Visual stability: perception of stable objects across saccadic eye movements

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I would like to thank my family, that supported me during these years, my supervisor for mentoring and giving helpful suggestions and all the PhD students for having great time here in Trento.

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Chapter 1:

Introduction

The ability of moving freely in the environment gives us the great advantage to directly interact with it, improving our discriminative abilities. For example, if we were to inspect an object without the chance to actively moving around it, then we could only rely on the information that we can extract from a single point of view with respect of the object. We would have restricted access to the object properties and we would then establish our decisions within those limits. Moving actively allow us to overcome these limitations and gain access to a more complete set of informations regarding the object. This would help us decide what to do next, whether or not to interact with an external object and, in case, providing hints on how to interact. To this extent moving and exploring the environment augment our discrimination abilities. Moreover, active movements help us to form a complete sense of space (Trinity-Crapse & Sommer, 2008).

However the remarkable ability to actively move and interact with the environment becomes adaptive only if the agent is able to distinguish whether a sensorial stimulation is the result of an external change in the environment ("exafference", Holtz and Mittelstaedt, 1865) or the effect of its own movement ("reafference"). Sensory receptors respond irrespective of the source of stimulation, and this could lead to potentially disadvantageous situations in which active movements of the agent are confused with changes in the external environment and vice-versa. The nervous system face this problem with a very general mechanism, keeping track of the movement commands and informing the sensory system of the incoming movement. This signal is usually referred to as *efference copy* or *corollary discharge* and consists on a copy of the movement command towards relevant sensory areas for that particular planned movement (Trinity-Crapse & Sommer, 2008).

In this way the system can resolve the exafference / reafference ambiguity taking into account the input changes, expected only on the basis of the expected movement. Being able to rapidly and efficiently resolve the ambiguous nature of the sensory input is crucial in order to move efficiently in the environment. It would be completely useless to be able to run if we could not easily reach the conclusion that the noisy input to the retina is not due to the world moving around us, but instead the consequence of our own movement.

In this review I will describe relevant literature about how the visual system takes into account upcoming movement signals in order to maintain a stable representation of the external world. The review will be based mainly on saccadic updating, remapping and trans-saccadic memory. Moreover I will review recent findings on saccadic updating and trans-saccadic perception using apparent motion displays across eye movements.

Eye movements and Visual Stability

Saccadic Updating

Making eye movements allow us to extract information from the visual field bringing the most sensitive part of the retina, the fovea, into relevant portions of the field. In normal conditions we mostly rely on visual inspection to decide how to move in the environment so it is evident that, especially in the case of eye movements, the nervous system had to deal efficiently with the exafference / reafference ambiguity to guarantee a fast and efficient processing of the constantly changing visual input.

Most strikingly, our subjective experience is that we are usually not aware to the changes in the retinal input due to eye movements, nonetheless eyes are frequently in motion. This subjective feeling is usually referred to as *visual stability.*

This subjective insight seems to suggest that we do not rely directly on a retinotopically organized input, but instead of an eye-position independent representation on the world (Mathot and Theeuwes, 2011). This would suggest that our conscious visual experience does not depend solely on our retinotopic input (Harrison & Tong et al, 2009), moreover there exist experimental evidence which suggest that also the corollary discharge signal that accompany each eye movement does not have a retinal source based on proprioceptive signals. In a series of elegant experiments (Mays, Sparks, & Porter, 1987; Sparks & Mays, 1983) it has been shown that when the eyes were passively set in motion by the experimenter, stimulating the motor neurons right before a saccade, compensation towards a previously shown saccadic target did not occur, the conclusion was that proprioception related to the eye-position could not have conveyed sufficient information to set the corrective saccade needed to reach the target (Wurtz, 2008). A subjective test of the relative independence of retinal signals to visual stability maintenance has been provided by Descartes, who pointed out that the world seems to move when the retina was passively displaced tapping on the side of the eye (Descartes, 1644 in Medendorp 2011).

Recently experimental evidence has been provided suggesting a more central nature of the corollary discarge generator through a pathway that runs from the superior culliculus (SC) through the thalamus till the frontal eye fields (FEF), (Sommer & Wurtz, 2006). Inactivation of this pathway lead to impaired performance on the classical double-step saccade task. In this task two saccade targets are briefly presented, after targets removal, the participants are instructed to perform two successive eye-movements to where the targets used to be. Crucially, the nervous system can rely on the retinotopic trace of the first target to perform the initial movement, but in order to correctly perform also the second saccade, target position needs to be updated according to the first eye-movement vector (see figure 1.1). An impairment on the second saccade landing position points

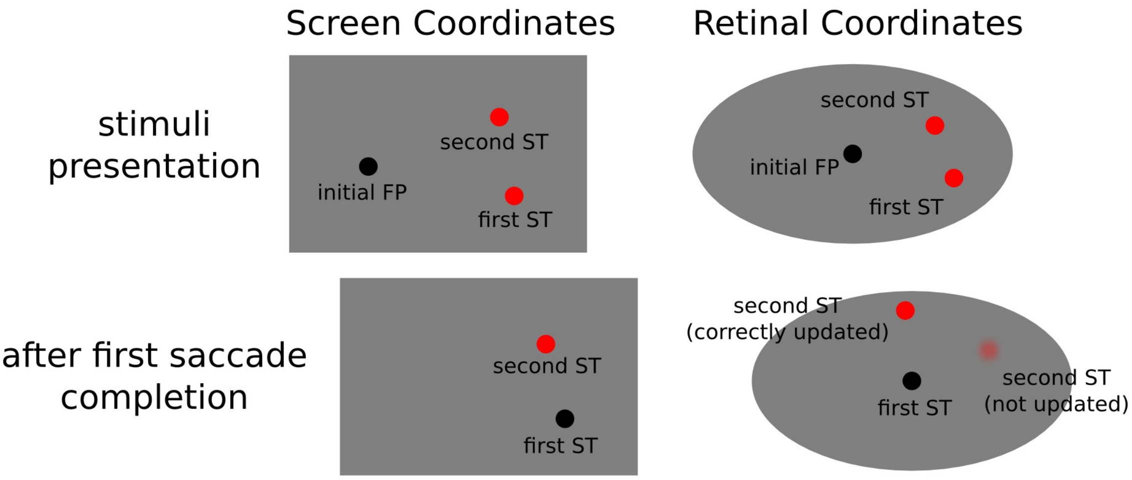


Figure 1.1: typical trial procedure in a double-step saccade paradigm, saccadic targets are reported with respect to the screen (leftward panels) as well as retinal coordinates (rightward panels), after the completion of the first requested saccade, the second fixation point needs to be updated correctly in order to perform the second eye movement (note that the second fixation point was not present on the screen during the planning of the second saccade)

following inactivation of the aforementioned pathway has been taken as evidence for a reliable source of the corollary discharge accompanying eye-movements, that allowed the system to take into account motion vectors in the resolving the exafference / reafference ambiguity.

Even though this was the first time that a clear signature of the corollary discharge supporting the updating process was shown, it has to be noted that the deficit on the updating task was limited to a 19%. This observation seems to suggest not only the existence of alternative pathways for the updating process, as could be suggested by in a cognitive degeneracy approach (Friston & Price, 2003), since the same function can be performed by a variety of different pathways in the brain. The clear advantage would be to have a system extremely resilient to damage, which could recover quickly and efficiently. Moreover we cannot exclude that other processes might be involved in maintaining visual stability and updating across saccades, possibly with different sources of the upcoming movement signal other than SC (Berbam & Wurtz 2008 and Prevosto et al 2009).

For example there exists experimental evidence for a direct involvement of parietal areas in saccadic updating in humans. Morris and colleagues (Morris et al, 2007) reported that stimulation of intra parietal sulcus (IPSp), distorts eye trajectories towards the contralateral hemifield on the second saccade of the classical double-step saccade task, while leaving unaltered end point and trajectory of the first one. This results suggest that IPSp is crucial for the ongoing updating mechanism of eye movements in humans. Evidence for the existence of a saccadic updating mechanism in humans has been reported also using fMRI (Medendorp et al, 2003; Merriam et al, 2003).

This is not the only existing proposed explanation tor the updating of sensory input with eye-movement information, another relevant proposal comes from theoretical neuroscience. In a remarkable attempt to model sensorimotor transformation through implementation of basis functions, it has been shown that an updating behavior to compensate for eye movements emerges as a natural property on the hidden layer of a a three-levels neural network. The aim of the network was to integrate eye position and eye-centered position (retinal location of a stimuli) on a single head centered representation (Deneve et al 2001). Notably, the authors took advantage of the neurally plausibile approach of population coding (Georgopulos et al, 1982), moreover this proposal did not assume the existence of any peculiar signal associated wit the eye movement, but only considers fixed eye position on the various fixations, as successive snapshots.

Nodes in the hidden units of the network showed a clear partially shifting behavior, meaning that receptive fields were not purely eye-centered since the preferential position in eye-centered coordinates changed consistently with eye position. Interestingly, this gain modulated shift was in the opposite direction of the eye displacement, as one would expect for a saccade compensatory mechanism. This kind of shifting behavior is consistent with what has been observed experimentally (Duhamel, 1997 Nature, the analysis was performed on a set of neurons on the ventral intraparietal area of the monkey, see figure 2.1). It's interesting to note that this view does not assume that the system does not update for reafferent sensorial information in order to compensate for shifts due to the eye movement, instead it states that the mechanism that takes into account sensory reafference is **built-in** in the architecture of the system itself, embedded as an emerging property.

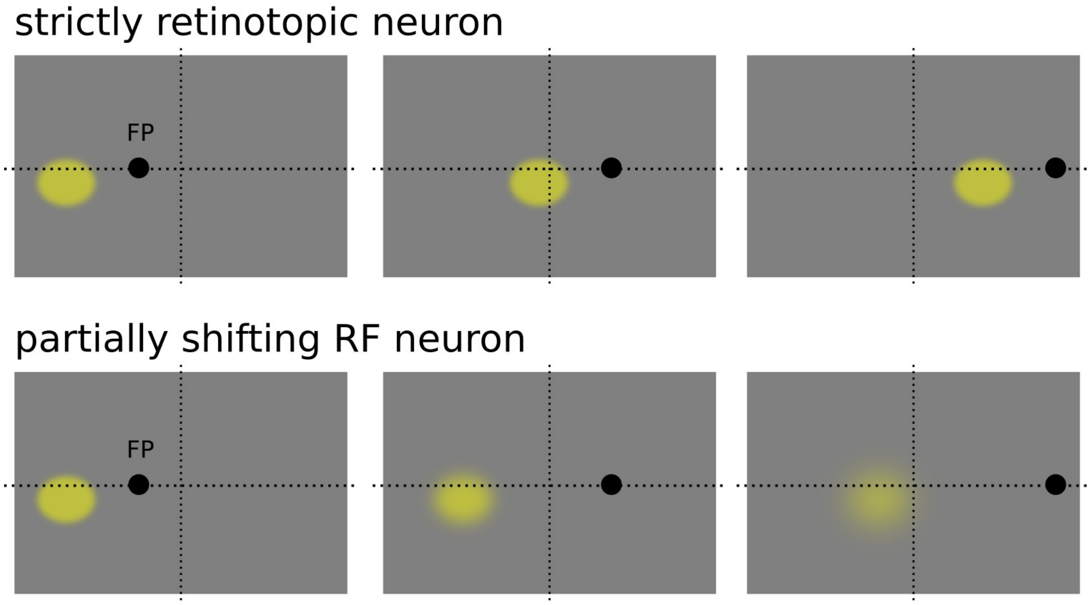


Figure 2.1: strictly retinotopic receptive field (upper panels) and partially shifting receptive field (downward panels) behaviour, in the former the receptive field changes its position according to the eye position, keeping its response unaltererd for a different position in space, in the latter eye position modulates the gain of the neuron response, with the neuron being sensitive to the same position in space

Predictive remapping

One additional mechanism that has been show to intervene whenever a monkey performs an eye movement is predictive remapping. Neurons in FEF and Lateral Intraparietal Cortex (LIP) have shifting receptive fields that predicts the response to the visual stimulus that will fall on the receptive field after the completion of the saccade (Duhamel 1992). The peculiar behavior of the response of these neurons is essentially different from those described above since their response is *predictive* of what will fall on the receptive field after the eye movement, it anticipates the movement itself. Not only a stimulus briefly shown right before the onset of a saccade elicit activity on the receptive field that will be stimulated only after the saccade but, the closer we get to the eye movement onset, the larger the response of the "future" receptive field (FF) will be with respect to the "current" receptive (RF) field (Kusunoky & Goldberg 2003, see figure 3.1). This peculiar process has been shown to have a dynamic nature that evolves during time along the perisaccadic interval, gradually decreasing the response on the current RF and increasing in the FF.

