of the retina is missing, motion interpolation is prevented and a different strategy must be used, for instance a simple prediction on when the target will reappear. Our second assumption was that in the absence of any spatial cues to indicate the end of the invisible trajectory, participants cannot predict when and where the target is going to reappear. When responding to the appearance of an occluded target, I was interested to know whether participants respond simply when they see the target appear (reaction time response) or whether (given the appropriate conditions) they can form a mental representation of the object in motion behind the occluder (Figure 20) and, on the bases of this, even anticipate its reappearance.

5.2 Experiment 1

In Experiment 1 I presented a moving target that travelled behind an eccentric occluder (average eccentricity 13 deg) over either the nasal (blind spot, BS) or the temporal retina, at a symmetrical distance from the fovea (symBS). Reaction time (RT) was recorded from when the target disappeared and from when it reappeared.

I hypothesize that, when the occluder is on symBS position, participants can perform the task by either interpolation of the invisible motion or just by prediction (estimation) of the reappearance time. Conversely, when the target travels across an occluder placed over the BS where the cortical representation of space is missing, interpolation is prevented and therefore, if anticipation occurs this can only result from prediction. Thus, I would not expect any difference in reaction time to the reappearance of the target if prediction occurs in both conditions. On the other hand, shorter reaction times with the occluder on the symBS would reflect interpolation: i.e. the capability of forming a spatio-temporal map of the moving target that allows participants to infer when the target reappears.

Figure 20

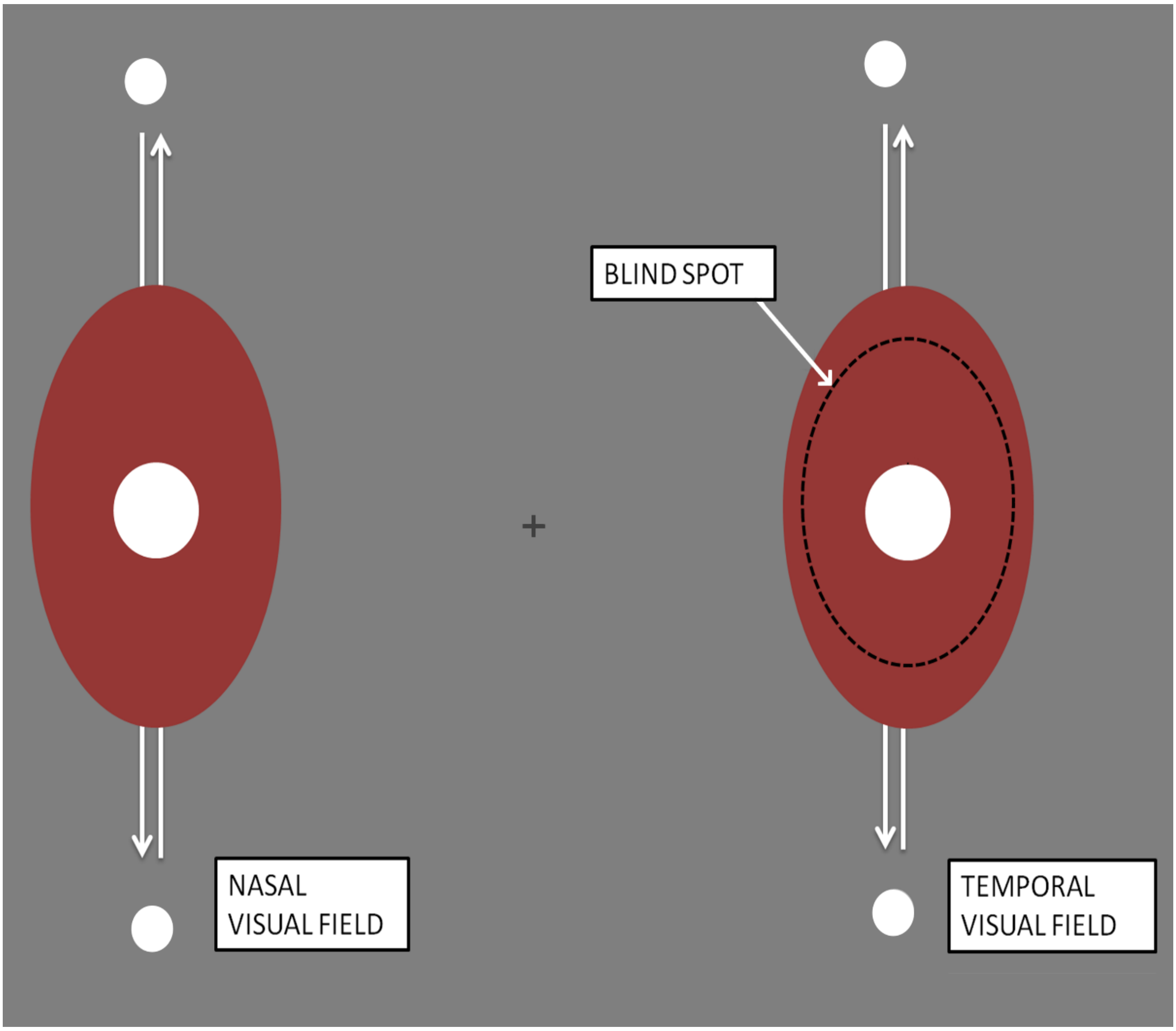


Figure 20. ***Illustration of the trial****: right eye. A moving circle traveling through an occluder was placed at 13 deg from the fixation cross (center to center). The occluder changed color every 66 ms in order to avoid the Troxler effect. In the center of the occluder a visible cue was presented which remained visible in the symmetrical condition but disappeared in the blind spot condition. Participants had to press a button to indicate when the target reached the leading edge of the occluder and also when the target reappeared from the trailing edge of the occluder. The target was presented randomly from either above or below the occluder and travelled towards the opposite side of the screen at a constant speed during each block.*

5.2.1 Method

Participants

Ten students from the University of Padova (8 female, 2 male; age 19-22 years) took part voluntarily in this experiment. Participants had normal or corrected-to-normal vision and were required to give written informed consent according to the Declaration of Helsinki. Participants remained unaware of the true aims of the experiment until completion of the task. They were then fully debriefed as to the true intentions of the experiment.

Stimuli and Apparatus

Participants were placed in a dark room, seated 57 cm away from the display screen. Viewing was monocular. Stimuli were generated with Matlab Psychtoolbox (Brainard 1997; Pelli, 1997) and displayed on a 24 inch Asus monitor with a refresh rate of 60 Hz. The screen resolution was 1920 × 1080 pixels. Each pixel was subtended ~2.5 arcmin. The luminance of the background was 0.8 cd/m^2. The target was a small circle of 0.5 degree of visual angle (deg) in diameter. A fixation cross was placed in the center of the screen with a length of 0.3 deg and with a width of 0.1 deg. Both had a luminance (Minolta LS-100 photometer) of 125 cd/m^2. The occluder was an oval shape with top-bottom and left-right mirror symmetry. During normal viewing, when a stationary object of a uniform texture is placed in the periphery of the visual field, this object would usually disappear from sight due to phenomenon known as the troxler effect (Troxler 1804). In order to avoid this problem the occluder changed its colour every 66ms (colours similar to the background were not used). This meant that the borders of the occluder would remain sharp and in focus even when placed in the peripheral vision. The size of the occluder (average: 7.5 deg in height and 5.5 in length) was adjusted very carefully over the blind spot for each participant. Centered in front of the occluder was placed a spatial cue with a diameter of 1.5 deg (not visible when the occluder was placed temporally as it fell inside the blind spot). The target appeared after a random interval between 0-2000ms from an acoustic cue, within a range of 8-10 deg from the upper or lower edge of occluder and travelled in a linear trajectory. The target continued this motion at a stable speed (3 deg/sec) and direction up until and behind the occluder, and reaching the end of the trajectory at a symmetrical distance from the opposite side of the occluder. (The speed of the target remained constant at 3 deg/sec throughout both the visible and invisible trajectory). To minimize head movements a chin rest was used for all participants.

Procedure

Within each block of 40 trials, 20 were devoted to upwards and 20 to downwards motion, the target direction was randomly presented either upwards or downwards. Participants were required to fixate monocularly on the white cross placed in the center of the screen. In each trial, their task was to press the response-key as fast as possible in two instances, when the target *just* reached the leading edge of the occluder (time-to-contact) and as soon as it reappeared from the far edge of occluder (time-to-reappearance). From the time-to-contact (TTC1) and the time-to-reappearance (TTR2) I subtracted the duration of the corresponding physical trajectory in order to obtain the first (RT1) and the second reaction times (RT2). Since the target is a moving object, I assumed that an RT equal to zero corresponded to the moment that the leading edge of the moving target reached the edge of the occluder. The experiment consisted of two blocks that were counterbalanced between subjects, one devoted to the blind spot condition and the other to the symmetrical position.

5.2.2 Results

A two way repeated measures ANOVA was carried out on the numerical differences between the reaction time response from when the target reappeared from the occluder (RT2) and the reaction time response for when the target disappeared behind the occluder (RT1), i.e. RT2 minus RT1. The two within-subject factors were the occluder position (blind spot or symmetrical) and direction (upwards or downwards).

Results (Figure 21) revealed a significant difference between the two occluder positions ($F_{(1,9)}=13.6$; $p=0.005$; $\eta^2_p=0.6$). Neither the main effects of direction nor the interactions yielded statistically significant results.