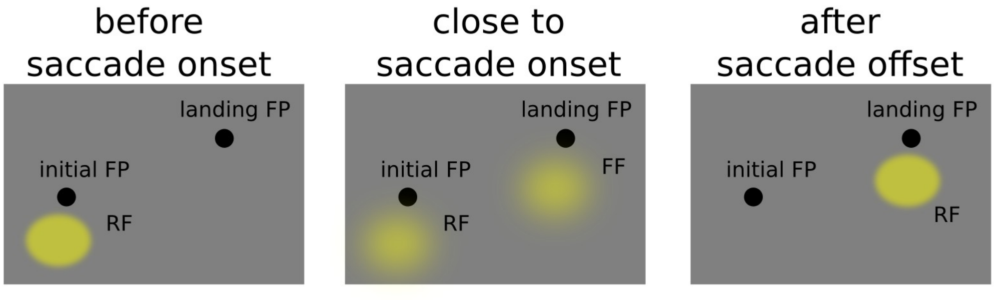
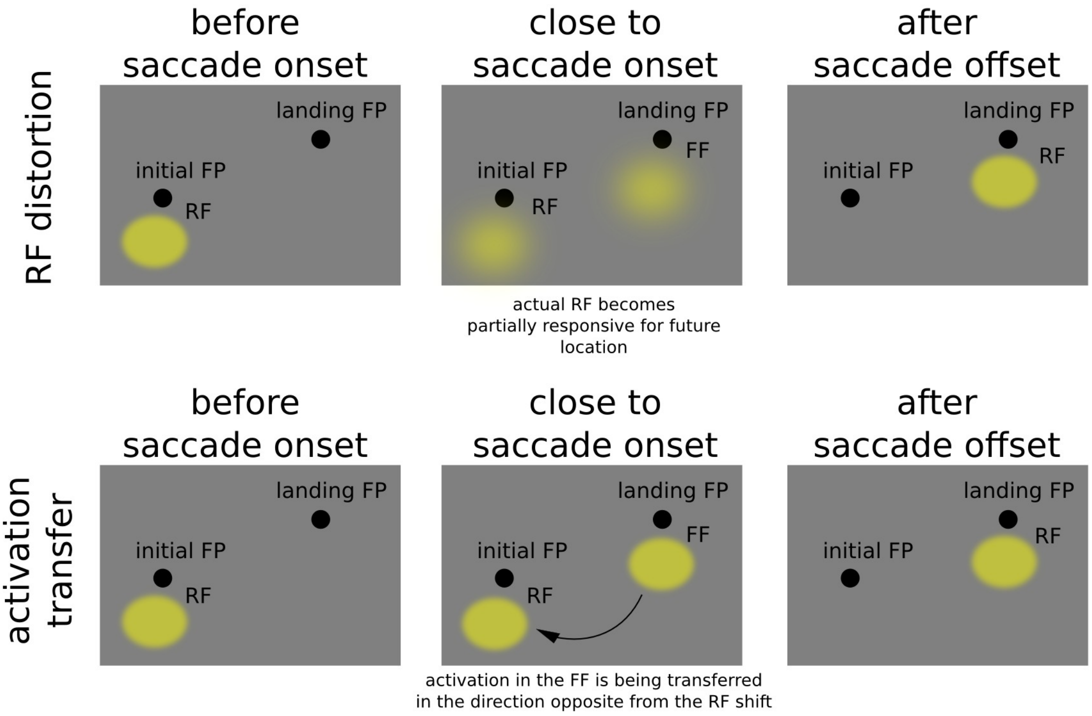


Figure 3.1: predictive behaviour of an LIP neuron, during the perisaccadic interval the neuron becomes sensitive to a spatial location that will be brought into the receptive field only after saccade completion. The neuron becomes gradually less sensitive to the current location and shifts its sensitivity towards the future location in space.

This neurophysiological evidence is tightly coupled with the well known behavioural phenomenon of perisaccadic mislocalization. When a stimuli is briefly presented around the perisaccadic interval participants reports its location as mislocalized along the direction of the eye movement. Such perisaccadic mislocalization has been studied and replicated various times (Honda 1989; Matin et al. 1970; Burr et al, 1997; De Pisapia et al, 2010). One possible explanation is that, in the highly spatially inaccurate moments around the onset of the eye movement, the brain extracts the location of stimulation as the average between the response of the current and the future receptive field associated with the stimuli, the first one being aligned with current fixation, whereas the second being shifted along the direction of the eye movement, averaging the two lead to gross mislocalizations of target stimuli along the direction of the eye movement (Kusunoky & Goldberg 2003).

It is important to note that neurophysiological data suggests that the receptive field associated with a particular location in space-time is actually *distorted* by the upcoming eye-movement, meaning that a particular neuron, right around the onset of the eye movement, becomes sensitive to stimuli **outside** the region of space that would elicit a response at stable fixation. Specifically this region is displaced along the direction of the intended eye movement.



before saccade onset

close to saccade onset

after saccade offset

actual RF becomes partially responsive for future location

activation in the FF is being transferred in the direction opposite from the RF shift

Figure 4.1: upper panels, neuron showing a predictive remapping behaviour, during the perisccadic interval it becomes sensitive for location that will be brought into the receptive filed only after saccade completion. Lower panels, alternative account based on an transfer of activation between the future towards the current receptive field

This form of remapping is not compatible with a simple mechanism that takes into account eye-movement vectors and just compensate saccade-induced shifts. In fact receptive fields distortions are in the same direction of the saccadic movement, not in the opposite.

Another proposal is that predictive remapping reflects an activation transfer right before the initiation of the saccade starting *from* the future receptive field *towards* the current one (Cavanagh et al 2010; Hunt & Cavanagh, 2011; Mathot & Theuvees, 2011, see figure 4.1), also this second proposal can be ruled out considering the nature of the perisaccadic distortion. This idea is intriguing because the transfer of activation would follow a direction opposite to the saccadic vector, then compatible with a compensation mechanism for the upcoming eye movement, reconciling the predictive remapping evidence with the saccadic updating data. But the supposed transfer of activation that should take place from the future receptive field towards the current receptive field cannot take place in practice, since current and the future RF are in fact the *same* receptive field. The difference in activation found along the perisaccadic interval for different spatial locations (Kusunoky & Goldberg, 2003) is the result of a different sensitivity of the *same* receptive field for two different locations, the current and the future (that are the location covered by the receptive field before before the eye movement and after eye movement completion, respectively). What changes during the perisaccadic interval is RF orientation in space-time of the visual receptive field, (Hall & Colby, 2011, Burr & Morrone, 2011), not an activation transfer among the same receptive field, how this dynamic change in space-time orientation might help to maintain visual stabilty is not clear yet, but various attempts has been made arguing that this distortion could lead to a form of local and transient spatiotopy across single fixations, an area in which extends temporally and spatially around the onset of the eye-movement that let information on the previous fixation to be integrated with upcoming information on the next planned fixation (Burr & Morrone, 2011).

Relation between saccadic updating and predictive remapping

Attempts has been made to investigate the relation between the two aforementioned mechanisms closely related to visual stability. As stated above it has been shown that SC inactivation leads to impaired performance on the dual-step saccade task, a task that requires efficient spatial updating across saccades to be performed correctly. Superior culliculus inactivation is thought to disrupt the neural pathway mediating the corollary discharge signal that informs the nervous system about the upcoming eye-movement. (Wurtz & Sommer, 2006). Moreover, it has been shown that visual neurons in the parietal cortex shift their activity in space right before the onset of the eye movement. Specifically the sensitivity of these neurons shift to a position that will be occupied by the receptive field only after the saccade, with this location being referred as future receptive field (Duhamel et al, 1992).

An open question is whether corollary discharge signal mediating spatial updating influences directly the shifting behaviour of the receptive fields shown in visual, parietal and frontal cortex (Hall & Colby, 2011) for perisaccadic presented stimuli. This empirical question has been investigated by Sommer & Wurtz (2006) by selectively impairing the middle dorsal (MD) thalamus (a crucial node in the corollary discharge pathway) and measuring the behavior of the FEF shifting receptive fields before and after inactivation. Results showed that the magnitude of the shifting receptive field on the tested neurons (as measured by future field activity) was severely reduced after inactivation. Notably, MD inactivation did not changed significantly activity on the current receptive field of the FEF area tested, moreover it did not modify monkeys ability to perform the actual eye-movement. The main conclusion of this study is that there is a direct link between the SC corollary discharge generator and the shifting behavior shown for retinotopic FEF neurons.

One question however remains open. It has been shown with neurophysiology and neuroimaging studies that neurons in visual, parietal (LIP) and frontal cortices shown a peculiar predictive behaviour during the perisaccadic interval, being responsive to locations that will be brought into view only after eye movement completion. On the other hand, experimental data (VIP neurons, Duhamel et al, 1997) and computational approaches to sensorimotor transformation showed how multisensory neurons (neurons integrating information between different sensory inputs, for example coding eye position and stimuli in retinal coordinated, eye-preferred positions) presented a gain field modulated partially shifting behavior. Crucially this dual “shifting” behaviour from a purely retinal based coordinate system (eye-centered reference frame) is in the opposite direction: along the same vector of the eye-movement on the perisaccadic remapping case, on the opposite direction for the partially shifting, gain modulated RF (see figures 2.1 and 3.1). How this evidence can be reconciled under the same theoretical framework is still a matter of debate. It could be that the two mechanism jointly act to update sensorimotor information separately, or they could be related to the corollary discharge signal generating in the superior colliculus (Wurtz & Sommer, 2006). As perisaccadic remapping signal seems to be directly related to this updating signal, also the gain modulated RF could be modulated by the upcoming signal, even though this second system is embedded in the architecture of the system. One way to tackle this issue would be to study the temporal dynamics of gain modulated RF in active vision, and test the eventual influence of CD on this dynamic.

Trans-Saccadic Perception

Other than egocentric cues providing information about saccade metrics and the expected reafference signal deriving from those movements (as the corollary discharge), the brain can also take advantage of allocentric cues, that is to derive object location by its relative position with respect of other objects in the world, independently of the observer's gaze.

A possible mechanism to maintain space constancy would be by matching images from successive fixations ignoring the attributes of the saccade vector (Deubel et al, 1996). However, the larger the saccade amplitude, the less the retinal overlap between subsequent images will be, so a mechanism based only this principle would be useless in the case of large retinal displacements, paradoxically the case where a process allowing space constancy would be more of use.

An alternative strategy would be the use egocentric cues (as those discussed in the previous paragraphs), combining the informations regarding the upcoming eye-movement with the positions of the relevant objects in the visual field, in a convenient frame of reference (that could be assumed to be the head, Pouget et al, 2008; Sommer and Wurtz, 2008). For example behavioural studies seems to suggest that stimuli location can be correctly updated across saccadic eye movements just on the basis of egocentric cues, as the characteristics of the upcoming saccades, in an experimental settings that aimed to remove as much as possible allocentric indexes (Prime et al, 2006).

Using the paradigm of saccadic suppression of intrasaccadic displacement (SSID, Bridgeman et al, 1975; Deubel et al, 1996) it has been shown that the nervous system uses a combination of both egocentric and allocentric cues to maintain a stable representation of the world (Nimeier et al, 2003). The basic SSID paradigm is the following. A target is displayed at a certain spatial location well before a saccade occurs. As soon as the eyes started to move and a saccade is detected the target is shifted towards another spatial location, usually in the same or opposite direction of the eye-movement, not in the orthogonally to saccadic vector. The task of the observer could be to report whether the change in location has been perceived or to report the perceived direction of displacement, if any, or to guess otherwise. The principal finding is that the displacement threshold is much higher in the saccadic condition than in a fixation condition. Up to one-third the size of the saccade (Bridgeman et al. 1975).

The influence of allocentric cues on this kind of task has been established (Deubel, 2004) as well as the active involvement of egocentric cues (Nimeier et al, 2003) showing how displacements thresholds scales with saccadic amplitude and post-saccadic eye position scatter ratios (post-saccadic eye position standard deviation. which is assumed to reflect the uncertainty of eye position towards saccadic target following the eye movement).

The proposed model of trans-saccadic integration shows that the brain uses eye-position signals in interpreting post-saccadic retinal information (egocentric cues), only when the retinal information provide a reliable measure for interpreting the new post-saccadic information inflow. The different weights associated with allocentric and egocentric cues in combination is a function of the reliability of these different sources of information, giving the overall percept of trans-saccadic visual stability. This observation reflects the quantitative counterpart of a crucial aspect of spatial constancy, that is the *assumption* of visual stability (Mathot and Theewues 2011). Our visual system exploits the fact that that world remains stable at least for the small duration of the eye-movement.

Even though this model is extremely intriguing theoretically and can predicted new empirical findings that found subsequent experimental confirmation its building blocks are not cognitive plausible. Its implementation takes the form of a Bayesian integration of information that changes the outcome of the predicted response as a function of the reliability of the input signals. Similar remarkable attempts has been made to build model to describe multisensory integration (Ernst and Banks, 2002; Alais and Burr, 2006) and positional information during the perisaccadic interval (Binda et al, 2008).

These models behave remarkably well in predicting participant behavior but it's not clear how the neural system could perform the computations to obtain these response. However, there has been attempts to implement a Bayesian explanatory framework in a biologically plausible network, taking advantage of a hierarchical scheme (Friston, 2002).

The main aim of the network was to inferring the causes of sensory input and learning the relationship between input and cause (sensory input) using the same unifying principle, that is to minimize the error between the observed inputs and the expected input based on a generative model aimed to infer which sensory stimulation caused that particular input. This idea is similar to what Irwine Rock stated about perception as an inferential process (Rock, 1997), but expressed using a mathematical formalism. The model has been successfully applied to model and predict electroencephalography phenomena (as the mismatch negativity wave and P300) as well as psychophysical results as priming. These attempts show how a powerful Bayesian explanatory framework can be implemented in a biologically plausible fashion, which further support that trans-saccadic perception may rely on a accurate weighting between allocentric and egocentric cues available in different conditions.

The case of Apparent Motion displays

Transformational Apparent Motion

Recent behavioral evidence seems to support and extend previous data on trans-saccadic perception suggesting that not only allocentric or egocentric cues are taken into account in order to keep vision stable across eye movements. Also features of relevant stimuli are taken into consideration and are likely to be updated across eye-movements (Fracasso et al, 2010).

Apparent motion phenomenon provide a series of interesting tests for trans-saccadic percetion. One interesting perceptual property of apparent motion is that our visual system fills in the entire motion path, rather than seeing two discrete events (Kolers, 1972; Morgan, 1976). A dot flashed in two different locations, given the right timing parameters, is seen to move through the entire trajectory between point A and point B. This property of apparent motion makes it the perfect test of the hypothesis that perception bridges the saccade. In fact, Rock and Ebenholtz (1962) had already reported a version of trans-saccadic apparent motion many years ago. In their experiment observers were asked to synchronize left/right eye movements with two alternating flashing lights visible through two vertical slits. In this way the illuminated vertical lines would be presented at the fovea after each eye movement. Various kinds of apparent motion exists, but one type of apparent motion is of particularly interest for trans-saccadic perception, namely transformational apparent motion (TAM, Tse & Caplovitz, 2006).

This particular type of apparent motion has been studied recently (Tse, 1998), it occurs when two spatially overlapping shapes are presented discretely in time, this results on a percept of a single object that transform smoothly and illusorily from the first shape into the second as if the sequence were animated, as shown in figure 5.1.

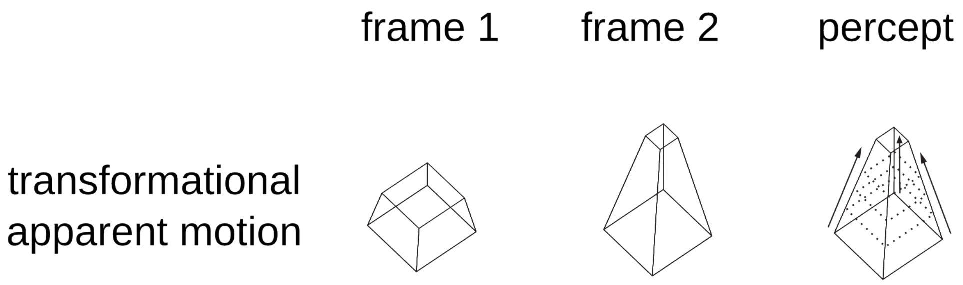


Figure 5.1: transformational apparent motion example, sequence of two subsequent frames and typical percept.

Crucially, figural parsing plays an essential role in determining the perceived direction of TAM (Tse et al., 1998; Tse and Logothetis, 2002). Figural parsing involves a comparison of contour and surface relationships among successive scenes. Based of contour and surface relationships between successive images in the sequence, the visual system appears to infer which figures at time 2 are derived from which figures at time 1. If a given figure has a different shape at different times, a continuous deformation between those shapes is constructed and perceived. It's likely that the new figure is inferred to be a change in the shape of an already existing figure, as if the two images were merged into a single spatio-temporal object. The processing of shape information must accompany the motion processing that subserves the percept of TAM. The perceived motion depends on how figures at time 1 have been matched to figures at time 2. The mechanism involved into TAM perception is two-fold: the first step is to identify candidates at both instants, and the second is to match them. Usually these steps are referred to *parsing* and *matching* steps.

These steps are of particular interest also in trans-saccadic perception since it is still a matter of debate whether object features are maintained across eye movements. The allocentric/egocentric sets of indexes that might help keeping a stable updating are focused on the maintenance of object location irrespective of large retinal shifts due to eye-movements. However it is not clear if also feature characteristics are in some ways stored and updated as object locations seems to be (Cavanagh et al, 2010; Melcher, 2010).

Interestingly, when participants were asked to perform and eye movement between the two images of the TAM sequence, they report perceiving a clear and vivid motion between subsequent snapshots (see figure 6.1), that did not differ significantly from a condition in which the stimuli in the sequence were aligned both in spatial and retinal coordinates (subjects were required to maintain stable fixation while presented with the sequence).

When retinal coordinates of stimulation were matched across the saccade motion reports were consistently lower than when stimulation was matched in spatial coordinates, see figure 6.1 for details.

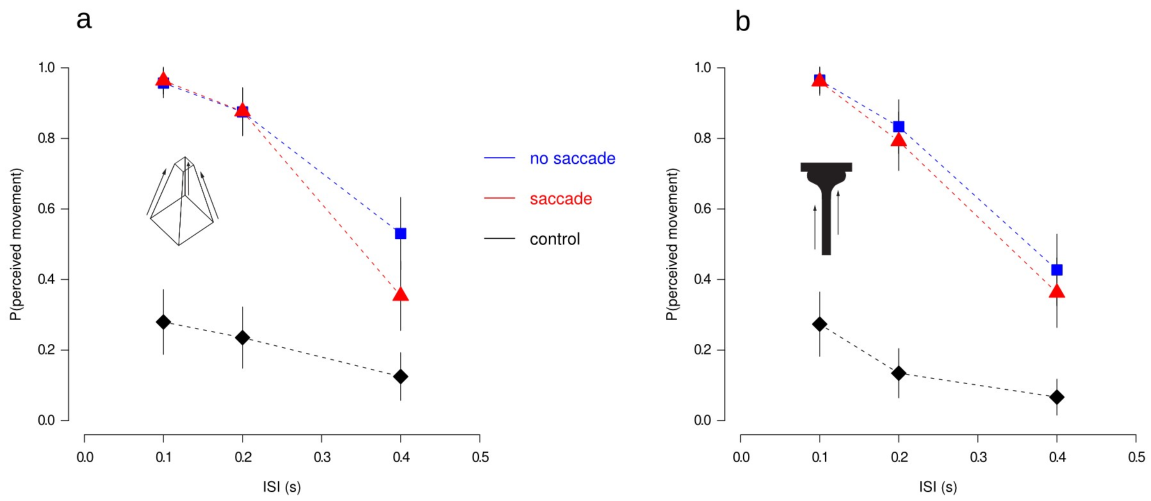


Figure 6.1: trans-saccadic perception of two tranformational apparent motion stimuli, necker cube and expanding bar, participants were asked to perform a 10° horizontal saccade while presented with the subsequent frames of the sequence, only trials where the saccade has been performed during the ISI were analyzed, in the control condition the sequence was matched in retinal coordinates while participants had to perform the eye movement.

These results suggests that the parsing / matching mechanisms involved in TAM perception continues across the eye movements even though the stimuli are not aligned in retinal coordinates. Moreover object location does not seem to be the only characteristics maintained across the eye-movement, also shape features seems to be updated to help keeping vision stable.

Line Motion Illusion

The line motion illusion (LMI) provides an interesting test for spatial updating across saccades and the role egocentric indexes on maintaining visual stability. This illusion occurs when a static line, shown shortly after an inducer (flashed stimulus) appears to radiate away from the location where the inducer had been presented (figure 7.1).

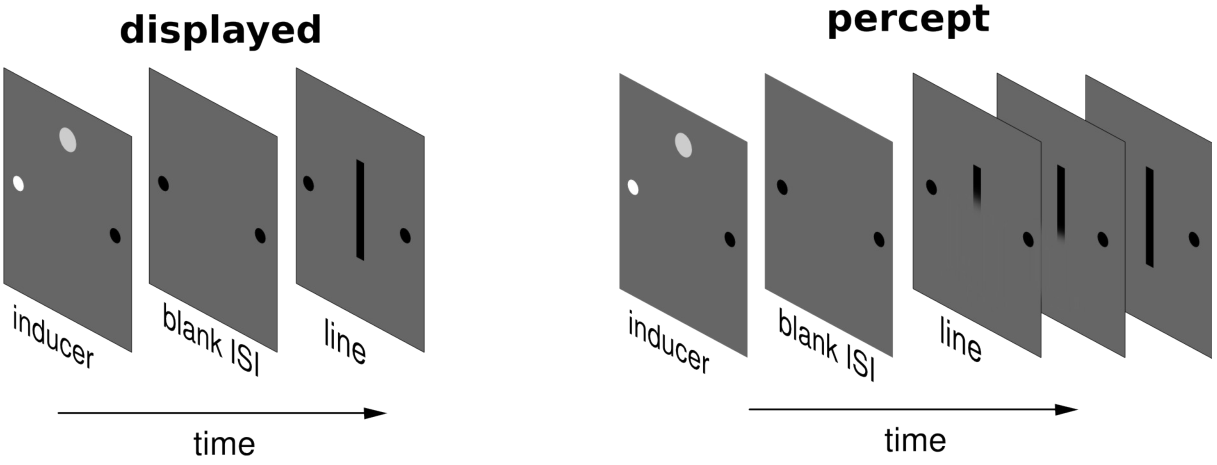


Figure 7.1: typical trial sequence for line motion illusion presentation (leftward panel) and percept (rightward panel)

Available data suggests that this illusion occurs independently of attention (Fuller and Carrasco, 2006). Together with the classical method of subjective reports of motion perception this particular apparent motion illusion can be measured using the motion cancellation method, giving an objective measure of its strength, less prone to subjective bias than simple subjective reports. To investigate the spatiotopic LMI, strength of the illusion was measured, as a function of the inducer’s contrast, for trials in which the eye was stationary or in which a horizontal saccade was made during the ISI between the inducer and the presentation of the line. We varied the timing of the stimuli with respect to the saccade to test whether the LMI effect was influenced by saccade timing, as would be predicted by an active remapping explanation for spatiotopic motion perception.

Either with subjective reports and the motion cancellation method results highlighted a cost in performing a saccade between the subjective snapshot of the apparent motion display. Moreover, subjective reports of motion were linked to the metric of the performed saccade, namely faster saccades lead to larger proportion of motion reports than slower eye movements. This latter effect was related to the distracter effect of the flash on the requested eye-movement, a form of a well known phenomena, the remote distractor effect (RDE, Bompnas and Sumner, 2009). When the flash was presented outside the RDE time window around the requested saccade signal, subjective reports of LMI across saccades increased consistently.

In trans-saccadic memory literature usually no cost of a single saccade is observed, with virtually indistinguishable capacity measures at fixation and when asked to perform an eye movement while presented with the subsequent frames (Prime et al, 2006).

It is important to note that the task adopted to measure visual memory across saccades usually employed a comparison of the subsequent snapshots presented across the eye movement (though see Bays and Husain, 2008).