Figure 21

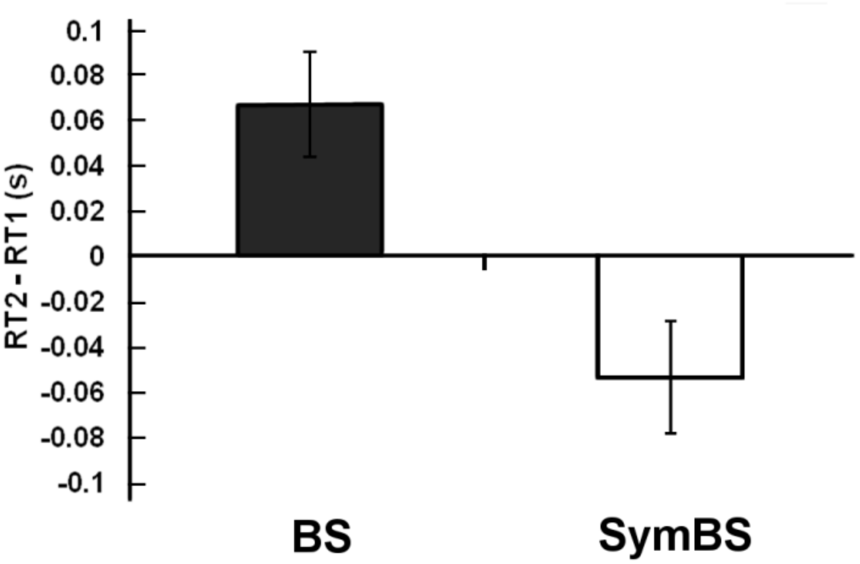


Figure 21. *The figure shows the difference between RT2 and RT1 in seconds obtained with an occluder placed either over the BS (black bars) or the symBS (white bars). Bars indicate one S.E.M with normalization for within subject design (Franz & Loftus 2012).*

Figure 22

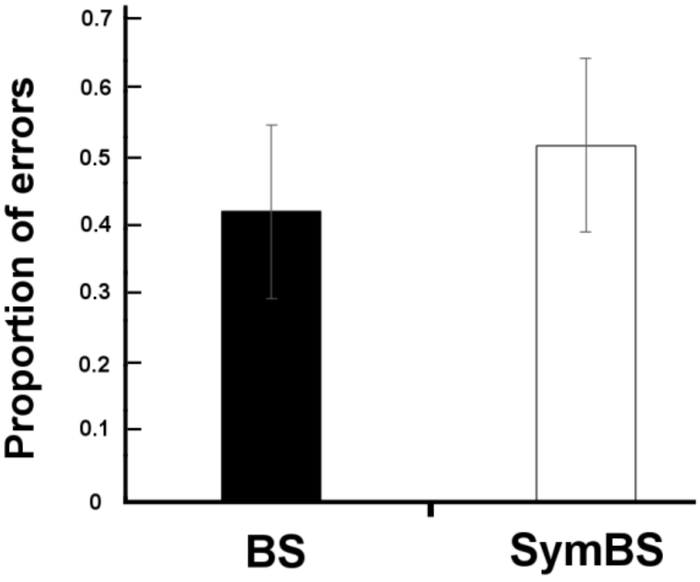


Figure 22. *Proportion of errors (button press before the reappearance of the target) in the BS (black) and symBS condition (white). Bars indicate one S.E.M.*

It was found that when RT1 was subtracted from RT2 a positive result was obtained only when the occluder was positioned over the blind spot (BS). On the contrary, when the occluder was positioned opposite (symmetrically) to the blind spot (symBS), the calculation of RT1 subtracted from RT2 yielded a negative result. Note that this occurs despite the response to the reappearance may be slowed by processing of the initial motion. Indeed, even if RT2 was slowed by the response to disappearance (RT1) (but this is unlikely given the long interval between the two responses) it was the case in both the BS and the symBS conditions. This surprising result would indicate that in spite the participants' requirement to respond when the target actually reappeared, they often responded before the reappearance of the target. Two results support this interpretation: first, RT2 in the BS condition is 212ms and the mean RT2 in the symBS position is 134ms, well beyond the human limit (table 1); second, (Figure 22), shorter RT2s, in the symBS condition, are associated with a larger number of errors ($t_{(9)} = 2.353$, $p < 0.045$), i.e., trials where the participants effectively responded before the target had reappeared. The dissociation between RT2 obtained in the two conditions may reflect the intervention of different mechanisms to judge reappearance: for example prediction in the BS, and interpolation on the symBS condition.

5.2.3 Control Experiments

An alternative explanation to account for the difference in RT2 between the two conditions could be a possible spatial distortion of the occluder size placed over the blind spot (Ferree & Rand 1912). I reasoned that if participants used a prediction strategy in both conditions and the occluder size is perceived as larger over the BS, they should judge the time to reappearance as longer. Although this is unlikely because spatial values around the BS are either preserved or perceived as being smaller (Ferree & Rand 1912; Triphaty, Levi & Ogmen 1996), I decided to control for this possibility. I used an invisible occluder (hence, the circle traveled behind the background) and I put two horizontal lines outside the BS at a distance of more than 1/6 of its diameter (the procedure to estimate the size of the blind spot was the same of Experiment 1) to indicate the upper and lower edge of the invisible occluder. Since the occluder was now invisible, there was no visual spatial distortion of the occluder. A new sample of 10 participants (6 female, 4 male; age 21-28 years) underwent the same task and procedure of Experiment 1.

Since the RTs obtained in the Experiment 1 were very small, here participants were instructed to respond when the circle disappeared and reappeared entirely in order to reduce anticipatory errors and focus more on the RT. I carried out an ANOVA with two within-subject factors: occluder position (BS or symBS) and direction (upwards or downwards). Results revealed a significant difference between the two occluder positions ($F_{(1,9)} = 6.36$; $p = 0.03$; $\eta^2_p = 0.4$). Neither the main effects of direction nor the interactions yielded statistically significant results. Moreover, as in Experiment 1, the symBS condition was associated to a larger number of errors ($t_{(9)} = 2.13$; $p < 0.035$). The results of this control experiment support the suggestion that participants interpolate invisible motion over the symBS.

Table 1. Reaction time from experiment 1 and control experiment.

Experiment 1	RT1	RT2	RT2 - RT1
BS	0.145	0.212	0.067
SymBS	0.188	0.134	-0.054
Control Experiment			
BS	0.388	0.278	-0.109
SymBS	0.382	0.227	-0.155

To further support this suggestion I checked, in a second control experiment, for the alternative possibility that temporal estimation of the time to reappearance differed in the BS and symBS condition and therefore prediction could still explain the differences in RT. A new sample of 9 participants (6 female, 3 male; age 21-27 years) were asked to make a magnitude estimation (Stevens, 1968) of the time taken by the target to reach the end of the trajectory. There was no occluder, therefore the target disappeared only when it passed through the BS (the BS served as a natural occluder). The target travelled over 5 different trajectories: 18.5, 19, 19.5, 20, 20.5 deg, employing 6.16, 6.33, 6.5, 6.66 and 6.83 s respectively. The starting position of the target trajectory was randomly jittered (within ± 1 deg range) in order to avoid temporal judgments based on spatial cues. Once the trajectory ended, the target did not disappear but remained static and visible until the participants pressed the appropriate button to start the next trial. All the other parameters were the same as in Experiment 1.

Participants were first presented with a block of 10 trials, in which they learnt that the estimated duration of a 19.5 deg trajectory over the symBS had a value of 10. This practice block was followed by two (BS and symBS) randomly presented 50-trials blocks (5 repetitions of the 5 different trajectory lengths for both upwards and downwards directions). During the target trajectory, subjects performed an articulatory suppression task (say the syllable /la/) in order to avoid a direct counting. In addition to pressing the response-key as fast as possible when the target stopped, participants had to estimate the trajectory duration by assigning a number to it, either greater, equal to or smaller than 10, depending on whether they perceived the duration was greater, equal to or smaller than that in the baseline condition.

Results are shown in Figure 23. The power function fitted to the estimated duration of the five physical durations resulted in a similar exponent in both the BS and the symBS condition. Indeed, individual slopes of the regression lines – obtained by plotting judged vs. physical duration on log-log axis so to transform the exponent of the power function into the slope of the regression line - did not show a significant difference ($t_{(8)} = -0.106$; $p = 0.918$). The reaction time did not differ in the two conditions either. From the results of the two control experiments I concluded that there is neither spatial nor temporal distortion due to (a possible) different representation of space or time within and near the blind-spot.

Figure 23

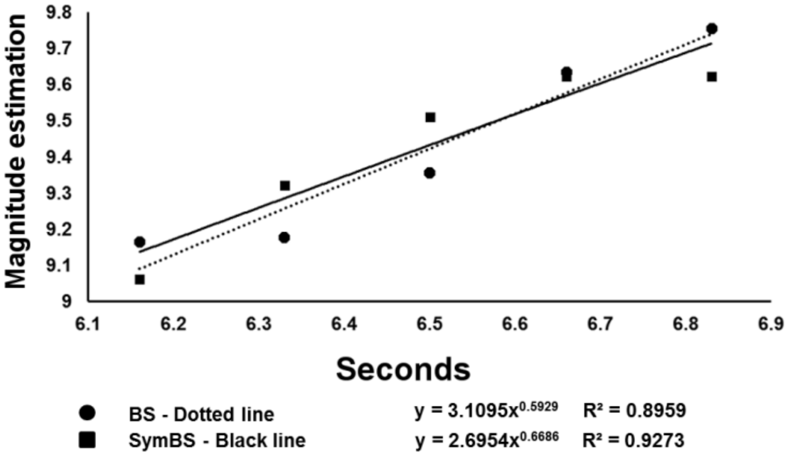


Figure 23. *Dots and squares represent the estimated duration of the different physical durations of target motion in the symBS (black squares) and BS condition (black dots) Dotted line represent the power function fitted for BS and black line represent the power function fitted for SymBS.*

5.3 Experiment 2. 'Testing the interpolation of invisible motion trajectories'

So far, results indicate that when the cortical representation of the BS is missing, participants cannot interpolate correctly, however they can still judge the target trajectory by pure prediction. Indeed, in Experiment 1, I used a classical paradigm with a visible occluder (or visible edge) and measured the time-to-reappearance (TTR2). Such a task does not exclude the possibility that the time to travel behind the occluder (estimated prior to target occlusion) can be predicted during the occlusion period (Weil & Rees 2011; Fiorani, Rosa, Gattass & Rocha-Miranda 1992). However, for this to occur, participants have to know, as they do under the conditions of Experiment 1, the point at which the trajectory ends. In Experiment 2, I wanted to investigate whether the dissociation between the RT2 - RT1 in the two conditions in Experiment 1 is suggestive of a true mechanism of interpolation in the sighted retina. Without a visible end point of the invisible trajectory participants can either rely on a spatial cue - an imagery of the occluder shape and length (note however that many trials are required in order to infer the shape of the invisible occluder) – or, they may rely on visuo-spatial cues: the point at which the target disappears and the point marked by the fixation cross indicating the middle of the trajectory. By interpolating these two points, participants can form an internal model of the target travelling behind the first part of the invisible trajectory and infer the second part by symmetry.