The case of line motion illusion in particular and apparent motion in general provide a different experimental setup in which the frames need not only to be **compared** but actually **combined** in order to obtain the motion percept. In our opinion the lack of any saccade cost in visual memory task as opposed to the drop in LMI strenght across eye movements described above can be accounted by this crucial difference in the underlying task, posing a difference between trans-saccadic memory and trans-saccadic perception.

Other recent studies of trans-saccadic perception using apparent motion displays aimed to study how performing an eye-movement lead to an illusory perception of the apparent motion display (Szinte and Cavanagh, 2011), given the updating error associated with each eye movement. This case is interesting since the perception of motion was so compelling that authors did not measured the strength of the illusion across saccades but focused directly on the estimation of the updating error. This provides another case of trans-saccadic perception across eye movements, irrespective large stimuli shift in retinal coordinates.

Conclusion

A number of phenomena contribute to reach visual stability across eye movement. The corollary discharge signal that accompany each eye-movement appear inform the sensory areas of the incoming reafference input signals due by the agent movement and not by actual changes in the external environment, this signal seems to be directly involved in the updating of information across eye movement, as tested with the well known double-step saccade task (Wurtz and Sommer, 2006). The phenomenon of shifting receptive fields seems to provide a mechanism that anticipate the outcome of the incoming eye movement, with retinotopic neurons being sensitive to information presented outside the spatial range of their receptive field during the perisaccadic interval. Most importantly these two neruphysiological phenomena seems to be strinctly related as recent evidence seems to suggest (Wurtz and Sommer, 2006), with corollary discharge signal directly modulating the amount of neurons showing shifting receptive field behavior across eye-movements in the frontal eye fields.

Not only internal neural signals representing the metrics of the upcoming eye movement are taken into account to solve the matching problem across saccades. Allocentric cues also plays a role since a reasonable assumption of the system is that the world does not change during the short time of a saccade. Moreover it has been shown that egocentric and allocentric cues are optimally combined, giving the overall percept of trans-saccadic visual stability (Nemeier et al, 2003).

Recent behavioral evidence seems to show how information between subsequent fixations can be combined to give a single percept, as in the case of transformational apparent motion and line motion illusion, even if retinal coordinates of stimulation are shifted in the direction opposite to the eye movement. With these kind of paradigm also the cost of a single saccade can be shown. The nature of this task seems to suggest that experimental setups where an active integration between fixations is needed are well suited to study the behavioural indexes underlying mechanisms of visual stability.

Chapter 2:

Continuous perception of motion and shape across saccadic eye movements

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Abstract

Although our naïve experience of visual perception is that it is smooth and coherent, the actual input from the retina involves brief and discrete fixations separated by saccadic eye movements. This raises the question of whether our impression of stable and continuous vision is merely an illusion. To test this, we examined whether motion perception can "bridge" a saccade in a two-frame apparent motion display in which the two frames were separated by a saccade. We found that transformational apparent motion, in which an object is seen to change shape and even move in three dimensions during the motion trajectory, continues across saccades. Moreover, participants preferred an interpretation of motion in spatial, rather than retinal, coordinates. The strength of the motion percept depended on the temporal delay between the two motion frames and was sufficient to give rise to a motion-from-shape after-effect, even when the motion was defined by a second-order shape cue ("phantom transformational apparent motion"). These findings suggest that motion and shape information are integrated across saccades into a single, coherent percept of a moving object.

Keywords: saccades, visual stability, transformational apparent motion, motion after effect

Introduction

The fact that we typically make several saccadic eye movements every second means that the position of objects on the retina is constantly changing. Thus, one of the fundamental questions of vision science is how we keep track of the location of objects across saccades (for review, see: Bays & Husain, 2007; Melcher & Colby, 2008; Wurtz, 2008). But a perhaps more basic question is how our naïve perception of a smooth and continuous visual flow is built out of a series of relatively brief visual snapshots that are separated by abrupt jumps, like in a poorly filmed home movie. This problem is made even more clear by the fact that the new input to the eyes in each fixation must travel through the visual system before it reaches awareness, necessitating around 120 – 200 ms (Genetti, Khateb, Heinzer, Michel, & Pegna, 2009; Liu, Agam, Madsen, & Kreiman, 2009; Thorpe, Fize, & Marlot, 1996), and that visual input is partially suppressed while a saccade is performed (Burr, Morrone, & Ross, 1994). The issue of achieving stable perception based on discrete and discontinuous input is particularly troublesome in the case of visual motion. While the brain is extremely efficient in integrating motion cues over time and space over a period of seconds (Burr & Santoro, 2001; Neri, Morrone, & Burr, 1998), motion detectors are typically assumed to operate in retinal coordinates (although see Ong et al., 2009). Unless motion forin applying for the available position the same object is integrated across saccades (Melcher & Morrone, 2003), then this impressive ability to integrate motion over time would be essentially useless.

There are essentially three main ideas about how visual stability is maintained (for review, see Melcher & Colby, 2008). The first is that our impression of smooth perception is essentially an illusion (Dennett, 1992). Failures to detect changes in the position of an object across a saccade (Bridgeman, Hendry, & Stark, 1975), for example, argue against detailed information being maintained across saccades. In the case of motion perception, this theory would predict that motion processing begins anew with each fixation, since any matching of object location across the saccade would be based solely on memory (Irwin, 1991).

A second idea is that our impression of visual stability comes from cross-saccadic priming, in which our post-saccadic perception is influenced by what was previously seen. A clear example comes from studies of reading, in which information about the word to the right of fixation (the "parafoveal preview") primes us to quickly read the word after the saccade (Rayner, 1998, 2009). Similar results, in which post-saccadic perception is influenced by what was seen before the saccade, have been reported for color perception (Wittenberg, Bremmer, & Wachtler, 2008), time perception (Burr, Tozzi, & Morrone, 2007), motion perception (Melcher & Morrone, 2003), object recognition (Van Eccelpoel, Germeys, De Graef, & Verfaillie, 2008) and face perception (Melcher, 2005; van Boxtel, Alais, & van Ee, 2008). Such cross-saccadic priming might contribute to the subjective impression that the world is stable, since the post-saccadic stimulus would be processed quickly and efficiently (Khayat, Spekreijse, & Roelfsema, 2004a, 2004b). However, this theory still maintains the idea that perception is essentially discrete and tied to individual fixations.

The third, and most radical, proposal is that conscious perception fuses information from before and after the saccade into a single, coherent percept. This idea agrees with the common, naïve impression of an unbroken stream of visual consciousness—although, of course, our intuitions could simply be wrong. In fact, early attempts to demonstrate the “fusion” of dot patterns across a saccade were without success (Bridgeman & Mayer, 1983; Irwin, Yantis, & Jonides, 1983). Likewise, the finding that changing the case of all letters in a word (McConkie & Zola, 1979) had little effect on reading behavior suggests that abstract codes are used in integrating information across saccades in reading.

More recently, however, the idea of trans-saccadic perception has been revived based on two types of evidence. The first is the discovery of dynamic receptive fields (RFs) which change their sensitivity around the time of eye movements (Duhamel, Colby, & Goldberg, 1992; Melcher & Colby, 2008; Wurtz, 2008). This “re-mapping” involves both prediction (before the saccade, the neuron responds to a stimulus in its future RF) and a type of memory trace updating mechanism in which a neuron continues to respond, after the saccade, to the stimulus in its old RF. One important implication of these findings is that the neural activity *bridges* the saccade, rather than showing discrete and discontinuous firing patterns. The second type of evidence comes from changes in visual perception, such as peri-saccadic mislocalization, which have been reported around the time of saccades (Matin & Pearce, 1965; Ross, Morrone, Goldberg, & Burr, 2001). These findings suggest that the brain anticipates the saccade and uses this information to update spatial information and match it across saccades. However, most experiments have looked at localization of briefly flashed stimuli in laboratory settings. It is less clear how everyday perception, in which objects rarely appear and disappear during saccades, would be influenced by dynamic receptive fields.

We directly tested the predictions of this third, trans-saccadic perception hypothesis by studying apparent motion. One interesting perceptual property of apparent motion is that our visual system “fills in” the entire motion path, rather than seeing two discrete events (Kolers, 1972; Morgan, 1976). A dot flashed in two different locations, given the right timing parameters, is seen to move through the entire trajectory between point A and point B. This property of apparent motion makes it the perfect test of the hypothesis that perception bridges the saccade. In fact, Rock and Ebenholtz (1962) had already reported a version of trans-saccadic apparent motion many years ago. In their experiment observers were asked to synchronize left/right eye movements with two alternating flashing lights visible through two vertical slits. In this way the illuminated vertical lines would be presented at the fovea after each eye movement. The displacement of the vertical line directly followed the size and direction of the saccade. Although the retinal position of the flash was constant, participants reported seeing motion in external (in their terms, “phenomenal”) space.

In line with this observation it has been shown that participants are able to detect changes in the position of a moving object across a saccade (Gysen, De Graef, & Verfaillie, 2002). In contrast to the Rock and Ebenholtz studies, recently replicated by Szinte and Cavanagh (2009), studies of change detection for moving objects measured the ability to notice *changes* in the expected position of the stimulus rather than to perceive smooth trans-saccadic motion. Thus, we adapted the Rock and Ebenholtz technique to study the perception of a coherent motion sequence across saccades.

In a new set of experiments, we built upon the Rock and Ebenholtz finding in four ways. First, we added motion orthogonal to the direction of the saccade in order to disentangle motion caused by the saccade from motion of the stimulus. This also resulted in the two stimuli being shown in different visual hemi-fields (and thus to different cerebral hemispheres), providing a greater challenge for mechanisms of trans-saccadic perception. Second, we varied the temporal delay between the two flashes in order to provide a more fine-tuned measure of motion perception. Third, and most importantly, we used “transformational apparent motion” (TAM), in which two differently shaped stimuli are perceived, when shown in an apparent motion display, as smoothly changing shape over time (Tse, Cavanagh & Nakayama, 1998; Tse, 2006; Tse & Caplovitz, 2006; Tse & Logothetis, 2002). Finally, we varied the amount of shape information in the stimulus to provide an estimate of the reliability of TAM perception judgments and used this stimulus to measure a transformational apparent motion after-effect.

The overall aim of these four experiments was to test whether motion can carry shape information—in addition to spatial location—across the saccade. If perception essentially begins anew with each fixation, then there should be little or no impression of smooth motion across saccades in the TAM condition. The ability to integrate the two stimuli into continuous shape-based motion, however, would provide strong evidence that pre- and post-saccadic information are combined into a single, trans-saccadic perceptual event.

Experiment 1: Percept of a motion event occurring across the saccade

The aim of the first experiment was to measure the smooth and continuous perception of motion across a saccadic eye movement. Following the example of Tse and Logothetis (2002), we presented two stimuli, which differed in location or shape, separated by a blank delay of varying duration (Figure 1.2). We expected that the perception of smooth apparent motion would decrease for longer blank delays (ISI) between the first and second stimuli. In addition, we investigated the influence of saccades on transformational apparent motion. While Tse and Logothetis (2002) had matched both the retinal and spatial location of the two stimuli, we investigated whether spatially matching the external location of stimuli across the saccade, despite a change in retinal coordinates, was sufficient to support the perception of object-based motion.

Varying the blank delay between the two stimulus frames was also important in order to allow sufficient time to make a saccade during this blank period between the first and second frames. We cued the subject to make the saccade while the first motion frame was still visible, so that the last

100 ms of the presentation of the first frame was spent preparing for the saccade (trials in which saccade onset was less than 100 ms were excluded from analysis). Then there was a blank delay, with no stimulus, during which participants moved their eyes to the new fixation position. As a result of the saccade, the two different stimuli were always shown in opposite visual hemifields. The minimum blank delay duration was chosen to be 100 ms for three main reasons. First, this allowed enough time for subjects to make a saccade on the majority of trials, even for the shortest blank delay duration (saccade onset less than 200 ms). Second, this brief ISI gave a strong impression of motion without a saccade. Finally, a blank delay of at least 100 ms was necessary to avoid the suppression of trans-saccadic displacement of the stimulus (Deubel, Bridgeman, & Schneider, 2004).

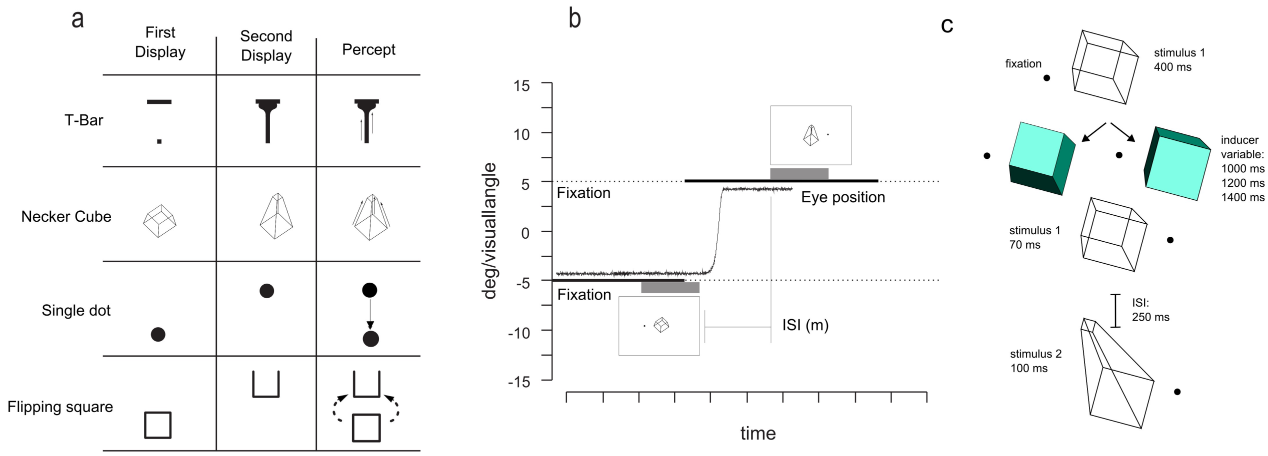

Figure 1.2: (a) Example of the stimuli adopted in Experiment 1; During the experiment, the direction of motion was varied randomly on each trial. (b) Trial procedure for Experiment 1 with time course and degree of visual angle of the screen on the x and y axis, respectively. Black lines represent the eye fixating the screen and gray rectangles represent the duration of the displays. Note that on saccade trials the first and second stimulus were always shown in different retinal positions, separated by the saccade. (c) Trial procedure and stimuli adopted in the Necker cube control experiment in order to bias the type of shape transformation (see Methods). Depending on the inducer, the shape appeared to either move forwards or backwards in depth.

Methods

Observers

Six observers participated in the experiment (two authors and four participants naïve to the aims of the experiment). Informed consent was obtained for all participants and all subjects reported normal or corrected-to-normal vision.

Stimuli and Apparatus

Stimuli were presented on a PC using Matlab software and presented on a gamma corrected Iiyama CRT 1900 monitor running at 85 hz (resolution: 1280 x 1024, short persistence phosphors). Figure 1.2a shows the four different types of stimuli used during the experiment; each configuration consisted of 2 frames in which the shape or vertical position of the stimulus was changed. Both shapes were modified from studies by Tse and colleagues (Tse, Cavanagh & Nakayama, 1998; Tse, 2006; Tse & Caplovitz, 2006; Tse & Logothetis, 2002). The T-bar stimulus subtended 8.8 x 4.5 deg/visual angle whereas the short and expanded Necker cube subtended 2.9 x 3.3 and 2.9 x 4.4 deg/visual angle, respectively. For these stimuli, background was set to white (CIE coordinates: x = 0.28; y = 0.30; luminance: 80 cd/m^2), and the stimuli were black (CIE: x = 0.35; y = 0.37; luminance: 0.25 cd/m^2). The fixation point consisted of a red (CIE: x = 0.56; y = 0.33; luminance: 70 cd/m^2) circle that subtended 0.4 degrees of visual angle.

The other two types of stimuli used in this experiment were a single black disk (1.4 deg/visual angle diameter) that could shift its vertical position from the first to the second frame by 4 deg/visual angle towards up or down (randomized across trials) and a flipping square apparent motion sequence whose first frame consisted of a black wireframe rectangle (2 deg/visual angle side) and the second frame consisted of the same square, shifted vertically by 2 deg/visual angle, with one side missing (Figure 1.2a). The typical percept for this sequence is that of a square that flips in the third dimension until it reach its final position depicted on frame 2, as described by Rock (1997). For this second group of stimuli (disk and flipping square), the screen background was set to gray (CIE coordinates: $x = 0.28$; $y = 0.31$; luminance: 8.8 cd/m^2).

For the control experiment, the stimuli were presented on a gray background. The Necker cube subtended 3.1 and 6 deg/visual angle for the contracted and the expanded version, respectively. Color used were CIE: $x = 0.20$; $y = 0.32$; luminance: 58.6 cd/m^2, CIE: $x = 0.27$; $y = 0.31$; luminance: 4.8 cd/m^2 and CIE: $x = 0.26$; $y = 0.34$; luminance: 9.8 cd/m^2. The fixation point consisted of a black circle that subtended 0.4 degrees of visual angle presented either to the left or the right of the stimuli (4.5 deg/visual angle).

Observers sat in a dimply lit room and viewed the screen binocularly at a distance of 57 cm, with their heads stabilized by a chin rest. Right eye position was monitored using an EyeLink 1000 Desktop Mount (SR Research, Ontario, Canada) sampling at 500Hz. Eye position was recorded for each trial and saved for offline analysis.

Procedure

Prior to the experiment, subjects were presented with practice trials showing examples of both smooth apparent motion (ISI between the two stimuli of ~105 ms) and non-motion (ISI of ~1200 seconds). During training, participants were shown the “no saccade” condition, which involved maintaining gaze on the fixation point throughout the trial. In the main experiment, all three viewing conditions (“no saccade”, “saccade” and “retinal control”) conditions were presented in separate, interleaved blocks in randomized order. The four different stimulus types were divided into two blocks, with two different types of stimuli presented in random order within each block. One type of blocks contained the T-bar and Necker cube stimuli, while the other blocks contained the moving disk and flipping cube apparent motion stimuli.

Each trial began with the participant looking at the fixation point and then pressing a button when ready. For the first group of stimuli (the T-Bar and the Necker cube), the first stimulus was presented for 400 ms, followed by a variable blank that could vary between 105 ms (9 frames), 210 ms (18 frames) or 400 ms (34 frames) and then the second stimulus display for a further 400 ms. In the “no saccade” condition, participants viewed a fixation point to the left or right of the display and stimuli were shown at the center of the screen.

In the “saccade” condition (Figure 1.2b), the fixation point was displaced during the trial to the other side of the screen, requiring a 10 degree saccade. This saccade cue occurred ~300 ms into the trial (25 frames), when the first stimulus was still visible, leaving participants ~210ms (18 frames) to ~500ms (43 frames) to move their eyes, depending on the condition.

Trials in which participants executed the saccade before the first stimulus disappeared (saccadic latency < 105 ms), as well as trials in which saccades were too short (amplitude < 8.5 degrees) or too slow (such that the saccade was not started by the onset of the second motion frame were excluded from further analysis (mean saccade latency was 184 ms, mean saccade amplitude was 9.8° visual angle). Please note that in the saccade condition, the spatial coordinates of the two stimuli *on the screen* were matched but they were always shown in different retinal coordinates. In total, 27% of trials on the saccade condition were excluded based on eye movements for these blocks of trials (30% for ISI = 105ms, 23% for ISI = 210ms and 28% for ISI = 400ms, see Figure 2.2).

In the other blocks (with the moving disk and flipping square apparent motion stimuli), the procedure was identical except that four different ISI's were tested (105, 210, 600 and 1200 ms) and subjects were requested to perform a 14 deg/visual angle saccade. Again, trials in which participants executed the saccade before the first stimulus disappeared (saccadic latency < 105 ms), as well as trials in which saccades were too short (amplitude < 12.5 degrees) or too slow, such that participants failed to make a saccade by the time of the second motion frame, were excluded from further analysis (mean saccade latency was 182ms, mean saccade amplitude was 13.4 deg/visual angle). In total, 22% of trials on the saccade condition were excluded based on eye movements (50% for ISI = 105ms, 26% for ISI = 210ms, 19% for ISI = 600ms and 12% for ISI = 1200ms, see Figure 2.2).

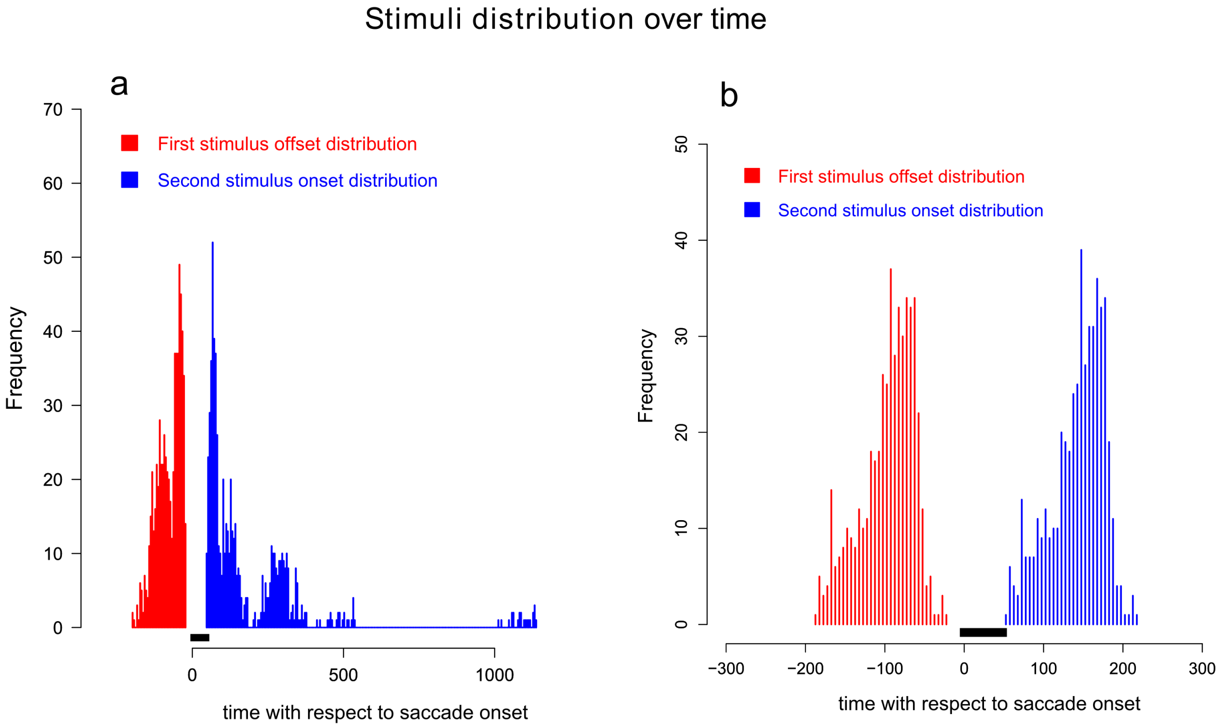

Figure 2.2: Timing of the stimuli with respect to saccade onset for (a) Experiment 1 and (b) Control experiment. Red bars represents the time of stimulus 1 offset (always before saccade onset), whereas blue bars represents stimuli 2 onsets (always after the saccade). The black filled rectangle along the horizontal represents the mean saccade duration.

The third condition provided a control for the saccade condition by replicating the same retinal stimulation but without the intervening saccade. The participant maintained fixation at the center of the screen. The first stimulus was shown on one side of the screen (distance of 5 degrees) while the second stimulus was shown on the opposite side of the screen. This condition tested the possible role of large receptive fields (radius of 10 degrees or more) which might integrate the two motion stimuli despite different retinal locations. Such large-range spatial pooling might have been a potential confound for the saccade condition, thus necessitating this control condition. In each of the three conditions, observers were presented with a total of 20 trials for each ISI level for the T-bar and the Necker cube (120 trials overall) and 10 trials for each ISI level for the disk and the flipping square stimuli (80 stimuli overall)

The motion stimuli were oriented along the vertical axis of the screen in the “saccade” and “no saccade” conditions (Figure 1.2). After each trial, subjects were requested to report whether they perceived motion in the vertical axis or, instead, perceived the appearance/disappearance of the stimuli. Subjects gave their responses by pressing a button on the keypad. For the T-Bar and the Necker cube trials, subjects could report one of the following three choices: no motion, moving up or moving down. These choices were included because it has been shown that the T-bar stimuli has a preferential direction of perceived motion that goes from the single point to the bar itself (Tse & Caplovitz, 2006), whereas the direction of the perceived motion for the Necker cube depends on the subjective interpretation of the first display orientation (Tse & Logothetis, 2002).