To test whether or not interpolation occurred, in Experiment 2 I substantially modified the paradigm used in Experiment 1. I measured RT using an invisible occluder, therefore, in the *absence* of a spatial cue at the end of an invisible trajectory. Note that both the surface and the contour of the occluder, an irregular polygon with left-right mirror symmetry, were completely invisible. I compared RT2 with and without pre-occluder motion. Whereas with pre-occluder motion participants could form either a spatial or visuo-spatial representation of invisible motion: without pre-occluder motion it is impossible to form a visual representation of target motion behind the occluder and obsevers can only respond when they see the target.

5.3.1 Method

Participants

Seven students from the University of Padova (4 female, 3 male; age 19-22 years) participated voluntarily in Experiment 2. Participants remained unaware of the true aims of the experiment until completion of the task. They were then fully debriefed as to the true intentions of the experiment.

Stimuli and Apparatus

The stimulus was an invisible (entirely) irregular polygon with left-right mirror symmetry. In one block the target (same as experiment 1) initiated a linear trajectory after a randomly chosen interval of 0-2000ms from an acoustic cue either 7.5 or 10 deg from the center of the screen. In the other block the visible trajectory was removed and the target motion started from the center of the occluder (target was invisible behind the occluder). The trajectory of the circle terminated 4 deg after reappearance. Target speed (either 3 or 6 deg/sec) was randomly selected within each block. The direction was randomly chosen within each block. Direction could begin from either side of the screen, from one of 8 specified directions. Each of these directions was separated by a 45 deg sector of a virtual circumference: 0-180 (5 deg), 45-225 (4.7 deg), 90-270 (4.9 deg), and 135-315 (4.7 deg). Once the target reached the polygon edge it continued its motion behind it along an invisible trajectory length that varied from 4.7 to 5 deg (4.84 deg on average) (Figure 24). Each block consisted of 64 trials: 2 repetitions of each direction, speed and starting position (7.5 or 10 deg). Viewing was monocular and both eyes were tested. In all blocks participants were required to fixate on a cross (60 cd/m^2) that also represented the center of the invisible occluder. A circle (1.5 deg; 120 cd/m^2) was placed over the blind spot to have double control of fixation (participants were told not to see it). A chin-rest was used to limit the head movement. The participants' task was to respond as fast as possible when the target "just reappeared". Only RT2 was measured. In the absence of pre-occluder motion participants knew that the trajectory started at the center of the invisible occluder but they did not know when it started since no temporal fixed cue was given to provide this information. The hypothesis was that for interpolation to occur, a visible trajectory needs to be present. Based on this hypothesis, I predicted shorter RT2 when visible motion was present with respect to when it was not.

Figure 24

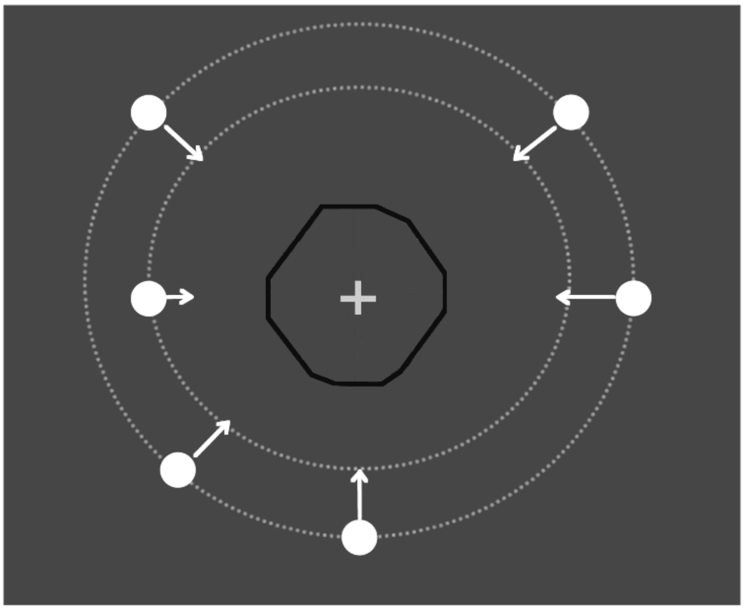


Figure 24. ***Illustration of the trial***. *A moving circle travelled through an* ***invisible*** *occluder (the black line is shown in the figure only for illustrative purposes, it was not visible to the participants) which had an irregular but mirror-symmetric polygon shape. The target (circle) started from eight different places at one of two different distances from the occluder. Participants had to press a response button as soon as the target reappeared. RTs were calculated assuming that RT was equal to zero when the leading edge of the target reached the edge of the invisible occluder.*

5.3.2 Results

A repeated measures ANOVA was carried out (Bonferroni correction) on the mean RT2 obtained when pre-occluder trajectory was present (control) and when it was absent. Factors were the speed of the target (3 vs. 6 deg/sec), the target direction (eight levels: 0-180 [horizontal], 45-225 [diagonal clockwise], 90-270 [vertical], 135-315 diagonal counterclockwise] deg and vice versa), the starting position of the visible trajectory (position: 7.5 vs. 10 deg from the center) and the eye (left vs. right). The Greenhouse-Geisser correction for degrees of freedom was applied where appropriate, i.e. when the sphericity of the data was violated as indicated by a significant Mauchly's test.

The effect of eye ($F_{(1,6)}$ = 0.46, p = 0.525, η^2_p = 0.07), position ($F_{(7,42)}$ = 0.44, p = 0.534, η^2_p = 0.07) and target direction ($F_{(2.836,17.014)}$ = 2.95, p = 0.07, η^2_p = 0.33) were not significant. Most importantly, the effect of condition was significant ($F_{(1,6)}$ = 20.44, p = 0.007, η^2_p = 0.77) (Figure 25). This indicates that the RT2 was shorter when pre-occluder visible motion was available, by 81 ms. Moreover, the effect of speed was significant ($F_{(1,6)}$ = 53.22, $p < 0.0001$) but not the interaction of speed x condition. This lack of interaction suggests that, although at high speed RT2 is slowed, (because of a difficulty to employ visuo-spatial attention to a fast stimulus when it reappears from the invisible occluder), this does not affect the difference in RT2 obtained with and without pre-occluder motion. None of the interactions were significant.

Speed-accuracy trade-off analysis (Figure 26) demonstrate that anticipation errors occurred only when pre-occluder motion was present ($t_{(6)}$ = 3.179; $p < 0.02$) and they increase as RT2 decrease. Conversely, with no pre-occluder motion, errors are almost absent and unrelated to RT2.

Figure 25

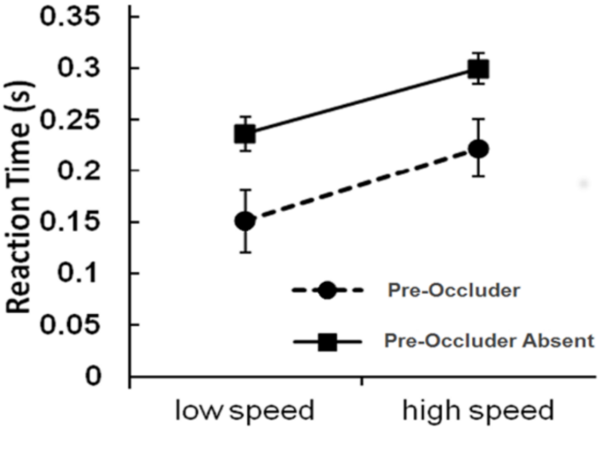


Figure 25. *RTs in seconds obtained in "Pre-Occluder Absent" condition (with visible trajectory, black squares) are longer than those obtained in "Pre-Occluder" condition (i.e., with visible trajectory before occlusion) in which interpolation was possible. Bars indicate S.E.M.*

Figure 26

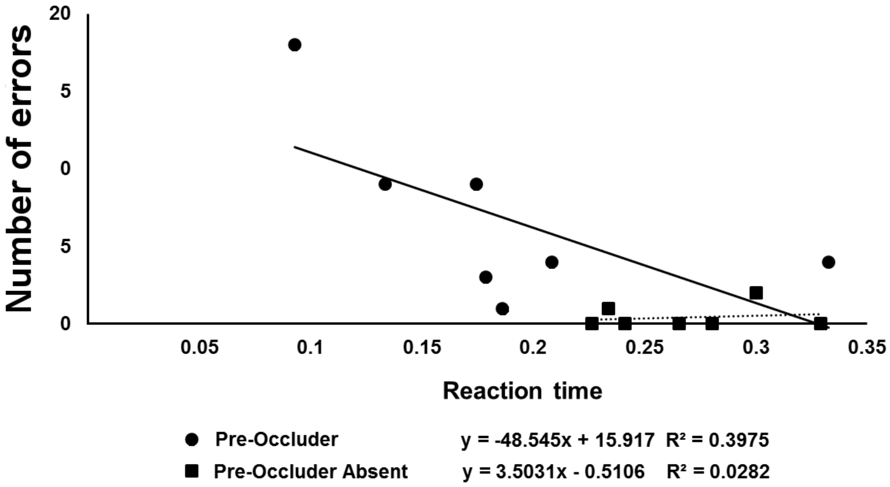


Figure 26. *Dots and squares represent the number of errors (button pressed before the reappearance of the target) as a function of mean reaction time for each participant. Empty dots indicate "Pre-Occluder" condition and black squares represent "Pre-Occluder Absent" condition. Dotted and black lines represent the linear Regression lines.*

These results suggest that pre-occluder motion allows participants to form a spatial representation of the hidden trajectory and anticipate target reappearance. The simpler way to do so is to "learn" the average length of the invisible trajectory (4.84 ± 0.12 deg) and predict when it would end. In this case, I would not expect a linear relationship between the TTR2 and the actual physical duration. Instead, as Figure 27 shows, the relationship between the TR2 and the actual physical duration *was* linear as it was in the baseline condition, where participants are forced to respond when they saw the target. The results demonstrated that with pre-occluder motion present, the duration of the invisible trajectory was isomorphic with the physical duration. This confirms that anticipation does not simply reflect an averaging strategy.

In sum, results of Experiment 2 showed that: i) participants often anticipate target reappearance even without knowing where it will reappear and ii) this does not occur by "learning" the average length of the invisibile trajectory.

Figure 27

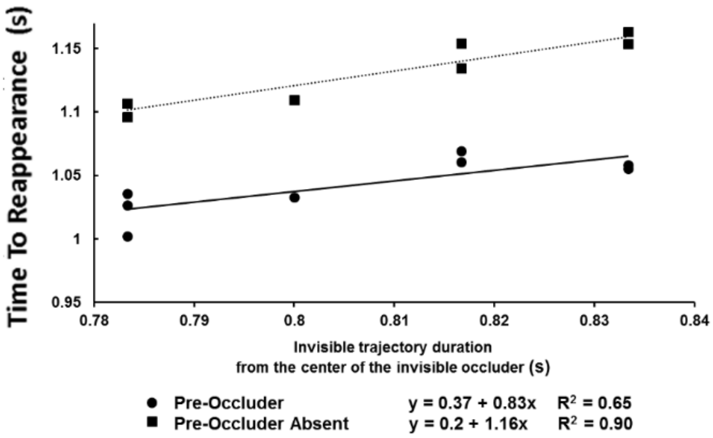


Figure 27. *Regression lines fitted to Time to reappearance data (calculated from the center of the invisible occlude to the button press) obtained in Experiment 2 in the condition where the interpolation is theoretically possible (black dot): i.e. visible motion before the disappearance and in "Pre-Occluder Absent" condition (black square). In "Pre-Occluder" condition the relationship between the TR2 and the actual physical duration was linear as it was in the baseline condition, where participants are forced to respond when they see the target. This indicates that the duration of the invisible trajectory is isomorphic with the physical duration and therefore cannot reflect a simple averaging strategy.*

5.4 Experiment 3. 'Testing for the sufficiency of spatial position information.'

In Experiment 3, I investigate how participants can anticipate target reappearance without a spatial cue to indicate where the target will reappear. Shiori and colleagues (Shiori, Cavanagh, Miyamoto, Yaguchi, 2000) have shown that participants can precisely judge the apparent location of a target in invisible motion relative to an imaginary cue. I asked whether participants could exploit this ability to form a visual representation of the target motion behind the occluder. By following its invisible trajectory they could first judge when the target reached the position behind the occluder marked by the central fixation and then, by symmetry, when it reappeared in an opposite symmetrical position relative to the point of disappearance (Figure

24). To test this possibility in Experiment 3 I compared the condition in which the fixation was available with the condition in which the fixation was absent. In the first case, participants could “follow” the moving target behind the occluder for the first part of its trajectory up to when it reached fixation, and then for the second part, its length was isomorphic to the first. In other words, they could interpolate the target motion. Conversely, when there is no fixation and the trajectory length is not constant, participants could “learn” the average length of the invisible trajectory by forming a visual representation of the occluder shape.

Experiment 3 is a replication of Experiment 2, with the novelty that pre-occluder motion was present in both conditions however, in one condition I removed the spatial cue (fixation cross) that indicated the center of the invisible trajectory. To assure fixation in this condition, a circle (1.5 deg; 120 cd/m^2) was placed over the blind spot (Participants were instructed not to see it otherwise fixation was altered). In the other condition, the central fixation was present. Seven students (5 women, 2 male; age 21-25 years) participated in this experiment.

The repeated measures ANOVA with the same factors as in experiment 2 revealed that the effect of eye ($F_{(1,6)} = 0.10$, $p = 0.761$, $\eta^2_p = 0.01$), position ($F_{(7,42)} = 0.002$, $p = 0.967$, $\eta^2_p = 0.001$) and target direction ($F_{(1,6)} = 3.50$, $p = 0.074$, $\eta^2_p = 0.36$) were not significant. None of the interactions were significant. However the effect of speed was significant ($F_{(1,6)} = 11.54$, $p = 0.015$, $\eta^2_p = 0.66$). Most importantly, the effect of condition was significant ($F_{(1,6)} = 17.78$, $p = 0.006$, $\eta^2_p = 0.75$). This indicates that the RT2 was lengthened by 81ms when the central fixation was absent (Figure 28). The number of errors are higher in the fixation conditions (4.07 vs. 2.07 in percentage), however the difference is not significant.

Moreover, with a central fixation, not only was RT2 shortened by 81ms, but also the relationship between the TTR2 and the actual physical duration was linear (Figure 29), suggesting that the invisible trajectory can be filled-in with high precision. Conversely, in the absence of a central fixation there was no linear relationship between TTR2 and physical duration, suggesting that target reappearance is judged on the basis of average trajectory length.

Figure 28

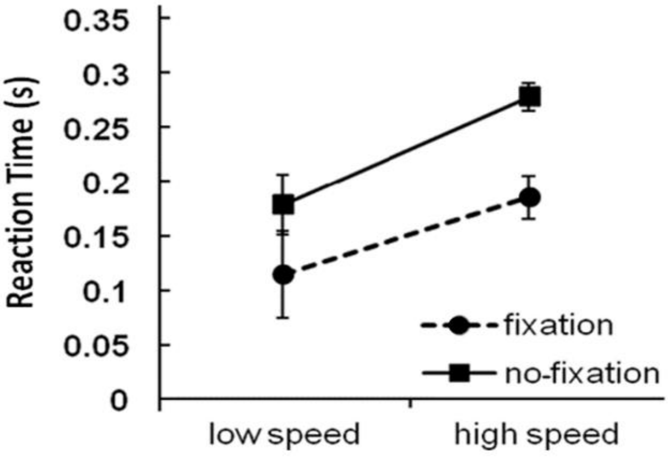


Figure 28. *Black squares represent RTs obtained in "No-Fixation" condition and white circles represent RTs obtained in "Fixation" condition). The RT was shorter when fixation cross was given. Bars indicate one S.E.M.*

Figure 29

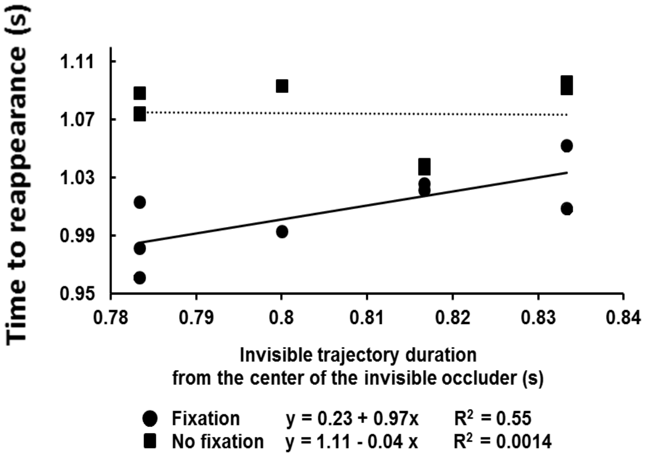


Figure 29. *Regression line fitted to TTR2 data (calculated from the center of the invisible occluder to the button press) obtained in Experiment 3 in the condition with (circle) and without*

fixation cross (square). In the fixation condition, the relationship between TTR2 and the actual physical duration is linear, indicating that TTR2 is isomorphic to physical duration and therefore cannot reflect a simple averaging strategy.

5.5 Discussion

To summarize I have compared RT2 in different conditions in which participants can respond to a target reappearing from behind an occluder:

a) They can respond when they actually see the target, as in the baseline condition of experiment 2, in which participants see the target appearing from behind an occluder without knowing where and when its trajectory started.
b) They can predict target reappearance when either they knew where it would reappear (as in the BS condition) or when they did not know but they could infer it by forming a visual representation of occluder shape (length), as in the absence of central fixation.
c) They can anticipate target reappearance by forming an internal representation of the moving target, judging the length of its trajectory from disappearance to when the target reached the central fixation and following its invisible motion to a symmetrical position.

Given the current findings, in these conditions (c) participants are able to fill-in (amodal completition) invisible motion by means of an interpolation mechanism.

How does interpolation of invisible motion lead to anticipate the reappearance of the target behind the occluder? Note that if reappearance is anticipated, it cannot rely on either co-occurring toward- and away-from-background changes at two spatial locations (Hock, Schöner & Gilroy 2009) or on cognitive mechanism such as long-range motion, which identifies a form and track its position over time.

A plausible candidate for interpolation may instead be the third-order motion mechanism. The image points behind the occluder (corresponding to the center of the invisible trajectory and its end point) may be made salient by a third-order motion system (Lu & Sperling, 2001; VanRullen, Reddy & Koch, 2005). In fact, the third-order motor system has been demonstrated to receive its input not only from motion sensors but also from task instructions. This in turn may trigger an attention-driven computation of marked locations in a spatio-temporal map or “saliency map” (Blaser, Sperling & Lu, 1999; Grassi & Casco, 2010) which provides the input for the neural circuit that processes motion in discrete sampling. The input to this cognitive system would be: the information from the visible motion, visuo-spatial cues (such as the fixation cross) and the instructions. The instructions would activate top-down attentional control mechanisms to increase saliency in the space and time of the image points behind the occluder. The output would be the “saliency map” and it would be used as the input for the next layer where low-level motion sensors compute motion in discrete sampling. Indeed attention, tested in a divided attention task, was proven to play a role. The RT2 in the full attention condition in which the procedure and the task were the same as the block with the fixation point in Experiment 3, were compared with those obtained in the divided attention condition: after pressing the key they had to report whether the fixation cross had changed its luminance during either a 33-1200ms interval (with low speed) or a 33-600ms interval (with high speed) after target disappearance (from 60 cd/m^2 to 70 cd/m^2 with 25% of probability). The analysis revealed a significant difference in RT2 (39ms) between the Attention and Divided Attention conditions ($F_{(1,11)} = 5.761$, $p = 0.035$, $\eta^2_p = 0.34$), suggesting that without full attention interpolation is less likely.

However, visual attention has also been found to be involved in other mechanisms of elaborating invisible motion, such as, motion extrapolation (Makin & Poliakoff, 2011) and feature tracking (Cavanagh, 1992; Verstraten, Cavanagh & Labianca, 2000; Shiori et al., 2000). Therefore, the established role of attention is not sufficient to conclude that interpolation is based on a third-order motion mechanism. Moreover, our results indicating that interpolation occurs at a long time interval from when the target disappears to when it reaches central fixation (805 ms), is not well predicted by a third-order motion model (Lu & Sperling, 2001). This model proposes that the motion of any salient object is signaled by the response of low-level Reichardt-like detectors that compute motion at short ISIs. Furthermore, third order motion requires “an hour or so of practice” to operate (Lu & Sperling, 2001) whereas interpolation did not require practice.