For the blocks of trials showing the black disk and flipping square apparent motion sequences, subjects could report one of the following three choices: no motion, translating or flipping, Thus, it was possible to explicitly test whether subjects perceived a shape change between the two frames in the transformational motion sequence.

In the case of the Necker cube, the direction of perceived shape change (forward or backward in depth) depended on the initial interpretation of the ambiguous shape. To directly test the perceived shape transformation, we ran an additional control condition (Figure 1.2c) which biased the perceived orientation of the Necker cube by presenting a solid cube (Tse & Logothetis, 2002). Participants were presented with 2 different conditions (“saccade” and “no saccade”), in interleaved blocks (48 trials for each block, 96 trials for each condition). Each trial began with the participant looking at the fixation point and then pressing a button when ready. The first stimulus of the Necker cube TAM (stimulus 1) sequence was presented for 400 ms (see Figure 1.2), followed by a solid biasing shape (inducer) remaining on the screen for a variable time (1000 ms, 1200 ms or 1400 ms), in order to prevent participants from anticipating the saccade. In the “saccade” condition stimulus 1 was shown again for 6 flips (~70 ms) together with a 9 deg/visual angle displacement of the fixation point on the other side of the screen. Participants were asked to perform a saccade towards the displaced fixation point. After an ISI of 250 ms, stimulus 2 of the transformational apparent motion sequence was presented for ~100 ms (9 frames). Thus participants had approximately 320 ms to shift their gaze to the new fixation position. Subjects were requested to report the direction of the perceived motion (“forward” or “backward” in depth, see Figure 1.2) or to report that no motion was perceived. The “no saccade” condition was identical except that the fixation point remained on the initial position. To ensure that subjects correctly performed the eye movement and maintained fixation as requested we implemented a gaze contingent display that checked eye position online. If a saccade was not performed correctly (the saccade did not occur during the 250 ms blank ISI between stimulus 1 and stimulus 2 or did not land inside an area of 3 deg / visual angle around the target fixation point) or if participants did not maintain fixation as requested in “no saccade” trials, then the trial was repeated at the end of the block. During offline analysis, an additional 12% of the trials were excluded due to loss of data acquisition due to eye-blinking and other factors.

Since the procedure for the Necker cube and the T-Bar, the black disk and the flipping square, and the control condition (with the Necker cube) were all run in separate blocks with different parameters, data was analyzed separately for each of these three types of trials.

Results

In the “no saccade” condition, the proportion of trials in which subjects reported coherent motion decreased as a function of the delay (ISI) duration between the two stimuli (Figure 3.2). In sharp contrast, participants did not report seeing coherent vertical motion in the control condition (Figure 3.2, diamonds). The main finding was that performance in the saccade condition (Figure 3.2, triangles) was similar to that found in no-saccade trials (Figure 3.2, squares) indicating that transformational apparent motion occurred across saccadic eye movements, in non-retinal coordinates.

For the Necker cur and the T-Bar stimuli we performed a repeated measures analysis of variance (ANOVA) on subject proportion of perceived movement (“up” and “down” responses were pooled together, given the bistability of the Necker cube). We also report *post hoc* comparisons reaching significance after Bonferroni correction. A 3 (ISI) x 3 (viewing condition) x 2 (stimuli) repeated measures ANOVA showed a main effect of ISI, $F(2,10)=18.366,\ p<.001,\ \eta^2=.79$, a main effect of viewing condition, $F(2,10)=18.386\ p<.001,\ \eta^2=.78$, and a significant ISI x viewing condition interaction $F(4,20)=8.249,\ p<.001,\ \eta^2=.63$. Stimulus type did not influence the proportion of perceived movement, $F(1,5)=0.435,\ p>.05,\ ns$. Bonferroni-corrected comparisons failed to reveal differences between the no-saccade and the saccade condition for ISI’s of 105ms ($p>.4, ns$), 210 ms ($p>.5, ns$) and 400ms ($p>.3, ns$).

Similar results were found with the moving disk and flipping square apparent motion stimuli. To look specifically at the change in shape in the flipping square trials, only "flipping" responses were examined (no motion and translation responses were pooled together). Again, there were main effects of ISI and viewing condition ($F(3,15)=33.137,\ p<.001,\ \eta^2=.86$ and $F(2,10)=23.108,\ p<.001,\ \eta^2=.82$, respectively) and a significant interaction between the two, $F(6,30)=11.998,\ p<.001,\ \eta^2=.70$. Also in this case Bonferroni corrected comparisons did not reveal any differences between no-saccade and saccade conditions at any of the ISI durations.

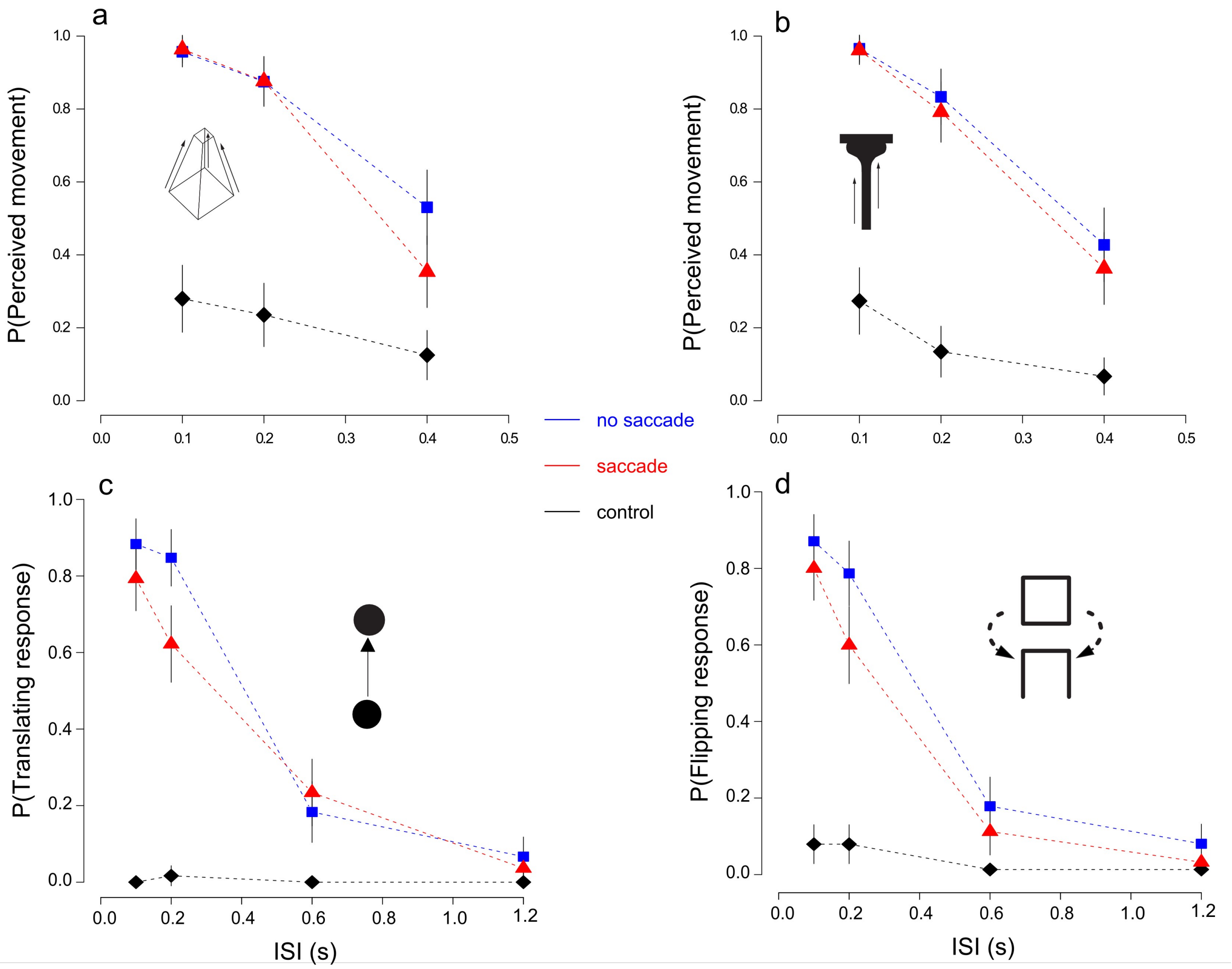

Figure 3.2: Experiment 1 results, different stimuli are plotted on different graphs (panel a: Necker cube, b: T-bar, c: single black dot, d: flipping square), vertical bars represents SEM, please note that the y scale differs in panels a & b from panels c &b, see text.

The results for the control condition with the "biased" Necker cube followed the same trend (Figure 4.2). The reported direction of motion was effectively biased by the inducer in both the saccade ($t(6)=3.566,\ p<.001$) and no-saccade ($t(6)=4.290,\ p<.001$) trials. There was no difference between and saccade and no-saccade conditions (t(6) < 1, n.s.).

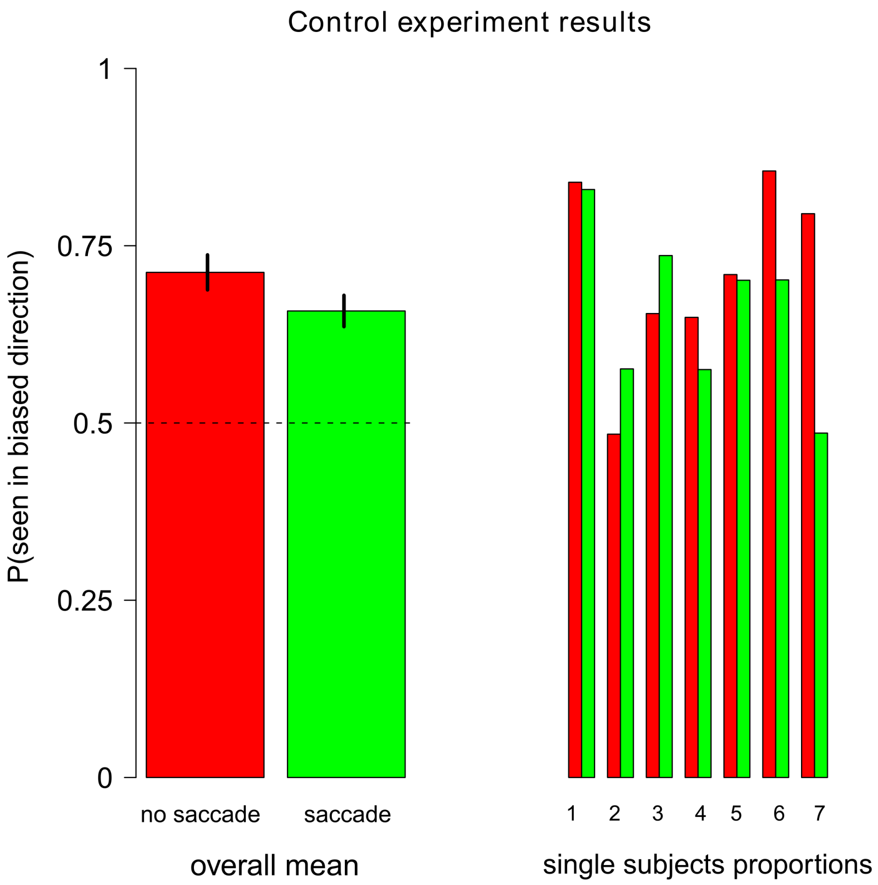

Figure 4.2: Proportion of trials in which the perceived motion was biased by the inducer. The left bars show average results for saccade and no-saccade trials. Error bars represent 1 SE. Individual subjects results are also shown (small vertical bars to the right of the figure).

Discussion

The main finding of the first experiment was that TAM and apparent motion perception continues across saccades. Participants reported a compelling percept of object transformation in both the no-saccade and the tran-saccadic motion condition. This finding suggests that the smooth perception of motion in non-retinal coordinates reported with location-defined apparent motion

(Rock & Ebenholtz, 1962; Cavanagh & Szinte, 2009; Szinte and Cavanagh, 2009) occurs also with a more complex, shape-defined TAM.

Previous studies have reported that the visual system performs poorly in detecting intrasaccadic displacements of stimuli (Bridgeman et al., 1975). At a first sight our results might seem to be in conflict with these reports, but there are considerable differences between our paradigm and the classic saccadic suppression of displacement (SSD) paradigm. First of all, in the SSD paradigm the saccadic target is displaced while in our method the stimuli were presented in the centre of the screen, not as the saccade target. Secondly in our case the displacement of the stimulus was considerably larger, around 4 deg/visual angle, than the usual displacement of ~1 deg/visual angle adopted in the classical paradigm. Thirdly, and perhaps most importantly, we included a blank delay between the vertical displacement so that it did not occur surreptitiously during the saccade (and during saccadic suppression). It has been shown (Deubel et al., 1996) that blanking the target considerably lowers the threshold for detection of saccadic displacements of target stimuli. Thus, it is perhaps not surprising that observers in our experiments could easily detect the shift between successive frames of the apparent motion sequence. What was more striking was the finding that subjects perceived coherent, vertical motion at the center of the screen even though the two stimuli were presented in two completely different retinal positions.

Experiment 2: Comparing retinotopic versus spatiotopic motion

In the first experiment, subjects were able to integrate two stimuli in different retinal positions into a coherent motion perception in spatiotopic coordinates. However, the spatiotopic percept was by far the simplest interpretation of the display. Thus, it is not clear whether the spatiotopic preference would still hold also when both a spatiotopic and a retinotopic interpretation of an apparent motion display could be possible. To test the preference for spatial or retinal coordinates in trans-saccadic motion, we included two different post-saccadic stimuli, one at the retinal location and one in the spatially-matched location on the screen.

Methods

Observers

Six observers participated in this experiment, two authors and four naïve observers, two of whom participated also on the first experiment, All observers had normal or corrected-to-normal vision. Informed consent was obtained for all participants.

Stimuli and Apparatus

Each stimuli comprised two frames: the first display consisted of a single bar (1 X 5 deg visual angle) with two possible orientations (90° or 45°), while in the second display two bars were presented, one in the same spatiotopic position of the screen and the other one in the same retinotopic coordinates after the saccade (see Figure 5.2a). The orientation of the bars in the second display depended on the bar orientation in the first display. If the bar in display one was at 90°, the orientations of the bars in the second display were 45° and 135°, while if the bar in display one was at 45°, the orientations were 0° and 90°. Background was set to white (CIE coordinates: $x = 0.28$; $y = 0.30$; luminance: 80 cd/m^2) stimuli color was set to black (CIE: $x = 0.35$; $y = 0.37$; luminance: 0.25 cd/m^2). The fixation point was a red (CIE: $x = 0.56$; $y = 0.33$; luminance: 70 cd/m^2) circle that subtended 0.4 degrees of visual angle.

Procedure

Experiment 2 was similar to the previous experiment, but only the “saccade condition” was tested. On each trial observers were instructed to perform a 10 degree saccade (following the change in fixation point position) between the presentation of the first and second display, with the direction of the saccade randomized between trials. The ISI between displays was fixed (~130 ms, 11 frames), so subject had ~230 ms (20 frames) to perform the eye movement. After each trial, subjects were requested to report the direction of perceived rotation (rotated to the left/right or towards up/down) by pressing key 1 or key 2 on the keypad. Unlike the first experiment, the participants had to choose (or guess) one direction or the other and could not report “no motion”. The orientation of the first and second bars and the rotation direction for retinotopic and spatiotopic coordinates was counterbalanced across trials. The direction of the motion with respect to the direction of the saccade was randomized across trials, in order to take account of the tendency to see motion in the same direction as the horizontal saccade (although any tendency to see motion as congruent with the saccade direction would tend to mask a preference for retinal or spatiotopic motion). The experiment was run in a single block of 120 trials. Trials in which participants failed to make the saccade during the blank delay, as well as trials in which saccades were too short (amplitude < 8.5 degrees), were excluded from further analysis (mean saccade latency 175ms, mean saccade amplitude 9.8 deg/visual angle). In total, 22% of trials were discarded.

Results

Participants reported motion consistent with the spatiotopic, rather than the retinotopic, interpretation on a majority of trials (Figure 5.2b). None of the participants preferred the retinotopic interpretation of motion. There was a clear preference across participants towards the spatiotopic position, which differed from 50% (no preference), $t(5)=8.982,\ p<.001$.

Of course, some saccades fell slightly short of the new fixation target or overshot the target (Figure 5.2c). Such saccade errors would lead to imperfect alignment of the stimuli, in both retinotopic and spatiotopic coordinates. However, participants clearly preferred the interpretation of motion which was defined by the spatial matching of the two bars, rather than the retinal position of the bars.

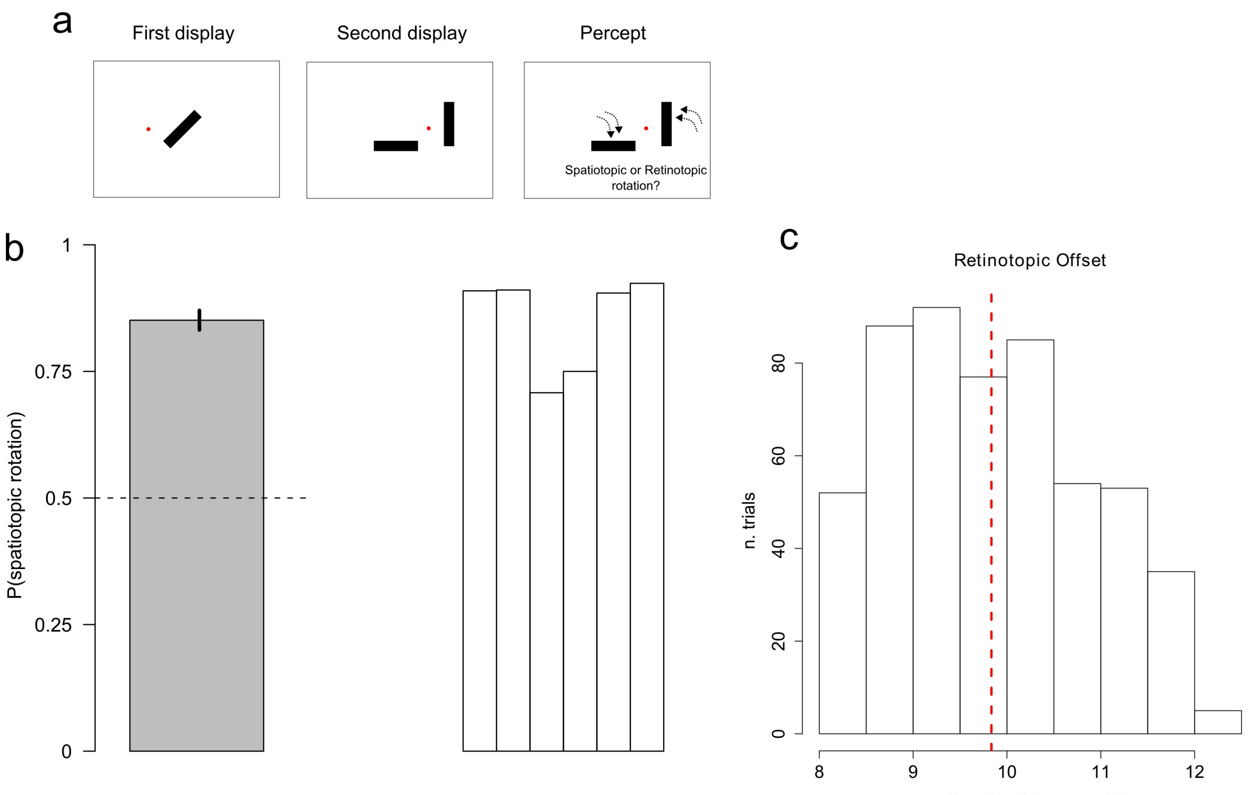

Figure 5.2: Experiment 2 stimuli and results: (a) stimuli adopted and typical percept (b) Mean proportion of spatiotopic response for six subjects, vertical bar represent 1 SE. Individual subjects results are also shown (thin white bars). (c) The distribution of saccade landing positions with respect to the target (presented at 10° of visual angle), dotted line represents mean landing position. Any under- or overshoot of the saccade would have resulted in a spatial mismatch between the two motion frames, both in retinotopic and spatiotopic coordinates.

Experiment 3: Perception of a second-order “Phantom TAM”

In order to provide a finer measure of motion perception we build upon the Tse’s idea of using second-order shape stimuli to build TAM configurations (http://www.dartmouth.edu/~petertse/, 2nd-order transformational apparent motion demo). This “phantom TAM” display gives an impression of motion without any motion energy. One advantage of this type of stimulus is that is makes it possible to modulate the amount of shape information presented on the TAM displays. Previous reports (Tse & Caplovitz, 2006) show that TAM perception relies on mechanisms that parse and match the images across successive fixations giving the impression of motion. By modulating the amount of shape information present in the first frame of the motion configuration, we expected to modulate the resulting TAM, thus providing a finer measure of the motion percept.

In addition, this stimulus provided an additional control to eliminate any hypothetical role of monitor persistence, since stimuli in this case are defined by a transient polarity inversion of pixels inside a predetermined area (see method) that lasts less than a frame (Bridgeman, 1998). Of course, in our study the measured persistence of the CRT monitor was well below the frame rate, but the use of the new phantom TAM would allow the stimulus to be more widely used, in the future, in LCD and other types of displays.

Methods

Observers

Five observers participated in the experiment (one authors and four participants who were naïve to the aims of the experiment). All subjects reported normal or corrected-to-normal vision.

Stimuli and Design

The basic design of the stimulus was that of a second-order apparent motion display, similar to the T-bar studied in Experiment 1 (but without the T on top), that involved a small region appearing to expand upwards or downwards into a larger region (Figure 6.2). In order to create this "phantom TAM" illusion, the region was defined by a change in the polarity of the dots. The rectangular stimulus (oriented vertically) was made up of random dots, which contained two different virtual regions: one at the top of the rectangle and one at the bottom (Figure 6.2). The greyscale random dot stimulus, which subtended 6.0 x 3.0 visual degrees, was centred on the screen and filled with dots (192 columns x 96 rows of square dots), randomly generated on each trial (mean luminance 9.4 cd/m^2). Each square had random brightness between 0 and 220 (greyscale RGB values) and subtended 0.028 visual degrees. This central stimulus was surrounded by a greyscale border subtending 7.2 x 3.8 visual degrees, centred on the screen and filled with dots, (230 x 122 squares). Each square in the background had random brightness between 0 and 150 (greyscale RGB values, CIE: x = 0.27; y = 0.32; luminance: 0.15 cd/m^2 and CIE: x = 0.28; y = 0.30; luminance: 13.8 cd/m^2, respectively). The overall impression given by the stimulus was of a grey rectangle oriented vertically, surrounded by a darker gray border.

In order to create a second-order region, within the rectangle, all dots inside one of two possible areas (at the top or bottom) of the central random-dot rectangle of the random dot stimuli abruptly inverted the polarity following the rule:

$$brightness_{new} = (brightness_{old} - 1) * -1$$

As a result, the area of dots in which polarity was reversed was perceived as a uniform shape that instantaneously appeared among the random dot stimuli. In Figure 6.2, this polarity-changing region is illustrated by a red rectangle (depicted with 1 in the figure). In order to ensure that the participant was fully able to perceive the region defined by the change in polarity, this polarity change was presented repeatedly three times at 2 Hz. Together, these three polarity changes over a total time period of 1500 ms gave the impression that there was a region, at either the top or bottom of the rectangle, which stood out as different from the rest. After the initial 1500 ms time period, in which three polarity changes occurred for the same virtual region at the top or bottom of the rectangle, the second part of the TAM display was shown. Specifically, both the polarity of first area (depicted with 1 on the figure) and the second area (depicted with 2 on the figure) was changed, such that a vertical bar comprising area 1 and 2 was perceived on the screen.

In order to vary the strength of the second-order shape information in the first part of the phantom TAM sequence, the proportion of the dots in frame 1 (see Figure 6.2) that changed polarity was varied among 6 different levels: 3%, 5%, 10%, 25%, 50% and 95%. This allowed for measuring a psychometric curve showing proportions of perceived motion as a function of the shape coherence (proportion of dots changing polarity). Subjects responded by choosing one among the following two choices: no motion or motion.

Procedure

Participants started each trial by directing their gaze to a fixation point positioned 5 deg/visual angle on the left or right of the screen. After a button press, the trial started and the random dot stimulus appeared on the centre of the screen. Region 1 was repeatedly presented on the screen, one repetition every 43 frames (~500 ms), then Region 2 was presented for 43 frames (Figure 6.2). After each trial subjects were asked to report whether they perceive the second frame rapidly expanding (motion response) or just the flash of the bar on the screen (no motion response), by pressing button 1 or 2 on the keypad.