Many of the properties of “feature tracking” mechanisms (Wertherimer, 1912; (Cavanagh, 1992; Verstraten, Cavanagh & Labianca, 2000; Shiori et al., 2000; Morgan, 1980; Watt & Morgan, 1983; Robins & Shepard, 1977) are on the other hand more compatible with the properties of amodal filling-in of invisible motion. Firstly, it involves attention to the imagery of moving features, and here I show that attention does plays a role. Secondly, feature-tracking uses a set of discrete spatial positions to form an internal model of the moving target which allows motion interpolation across intermediate spatial positions. Thirdly, interpolation by feature tracking is linear, consistent with our results found in Experiments 2 and 3 where the duration of the invisible trajectory is isomorphic with the physical duration. Fourthly, interpolation by feature tracking produces location judgments as well as it does for continuous motion. Therefore, it may well account for anticipation of the reappearance of the moving target. Fifthly, feature tracking occurs at relatively long SOAs (Shiori et al., 2000; Bex & Baker, 1999) and the duration of the invisible trajectory from disappearance to the position marked by central fixation is indeed 805 ms at low speed. Finally, Shioiri and colleagues (2000) showed that the critical factor for feature tracking is SOA and not speed, and indeed in the present work I found similar interpolation results at low and high speed (see Figure 28).

In sum, our results agree with the suggestion that amodal filling-in, based on visual representation, of motion behind the occluder is indeed possible. Previous studies have distinguished three types of filling-in phenomena: blind spot, artificial scotoma and pathological scotoma. Filling-in at the optic nerve head and at artificial scotomas are very different in nature (Ramachandram, 1993; Durgin, Triphaty & Levi, 1995). While the artificial and pathological scotomas can be filled-in (Ramachandran & Gregory, 1991; DeStefani, Pinello, Campana, Mazzarolo, Giudice & Casco 2010), other studies, which have investigated filling-in in the blind spot, could not find evidence that it can really occur (Triphaty & Levi, 1994, Maertens & Pollman, 2007). Those who claim the contrary cannot really rule out the possibility that, instead of being filled-in, the area of the blind spot is simply ignored or unattended to. Our results are compatible with this distinction, implying that only in the symBS does amodal filling-in occur.

The evidence presented in the present study is consistent with an active interpolation process, which produces an internal model of the moving target, possibly mediated by high-level visual areas. Our model does not emphasize attentional tracking, time processing, or the visuo-spatial update of the attention spotlight (Tresilian 1995; 1999; Makin, Poliakoff, Chen, Stewart, 2008). Instead, I want to highlight that the elaboration of occluded motion is an active process that requires cortical representation, interpolation and top-down mechanisms resulting in an amodal filling-in.

Chapter VI

New application in biomedical industry: a low cost perimetry for people with macular degeneration, preliminary result.

6.1 Introduction

The dramatic increase in average life expectancy during the 20th century ranks as one of society’s greatest achievements. The U.S. national institute of reported that although most babies born in 1900 did not live past age 50, life expectancy at birth now exceeds 83 years in Japan and is at least 81 years in several other countries. Consequently, age-related diseases have increased. One of them is the macular degeneration, a medical condition which usually affects older adults and results in a loss of vision in the center of the visual field due to damage to the retina. It is a major cause of blindness and visual impairment in older adults (>50 years). Macular degeneration can make it difficult or impossible to read or recognize faces, although enough peripheral vision remains to allow other activities of daily life (de Jong, 2006). In this part of the thesis, I will not go into details about the cause and risk of macular degeneration, but my focus will be on the practical application of ME with a clinical population. To measure the size of the retinal scotoma there are numerous perimetry tools/techniques, a very simple one is the Amsler grid, used since 1945, is a grid of horizontal and vertical lines used to monitor a person's central visual field. The grid was developed by Marc Amsler, a Swiss ophthalmologist. It is a diagnostic tool that aids in the detection of visual disturbances caused by changes in the retina, particularly the macula (e.g. macular degeneration, Epiretinal membrane), as well as the optic nerve and the visual pathway to the brain. In the test, the person looks with each eye separately at the small dot in the center of the grid. Patients with macular disease may see wavy lines or some lines may be missing. Amsler grids are supplied by ophthalmologists, optometrists or from web sites, and may even be used to test one's vision at home. The original Amsler grid was black and white. A color version with a blue and yellow grid is more sensitive and can be used to test for a wide variety of visual pathway abnormalities, including those associated with the retina, the optic nerve, and the pituitary gland. Another perimetry tool is the Goldmann perimeter that is a hollow white spherical bowl positioned a set distance in front of the patient. An examiner presents a test light of variable size and intensity. The light may move towards the center from the perimetery (kinetic perimetry), or it may remain in one location (static perimetry). The Goldmann method is able to test the entire range of peripheral vision, and has been used for years to follow vision changes in glaucoma patients

(Cunningham & Riordan-Eva, 2011). However, Goldmann perimetry is expensive and a trained technician (or nurse) or physician is required who manually map the visual field without the aid of a computer algorithm. Moreover, to account for reaction time, the perimetrist should consistently adjusts the location of the mark, therefore the size of the scotoma depends on this subjective adjustment. Nowadays automated perimetry is more commonly used. One of the best and accurate perimetry tool to measure the size is the NIDEK's MP-1. The Nidek MP1 microperimeter is a hybrid between a fundus camera and a perimeter, capable of imaging the fundus while simultaneously measuring the visual field using either static or kinetic stimulus presentation. Stimuli are generated by means of an LCD display, which is incorporated into the imaging system of the fundus camera. Landmark features on the fundus such as blood vessels are used to accurately track eye movements and precisely position light stimuli. The visual field results are superimposed over the fundus image, thus allowing for accurate mapping and monitoring of eye diseases ranging from optic nerve head disorders to maculopathy and more general diseases of the retina. The spatial resolution of visual field stimuli is much higher than can be obtained using conventional perimeters, making the instrument particularly useful for the investigation of maculopathy. The accurate and constant mapping of fixation enables the instrument to be used to train fixation for eccentric viewing in maculopathies which have damaged the foveal region. To summarize NIDEK's MP-1 is a fundus tracking perimeter that provides true retinal sensitivity data as well as a quantitative analysis of fixation location and stability. Unfortunately, this system is very expensive and requires an ophthalmologist or a trained technician to be administered. The scotoma of people with macular degeneration is similar to the occluder that I used in the previously discussed experiment to study motion extrapolation and interpolation. In Chapter V, I showed that participants could not interpolate, when the moving target passes in a zone over retinal areas that do not project to the visual cortex (blind spot) and when the central fixation cross is absent. In other words, they could not "fill-in" the object trajectory because they did not know where the object was headed and where it reappeared. In this case, observers perform a true reaction time task and do not anticipate the response. Patients with Macular degeneration (MD) cannot see with their fovea since it is damaged and if they ignore the dimension of their scotoma they cannot infer when the moving target will reappear and therefore they should respond only when they actually see the target. If people with MD cannot predict when the target is going to reappear because they ignore the dimension of the scotoma they should press the response key when either they no longer see the target because it disappears or when the see the target reappearing again, depending on the task. However, even if there is no input from the damaged fovea, the cortical representation of the space may be preserved (DeStefani et al., 2010). In fact, in the everyday life they continuously experience objects that disappear and reappear across their scotoma, so they could have learnt the dimension of their scotoma. Based on this acquired "experience" of the scotoma dimension they may be able to track the occluded target and predict when and where it is going to reappear. However, as suggested by previous data the scotoma area in this patients may be perceived as smaller (Safran, Achard, Duret, & Landis, 1999; Cohen, Lamarque, Saucet, Provent, Langram, & LeGargasson, 2003; Mavrakanas, Dang-Burgener, Lorincz, Landis & Safran, 2009). Indeed cortical change occurs immediately after the retinal lesions, with neurons that responded to a regions near the lesion that increase in size of receptive fields and shift in location, probably thanks to change in efficacy of pre-existing synapses and sprouting (Das & Gilbert, 1995). Based on these considerations we asked MD patients to press a button when a moving target disappears into their scotoma and to press another button when it reappears, the length of their scotoma can be measured along that linear trajectory. By using linear trajectories starting from different position and interpolating the spatial point on the screen in which MD patients report that the target disappears and reappears, we obtained an approximate measure of the size and shape of the scotoma. Note that in this case I mean the term "interpolation" in a mathematical way. In other words, connecting the spatial point in which the target disappear and/or reappear in a plot graph (see Figure 32) I should get approximately the dimension of the scotoma. Note that the relevance of this information is not only practical. Indeed, by connecting only the points where the target reappears, and comparing the size of the scotoma obtained with the size measured with Nidek MP-1 that has a very high precision, one can infer if MD patients pressed the response key when they predicted the reappearance of the target or when they actually saw the target. Prediction would produce a scotma size similar or even smaller to the size measure with the Nidek-MP1. An overestimation is instead expected if the response occurs at target reappearance. Indeed, because of the delay in response time due to motor reaction time, the size measured when the target reappear will be overestimated. However, the same delay in response time when the target disappears would produce an underestimated size so that, by averaging this two scotoma sizes obtained from the disappearance and reappearance task the errors due to reaction time would be cancelled. I would expect a high correlation with the Nidek-MP1 in this case, and therefore I can obtain a low cost perimetry very easy to implement and run in every PC.

6.2 Nidek-MP1

BRIEF SUMMARY OF THE NIDEK-MP1

The present tool provides a novel and much more “user-friendly” device and method for testing the visual field of a patients suspected of having diseases affecting the visual system and corresponding neurological pathways. With the Nidek-MP1 tool, the patient wears a head-mounted display, with a gaze fixation target. Various visual stimuli, such as icons of various shapes, sizes, colors, and luminosity, are displayed for the patient to observe, at various locations throughout the display. The patient signals his observation of these stimuli only by shifting his gaze from the gaze fixation target to the visual stimuli, then back to the gaze fixation target. The patient affected by macular degeneration does this task with their preferred retinal locus (PRL), that part of the peripheral retina that patients with macular degeneration spontaneously use as a new fixation point. The patient wears a wrap-around “head-mounted display” (“HMD”), which can be in the form of a helmet configuration, or wrap-around goggles or glasses. The visual field testing, then, can be performed in a “virtual-reality” environment. A computer with appropriate software interfaces with the head-mounted display via a controller. In addition to sending signals to the patient, the computer receives incoming response signals from a gaze tracker mounted within the HMD. In addition, the computer system provides audio feedback to the patient via headphones or earphones. Such audio cues monitoring the patient's performance eliminate the need for a technician to be continuously involved with the patient during the examination. The system is designed to perform interactively with the patient, in real-time. In the preferred embodiment, the patient is instructed to look at a central fixation target or icon. This central fixation icon remains illuminated and in a stationary position in the center of the patient's visual field throughout the entire visual field test. The first step is to monitor the patient’s eye with an eye tracker, mounted in the HMD, in order to ensure that patients are fixating (MD patients fixate with their PRL) the central icon. After central gaze has been recognized by the computer as having been established, via the gaze tracker, a stimulus such as a visible light is presented in the peripheral visual field of one eye in the form of a “peripheral stimulus icon”. The instruction given to the patient is to shift fixation from the central icon to the peripheral one. The test is completely automated, and, based upon information received by the computer from the patient, the software within the computer determines the location within the patient's peripheral visual field where the peripheral stimulus icon will next be displayed, as well as its luminosity, size, shape, color, etc. When the peripheral stimulus disappears, the patient must return to fixating at the central icon which remains visible during the entire procedure. The gaze tracking software analyzes eye movements and rejects random saccade movements. A new important aspect is that even though the central fixation icon is presented to both eyes, the peripheral stimulus is only presented to one; therefore, both eyes can be tested simultaneously. Moreover, the peripheral stimulus is illuminated for only a rather short period of time, namely, long enough to trigger the mental response and the neurological response to direct the eyes to shift fixation and perceive the peripheral stimulus icon, but not long enough to allow prolonged, random searching eye movements. A computer with appropriate software directs the controller, which in turn sequentially presents peripheral stimulus icons throughout the visual fields of the left or right eyes. For further information refer to Massengill, McClure, & Braeuning, J. (2001). *U.S. Patent No. 6,290,357* and Rohrschneider & Springer (2005).

6.3 Method

Participants

Five MD patients (2 female, 3 male; age 41-64 years) participated voluntarily in this experiment. None of these patients had cognitive or motor diseases. They were recruited from Centro di Riabilitazione Visiva Ipovedenti, Istituto L. Configliachi. The following are patient characteristics:

AG, 41 years old, affected by Stargart desease; visual acuity: 1/20 and instable fixation in both eyes.

FM, 49 years old, affected by Stargart desease; visual acuity: 1/10 and instable fixation in both eyes.

FB, 58 years old, affected by Best desease; visual acuity: 2/10 and instable fixation in both eyes.

NL, 64 years old, atrophic maculopathy; visual acuity: 1/50 in the right eye and 1/20 in the left eye, fixation instable in both eyes.

AM, 62 years old, cony dystrophy, visual acuity 1/20 in the right eye and 2/10 in the left eye, fixation instable in the right eye. Only the right eye was tested.

Informed consent according to the declaration of Helsinki, was obtained from each participant before starting the experiment.

Apparatus and Stimuli

Stimuli were gerenated using Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997) on a Screen Asus 24 in, 1920 x 1080 with a refresh rate of 60 Hz. One pixel is ~ 2.5 arcmin. Background luminance was 0.8 cd/m^2. Target stimulus was a white moving dot (0.5 in diameter, 125 cd/m^2). The luminance was measured with a Minolta LS-100. An acustic cue (300 Hz) advised the patients that at a random interval of 0.5 s the target/stimulus appeared 12.5 deg from the center of the screen. Target started along 8 different positions along 4 axes: vertical, horizontal, diagonal clockwise (upper left - down right and vice-versa) and diagonal counterclockwise (upper right - down left and vice-versa) (Figure 30). The target disappeared after 25 deg. Target speed was either 3 deg/s or 6 deg/s.

Figure 30

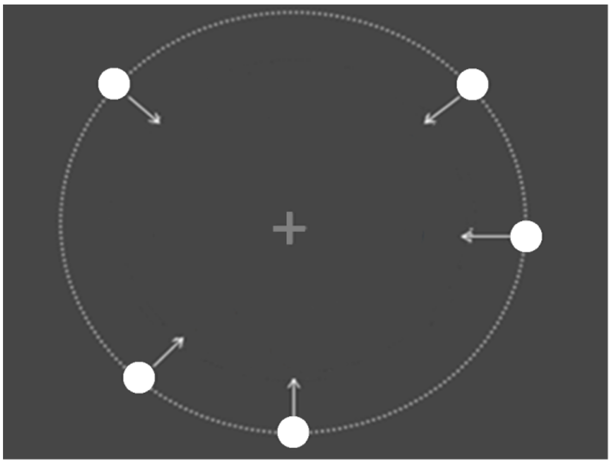


Figure 30. ***Illustration of the trial***. *A moving circle travelled along a rectilinear path. The target (circle) started from eight different places at 12.5 deg from the occluder. MD patients had to press a response button as soon as the target disappeared in their scotoma and to press again the button when it reappear.*

Fixation

Before starting the experiment, a white circle, 2.5 deg in diameter (125 cd/m^2), was placed about 14-15 deg in the temporal region of the visual filed. Patients were told to explore the screen and to hide this stimulus with their blind spot. After that, the experiment started. If they see the white circle during a trial, they had to adjust the position of their eye in order to once again hide the white circle and report it verbally to the experimenter that removed the trial offline. However, this task was not difficult at all and patients were able to hide the white circle during all 64 trials (no trial rejection).

Experimental procedure

MD patients performed one block of 64 trials per eye (8 direction x 2 levels of speed x 4 repetitions) (Figure 31), except AM where only his right eye was tested. The task consisted in pressing (as fast as possible) a button on a keyboard when the moving target disappeared from their visual field and pressing it again when it reappeared. Since it is a preliminary study only eight trajectories were used, but in order to measure the scotoma more appropriately and accurately, more trajectories are needed. A software interpolated (connect) in graphical format the spatial point in which participants pressed the button to indicate that the target disappeared or reappeared (from now on I refer to this low cost perimetry as “connecting-dynamic perimetry, CD-perimetry”). This way, nine graphs of the scotoma were obtained: 1) disappearance of the target with low speed, 2) reappearance of the target with high speed, 3) disappearance of the target with high speed, 4) reappearance of the target with high speed, 5) disappearance of the target with high and low speed averaged, 6) reappearance of the target with high and low speed collapsed, 7) low speed with disappearance and reappearance values collapsed, 8) high speed with disappearance and reappearance values collapsed and finally 9) the scotoma measured averaging the speed and the disappearance/reappearance (for an example see Figure 32).

Figure 31

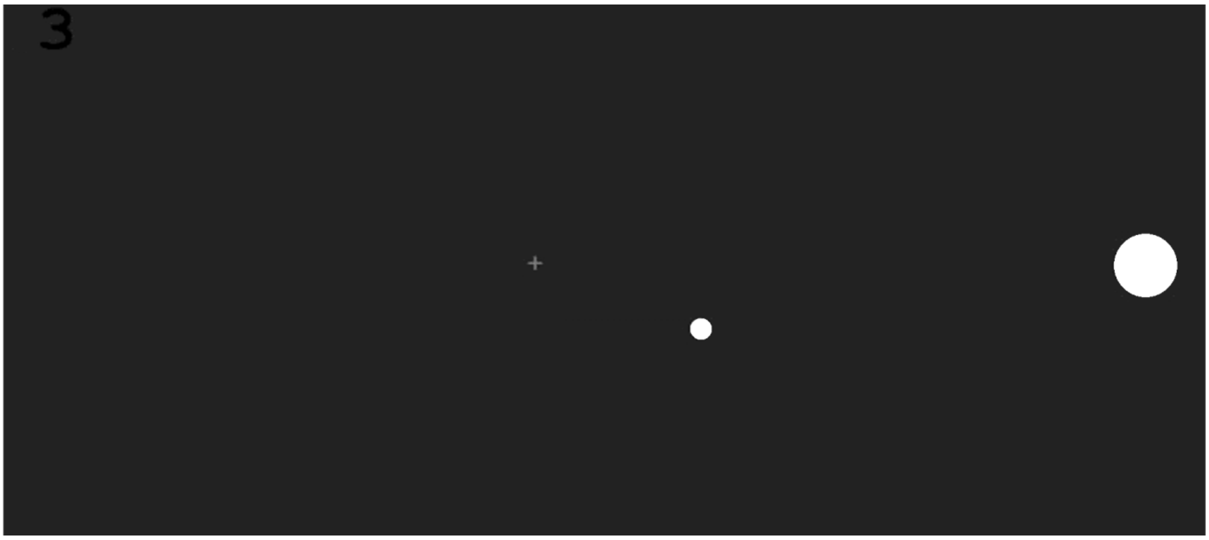


Figure 31. ***Illustration of the trial.*** *MD patients cannot fixate the cross with their fovea since it is damaged; therefore, they were instructed to hide the large white circle with their blind spot. Once this was achieved the task started and they were told to maintain their eyes as still as possible.*

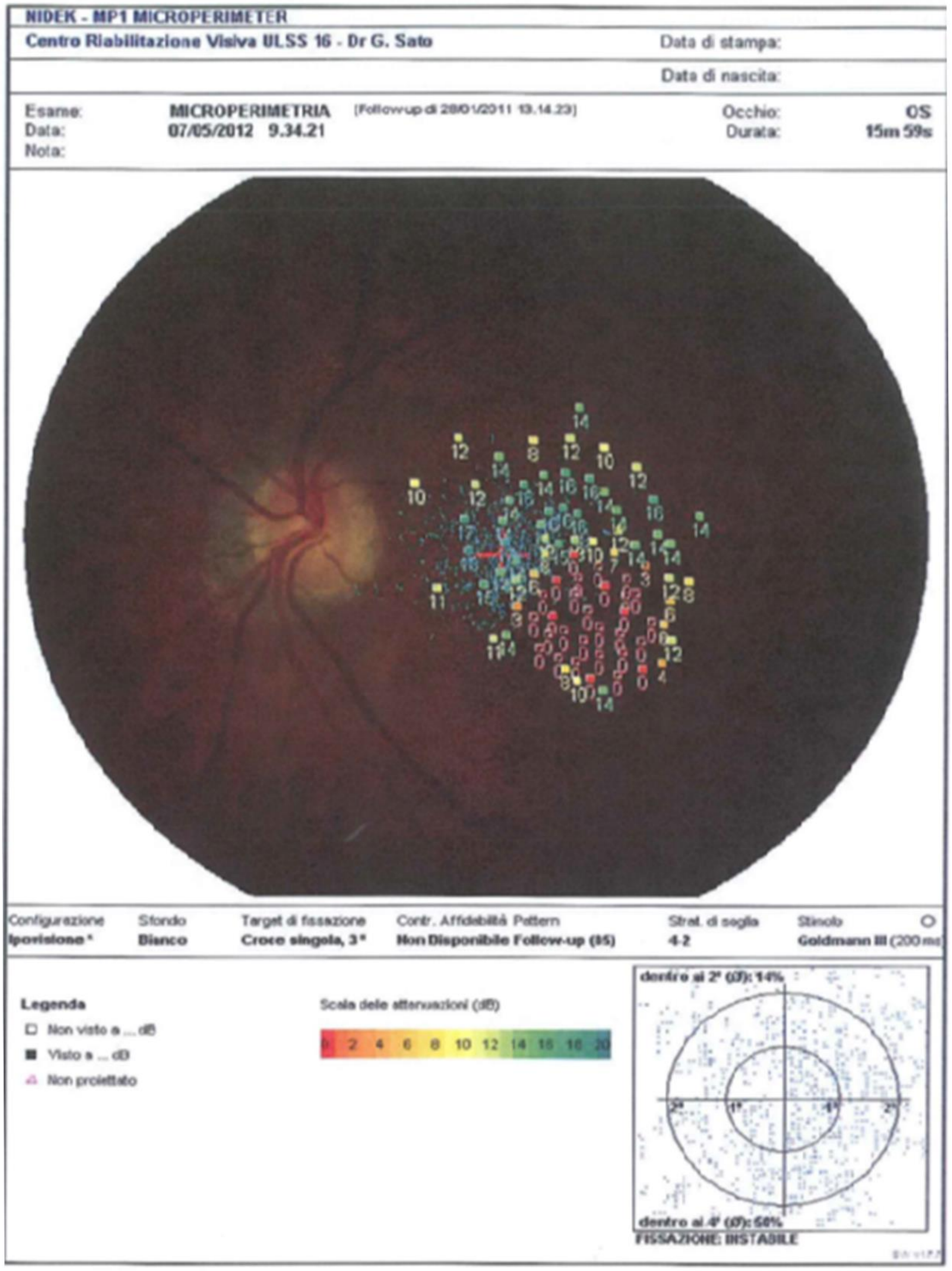
Figure 32

Figure 32. ***Example of the Connecting-Dynamic perimetry (CD-perimetry output.*** *The fixation cross represent the center of the screen, the empty circles represent the mean point in which the moving target disappear and reappear.*

Perimetry Nidek mp-1

Perimetry was performed using the Nidek MP1 (NAVIS software version 1.7.2; Nidek Technologies). This instrument allows the examiner to view the fundus on the computer monitor while it is imaged in real time by an infrared (IR) fundus camera (768 x 576 pixels resolution; 45° field of view). Fixation target and stimuli are projected onto the liquid crystal display (LCD) within the MP1 for the subject to view. The examiner, an ophthalmologist, can also view the overlaid graphic of the threshold values and fixation loci as part of the video IR image on the computer monitor. Background luminance was set at 3 cd/m^2, white, within the high-mesopic range. Stimulus used was a Goldmann III (visible light, 26 arcmin). As already stated in a previous paragraph, the MP1 also incorporates an automated tracking system to compensate for eye movement during examination. An infrared image of the fundus is captured immediately before the examination to allow areas with high contrast (e.g., large vessels, disc margin, or pigmented lesions) to be chosen for tracking. This reference landmark is tracked every 40 ms (25 Hz) to allow correction of the stimulus position on the internal LCD to maintain the same test locations on the fundus relative to landmark. An example of the output is given in Figure 33.

Figure 33



NIDEK - MP1 MICROPERIMETER

Centro Riabilitazione Visiva ULSS 16 - Dr G. Sato

Data di stampa:

Data di nascita:

Esame: **MICROPERIMETRIA** (Follow-up di 28/01/2011 13.14.23)
Data: **07/05/2012 9.34.21**
Nota:
Occhio: **OS**
Durata: **15m 59s**

Configurazione	Sfondo	Target di fissazione	Contr. Affidabilità Pattern	Strat. di soglia	Stimolo
Iposvisione *	**Bianco**	**Croce singola, 3°**	**Non Disponibile Follow-up (85)**	**4-2**	**Goldmann III** (200 ms)

dentro al 2° (Ø): 14%
dentro al 4° (Ø): 50%
FISSAZIONE: INSTABILE

Figure 33. ***Illustration of the Nidek-MP1 output***. *Red zeros indicate that the patient cannot see anything in that region whereas the yellow and green numbers indicate correct responses. Red cross indicate the PRL.*

6.4 Results

An ANOVA was conducted on the size of the absolute scotoma measured with the Nidek-MP1 (region in which MD patient reported no stimuli detection with the Nidek-MP1) and the interpolation perimetry with conditions (scotoma measured with: interpolating the point in which the target 1) disappears at low speed; 2) disappears at high speed; 3) reappears at low speed; 4) reappears at high speed and 5) with the Nidek-MP1) and direction (vertical, horizontal, diagonal clockwise, diagonal counterclockwise) as factors. No significant results were obtained. In order to see which condition lead to better or worse performance, an ANOVA was conducted on the subtraction between the value obtained with the CD-perimetry and the value obtained with the Nidek-MP1 (CD-perimetry minus Nidek-MP1). The factors were: conditions (disappear vs. reappear), speed levels (3deg/s vs. 6 deg/s) and directions (vertical, horizontal, diagonal clockwise, diagonal counterclockwise). There were no significant results. Further quantitative and qualitative analyses were run. A linear correlation was performed between data obtained with the CD-perimetry (dependent variable) and Nidek-MP1 for each trajectory. The b coefficient and the R^2 are shown in table 1 and 2 respectively.

Table 1. Coefficient b.

Trajectory	Disappearance low speed	Reappearance low speed	Disappearance high speed	Reappearance high speed
Vertical	0.5518	1.3919	0.766	0.6955
Horizontal	1.266	0.8218	0.4176	0.6816
Diagonal clockwise	0.8676	0.7621	0.4344	0.7791
Diagonal counterclockwise	1.225	0.9477	0.5173	0.7431
Mean	0.5036	0.8987	0.5127	0.7292

Table 2. R^2

Trajectory	Disappearance low speed	Reappearance low speed	Disappearance high speed	Reappearance high speed
Vertical	0.2724	0.841	0.3929	0.7449
Horizontal	0.6687	0.7763	0.5115	0.7801
Diagonal clockwise	0.3893	0.8421	0.4656	0.8239
Diagonal counterclockwise	0.5124	0.8239	0.5785	0.9357
Mean	0.5036	0.8549	0.4819	0.9008

Results from the linear correlation, clearly showed that generally the size of the scotoma is underestimated (coefficient lower than 1) with the CD-perimetry compared to the Nidek-MP1 (table 1a and b). However, the scotoma measured when the target disappeared with low, high or with the speed averaged, is not reliable, in fact the R^2 that shows that the strength of the correlation is a weak (average R^2=.47. On the other hand, when the scotoma is measured when the target reappears the R^2 showed always a strong correlation (mean R^2 is .82). In this condition of target reappearance, the best measure of the size of the scotoma is obtained when the target travels at 3 deg/s (averaged length Nidek-MP1 = 6.8 deg, averaged length CD-perimetry = 5.6 deg). Indeed the coefficient of the linear regression is very close to one (Figure 34). To better clarify the effect of speed at target reappearance, an ANOVA was conducted with conditions (CD-perimetry [target 3deg/s and interpolating reappearance point] vs. Nidek-MP1) and trajectories (vertical, horizontal, diagonal clockwise and diagonal counterclockwise). The results did not show any difference between the two perimetry conditions.

Figure 34

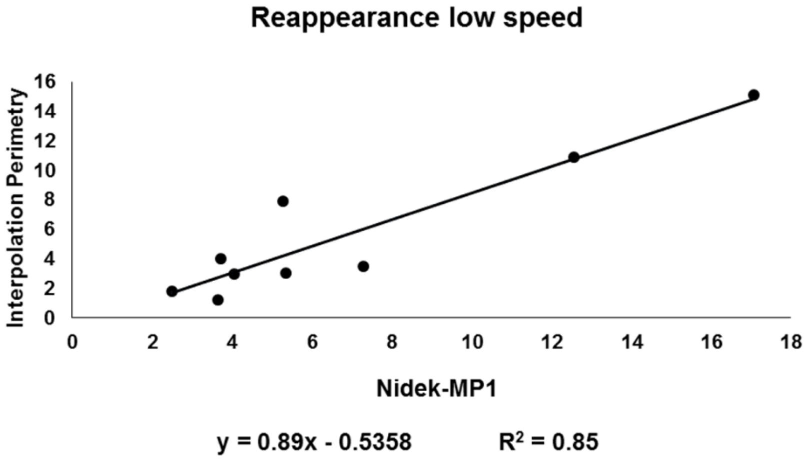


Figure 34. Regression line that show the c*orrelation between the size of the scotoma measured with the Nidek-MP1 and the CD-perimetry.*

An ANOVA was also run in order to check if the size of the scotoma is really underestimated. The factors were conditions (CD-perimetry [target 6 deg/s and interpolating reappearance point] vs. Nidek-MP1) and trajectories (vertical, horizontal, diagonal clockwise and diagonal counterclockwise). This ANOVA reveals a significant effect of conditions ($F_{(1,8)} = 7.341$, $p = 0.027$, $\eta^2_p = 0.48$) indicating that the length of the scotoma measured with the CD-perimetry and using a target with high speed is truly underestimated (averaged length Nidek-MP1 = 6.8 deg, averaged length CD-perimetry = 5.2 deg). In sum, results show that the best condition to obtain data isomorphic with the Nidek-MP1 are those resulting from the condition of target-reappearence at low speed. Indeed, Figure 35 shows an example of and Nidek-MP1 and the CD-perimetry of patient AM in the condition with low target and connecting the spatial point in which the target reappear. For this patient, there is a good-overlap between the Nidek-MP1 and the CD-perimetry (black line), this demonstrate that CD-perimetry can be as accurate as the Nidek-MP1.

Figure 35

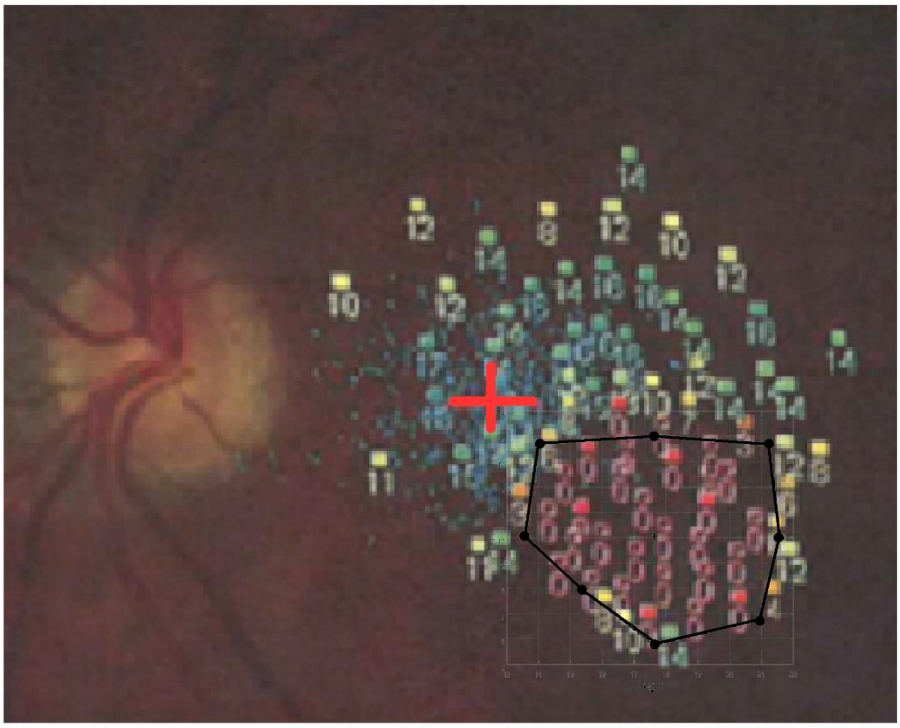


Figure 35. Illustration of the output of the two perimetries overlapped. *Figure represents the perimetries of patient AM. For this patient, there is a good overlap between the Nidek-MP1*

and the CD-perimetry (black line) in the condition with low target speed and connecting the spatial point in which the target reappear. .

6.5 Discussion

In this Chapter, a new, low cost and easy tool was presented to measure the visual field (CD-perimetry). Indeed, with MD patients it is vital to know the dimension of the scotoma in order to decide which part of the retina needs to be trained in order to substitute the damaged fovea and where to place the stimuli for the training (Maniglia, Pavan, Cuturi, Campana & Casco 2012; Maniglia, Pavan, Trotter 2014). This study show that only in some cases the CD-perimetry is reliable. Indeed, considering only the point in which the target disappears, the size of the scotoma is underestimated due to the error resulting from reaction time but the data are not reliable since there is a weak correlation between the CD-perimetry and the Nidek-MP1, suggesting that this measurement is not very accurate. On the other hand, when the scotoma is measured by interpolating the point at which the target reappears at low speed, the measurement is slightly (not significantly) underestimated (mean error = -1.2 deg, SD = 1.8), whereas when the target is presented at a high speed the size of the scotoma is significantly underestimated (mean error = -1.6 deg, SD = 1.7). To summarize connecting the point in the space in which the reappearing target moving at low speed (3 deg/s) reappears, is possible to get a quite accurate measurement of the scotoma, even though slightly underestimated.

My perimetry seems a very useful tool to measure reliably the scotoma size but, of course, an eye tracker has to be incorporated to monitor the patient's eye movements. Indeed the way I used to control for eye movements by using a stimulus placed over the blind spot may not be very appropriate. For example, during the task, the MD patients might be too focused on the task and they could simply ignore the stimulus over the blind spot and forget to report it. Moreover, the stimulus placed in the blind spot was 2.5 deg in diameter, when the horizontal length of the blind-spot region in the visual field is roughly 4 deg, so they could move their eyes more than 1 deg without actually see the white circle in the periphery). Another limitation is that only five MD patients (nine eyes) were tested and to give more credibility a larger sample size is required. Nevertheless, Figure 35 showed a good overlap between the Nidek-MP1 and the CD-perimetry and the coefficient b is close to 1, single data points showed that for some MD patients with a scotoma measured with the Nidek-MP1 between 4 and 8 deg the CD-perimetry measured a scotoma with an error even greater than ±2 deg. The variability across participants must be considered as another limit. I expect that increasing the number of judgments for each trajectory (now only two judgments are obtained) should reduce consistently this subjective variability.

Assuming that limits outlined above produces casual errors (therefore, they do not produce bias towards either an underestimation or overestimation of the scotoma) it is very interesting the underestimation found in the condition of target reappearance. In fact, considering also the reaction time (delay from the target reappearance and the button press) I would have expected to obtain an overestimation. To check if this result is typical of MD patients I tested nine student of University of Padova (4 male, 5 female, age between 21-28) with an artificial scotoma. The experiment was the same of that run with MD patients with the difference that the moving target disappear behind an invisible polygon placed at the center of the screen. The vertical, horizontal and diagonal clockwise invisible trajectory behind the polygon was 4.5 deg and the diagonal counterclockwise trajecotry was 4 deg. Fixation was controlled as in previous experiment (participants were told to hide the circle in the blind spot). An ANOVA with speed (3 deg/s vs. 6deg/s), trajectories (vertical, horizontal, diagonal clockwise, diagonal counterclockwise) and condition (reappearance vs. disappearance) was run. The main effect of condition was significant ($F_{(1,8)} = 6.567$, $p = 0.034$; $\eta^2_p = 0.45$) indicating that the size of the artificial scotoma is smaller when measured interpolating the point in which the target disappear compared to when the target reappear. The mean value of the invisible trajectories measured with the CD-perimetry with the disappearance of the target was 4.03 deg, with the target reappearance was 4.87 deg and the actual value was 4.375 deg. A t-test did not show significant difference between the actual value and the value obtained in a target disappearance condition, however it is significant between the actual value and the target reappearance indicating overestimation (error = 0.54; SD = 0.55, $t_{(8)} = 2.92$ $p = 0.02$). Considering the problem of the reaction time (delay from when the target reappear and the button press), this pattern of result was expected. However, it is very interesting the fact that participants with normal sighted overestimate the size of the artificial scotoma with the CD-perimetry in reappearance target condition whereas MD patients underestimated their pathological scotoma in the same condition. It is well known that following the loss of the visual input from the retina a reorganization of the cortical representation of the scotoma occurs(Darian-Smith & Gilbert, 1994, Gilbert & Darian-Smith, 1995; Das & Gilbert 1995, Baker, Peli, Knouf & Kanwisher, 2005; Baker, Dilks, Peli, & Kanwisher, 2008; Dilks, Baker, Peli, & Kanwisher 2009) , which leads to a perceptual modification (Safran et al., 1999; DeStefani et al., 2010, Cohen et al., 2003; Mavrakanas et al., 2009). When the target reappears, MD patients should press the response button only when the target actually reappears. Surprisingly, the CD-perimetry reveals an underestimation of the size of the scotoma, suggesting that MD patients could predict when the target will reappear and press the button of response before they actually see it. A fundamental question is how prediction of target reappearance may occur. In everyday life, MD patients continuously see object disappear into and reappear from their scotoma and perhaps they could have “learnt” the dimension of their scotoma. An alternative speculative explanation is that a moving target is a stimulus more “detectable” than a static target as the one used with Nidek-MP1. Although the Nidek-MP1 used the brightest Goldman III stimulus, this was presented for on 200ms, an interval which may be too short for showing relative detection capability in retinal areas with some residual vision. Indeed Rohrschneider, Beker, Krastel, Kruse, Völcker, & Fendrich (1995) reported that for object smaller than 0.41 deg, temporal summation requires up to 400ms. Instead, the moving high contrast stimulus I have used, because of its spatial and temporal summation properties may have been detected at the borders of the scotoma. Indeed, the visual system pools over time signals from the moving target, thereby rendering it more visible (Burr, 1981). Moreover, psychophysical studies suggest that the size of the receptive fields of motion detectors increase with velocity preference (Anderson & Burr, 1987, 1991; Burr & Thompson 2011) allowing spatial summation of the signal over a larger area. This can explain why the CD-perimetry underestimates the size of the scotoma at 6 deg/s compared to the Nidek-MP1. In addition, at the inner and outer borders of the scotoma summation may be even more efficient, because it is well known that receptive field size increases due to cortical reorganization that allows stimulation of the neurons with the receptive field at the borders of the scotoma to recruit neurons with their receptive field inside the scotoma, due to unmasking of connections (Darian-Smith & Gilbert, 1994, Gilbert & Darian-Smith, 1995; Das & Gilbert 1995, Baker, Peli, Knouf & Kanwisher, 2005; Baker, Dilks, Peli, & Kanwisher, 2008; Dilks, Baker, Peli, & Kanwisher 2009). Tomaiuolo, Ptito, Marzi, Paus, & Ptito (1997) even found spatial summation across the vertical meridian of the blind region in hemispherectomized patients. These findings may account for the result that both disappearance and reappearance produced underestimation and that underestimation is increased with high speed, i.e. with larger spatial summation. Further investigation is however needed in order to address this issue.

CD-perimetry however, might have a great advantage compared to others dynamic perimetry such as the Goldmann perimetry. The latter one is expensive and a trained perimetrist is required who manually map the visual field . The reaction time is an issue that is addressed by the ability of the perimetrist to adjust the spatial point to mark. Therefore, the Goldmann perimetry suffers of subjective response from the perimetrist. The CD-perimetry instead, might be a very low cost and easy perimetry, indeed it requires only a pc or laptop and an algorithm calculate the size of the scotoma along the trajectories tested, that in this way does not depend on the ability of the experimenter.

To summarize, the CD-perimetry is not a very accurate and reliable tool when one considers the scotoma measured by connecting the points at which the target disappears. It measures a smaller scotoma when one interpolates the points at which the target with high speed reappears indicating that probably MD patients can somehow predict target reappearance by pressing the response button even before actually seeing the target again (prematurely) or they can actually see the moving target thanks to the temporal and spatial summation of the motion signal. However, when the target has a low speed, the CD-perimetry measures the dimension of the scotoma quite well (with very little and not consistent underestimation) showing a strong correlation with the Nidek-MP1. This suggests, that when the Nidek-MP1 is not available, (note that it is very expensive and not all the ipovision centers can provide one), this new, low cost perimetry could be a fast and effective substitute.

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