Before each block subjects were informed about whether they would be cued to make a saccade within each trial. In the “fixation” condition, the fixation point maintained its position throughout trial duration, while in the “saccade” condition, the fixation point shifted its position, after ~150 ms (13 frames) from the third repetition of the polarity change in Region 1, to a position 10 deg/visual angle away on the opposite side of the screen, and then frame 2 was presented. In this way subjects had about 350 ms (30 frames) to move their eyes. Trials in which participants made a saccade before the fixation cross changed position or executed the saccade after the presentation of the second frame of apparent motion sequence were excluded from further analysis. Likewise, all trials in which saccades were too short (amplitude < 8.5 degrees) were excluded. Overall, the mean saccade latency of the saccades in the good trials was 186ms and the mean saccade amplitude was 10.7 degrees of visual angle. Overall, 17% of trials were discarded.

The experimental session consisted of 8 blocks of 36 trials each. The fixation and saccade conditions were run in interleaved blocks. Starting block was randomized across subjects. In addition, there was an initial training period, before running the main experiment, in which participants were familiarized with both the saccade task and the second-order TAM stimulus. To practice making the cued saccades, subjects sat in a dimly illuminated room and were presented with a single fixation point (black circle, 0.32 x 0.32 visual degrees) shifted 5 degrees of visual angle to the left or the right of the stimuli (randomized across blocks). In each practice trial, fixation point shifted its position from left to right (or vice-versa) for 10 times with a frequency of ~2 Hz (every 43 flips) and the task was to follow the fixation point. The training consisted on five blocks of 10 trials each.

In the second-order TAM familiarization procedure, participants were shown a repeated presentation of the motion stimulus. On each trial subjects maintained their gaze on a fixation point positioned 5 deg/visual angle to the left or right of the screen centre. After they pressed a button the random-dot rectangle stimulus appeared on the centre of the screen, followed by the two-frame TAM sequence. The sequence was shown 10 times, at a frequency of 2Hz, with the direction of motion constant within each trial (but randomized across trials). Subjects were asked to report whether they perceived the configuration as moving and in which direction. One subject who was unable to consistently perceive the TAM direction was excluded from the main experimental session.

Results

The transformational apparent motion was clearly perceived by subjects. As expected, the perception of vertical motion was strongest when the percentage of dots in the first region (at the top or bottom of the rectangle) was highest (Figure 6.2b). A repeated measures analysis of variance (ANOVA) revealed a main effect of shape information (proportion of dots changing polarity), $F(5,20)=32.294,\ p<.001,\ \eta^2=.88$. Neither the viewing condition (saccade versus fixation) nor the interaction between shape information and viewing condition yielded significant results ($F(1,4)<1,\ p>0.8,\ F(5,20)<2,\ p>0.2$, respectively). Bonferroni-corrected pair-wise comparisons failed to show any significant differences between saccade and fixation conditions.

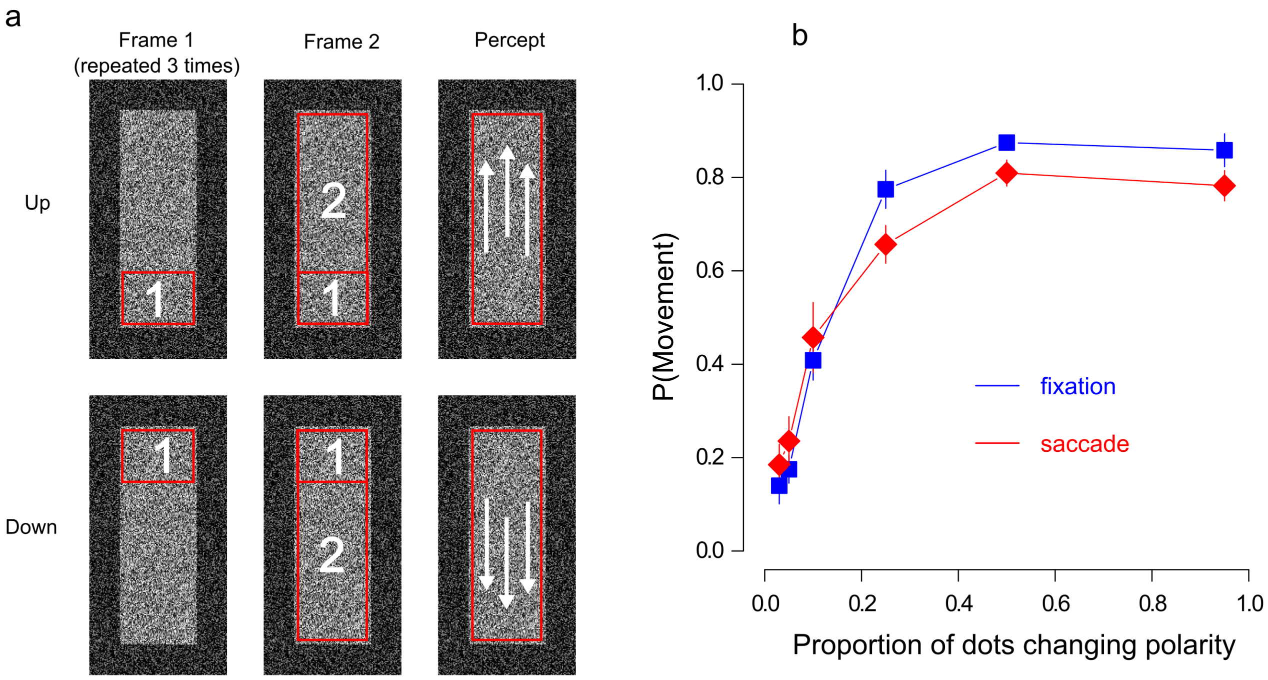

Figure 6.2: Experiment 3 stimuli and results: (a) The two different arrangements implemented to obtain motion impression towards up or down.

Experiment 4: Measuring a second-order TAM after-effect

Although participants reported seeing motion in the TAM displays, a nagging question in apparent motion studies is whether what subjects perceive is “really motion” (ie. a visual signal that taps into neural motion detectors) or rather a more abstract interpretation (Anstis, 1980). One generally accepted indicator of “real motion” is the motion after-effect (MAE), which is thought to be caused by the adaptation of motion-tuned detectors. There is some evidence that apparent motion can evoke an MAE: a prolonged adaptation phase with stroboscopic apparent motion stimuli can bias the perceived direction of a subsequent flickering test (von Grünau, 1986). But there are no existing reports showing MAE following TAM adaptation. We tested to see whether the second-order phantom TAM was capable of evoking a motion after-effect. The use of the random-dot stimulus allowed us to build a MAE probe whose structure closely resembled the adapting stimuli, a general rule of thumb adopted to elicit visual after-effects (Thompson, 1994). Specifically, we used a dynamic probe, considered more sensitive than a static probe, and easier to judge by subjects when measuring MAE (Thompson, 1994). The importance of using a dynamic test probe was also suggested by parallels between second-order motion and TAM stimuli (Tse & Logothetis, 2002), since it is well established that following second-order motion adaptation a MAE can be elicited only when tested with a dynamic test (Nishida, Ashida, & Sato, 1994; Nishida & Sato, 1995).

Methods

Observers

Four observers participated in the experiment (one authors and three participants naïve to the aims of the experiment). All subjects reported normal or corrected-to-normal vision.

Stimuli

The testing conditions were similar to the previous experiment, except that the stimulus and procedure had to be adapted to create, and then measure, the MAE. As in the previous experiment, the phantom TAM stimulus was made up of random dots. In this case, however, there were four different virtual regions defined within the random dot rectangle. One complete adaptation cycle consisted of 4 different frames (one frame every 500 ms) each of which was visible by the instantaneous polarity inversion of the squares composing the area (Figure 7.2a). Four frames (resulting in two bars) were used instead of two to minimize the chances of perceiving Illusory Rebound Motion (IRB) which has been reported with random dot stimuli (Hsieh, Caplovitz, & Tse, 2005), such as those implemented here. There were two different adaptation directions, towards up or towards down, and the arrangement of the four areas defining the stimuli changed accordingly to the direction (see Figure 7.2a).

As can be seen in, which shows a modified version of the adapter in which only the two tall bars are shown without any TAM, the appearance of the virtual regions, defined by the reversal of polarity, provides a much more compelling percept than any local motion cues given by repeatedly showing random dots. This movie also makes clear the difference between the phantom TAM, which gives a strong motion percept, and the mere appearance of second order bars.

The MAE probe (“test”) consisted on a first order motion stimulus with the same size as the inner rectangle where the phantom TAM had been shown. For high percentages of coherence, motion direction could easily be detected whereas, with low motion signal, the test was perceived as a dynamic visual noise pattern. In each test probe, a given percentage of squares moved towards up or down throughout the test duration (2000 ms) at 0.88 deg/second, with a frequency of ~8.5 Hz (every 10 frames with 85Hz refresh rate). Each square which made up the MAE probe stimulus subtended 0.028 visual degrees and was initially assigned a random brightness between 0 and 220 (greyscale RGB values, CIE: $x = 0.27$; $y = 0.32$; luminance: 0.15 cd/m^2 and CIE: $x = 0.28$; $y = 0.30$; luminance: 48 cd/m^2, respectively) kept constant throughout test duration. The remaining points of the test stimuli were redrawn at each refresh with a random brightness between 0 and 220 (greyscale RGB values). The percentage of coherent motion on each trial was randomly chosen among five different levels (-50%, -25%, 0%, 25% and 50%, positive and negative numbers represent movement towards up and down, respectively).

Procedure

Each subjects participated in 3 separate sessions on three non-consecutive days, each of which comprised 8 blocks of 15 trials each. During the first session the test stimuli were presented without prior adaptation to provide a baseline condition. Each trial started with the presentation of a single fixation point (black circle, 0.32 x 0.32 visual degrees) shifted 5 degrees of visual angle to the left or the right of the stimuli (randomized across blocks). Subjects pressed a button to start each trial, were instructed to pay attention to the adapter, and then after the presentation of the test (MAE probe) were cued to report the direction of perceived motion of the test probe by pressing button 1 (up) or 2 (down) on the keypad. In the two remaining experimental session the adapting stimuli was presented prior to the test. The eye tracker was calibrated using a 5 points calibration sequence before every block on each session.

In the adaptation blocks, a top-up procedure was implemented to measure the strength of the MAE, with the first trial using a long adaptation period (40 s) and then a 6 s adaptation period in the subsequent trials. The adaptation direction in the first session was randomized between subjects. The same adaptation direction was kept constant throughout the session. After the disappearance of the adapter, there was a blank gray screen with the fixation point for 105 ms (9 frames). Then, the test pattern was presented for 2 s. The test probe began with the exact same pattern of dots as had been presented in the final frame of the adapter, in order to avoid any local first order motion. Then, starting with that pattern of random dots, the first order motion was added to the dynamic test probe (see Stimuli, above, for details). After the test presentation, subjects were given a two-alternative forced choice direction discrimination test for the test probe. Then the next adaptation sequence started 500 ms after the response was collected.

Data Analysis

The percentage of “up” responses was computed for each combination of test coherence and adaptation condition (baseline, adapt up and adapt down). Data were analyzed for each subject to derive three psychometric curves for each participant, one for each adaptation condition. Psychometric curves were obtained using an approximate Bayesian inference method (Kuss, Jakel, & Wichmann, 2005) fitting a logistic function to our data. As a lapse rate prior we used a beta distribution with $\alpha = 2$ and $\beta = 50$. For the location parameter we chose a Gaussian distribution with mean = 0 and SD = 0.7, whereas as prior for the width parameter we choose a gamma distribution with $\alpha = 5$ and $\beta = 10$. Acceptance rates for 2000 MCMC generated parameters across subjects ranged from 68% to 81%.

Results

A strong MAE was found for each of the observers, as shown by the shift of the psychometric curves in the opposite direction from the adapter motion (Figure 7.2b). When presented with upwards TAM adaptation, subjects were biased to respond “down” (mean = 11%), whereas the opposite tendency was found for down adaptation (mean = -17%). The estimated width parameter of the psychophysical curve was constant between adapting conditions, (mean = 0.41 and 0.43, adapt up and down respectively). A slightly higher value was found for the baseline condition (mean = 0.50). In the baseline condition, there was a slight tendency to report the motion moving upwards in 3 subjects out of 4 (see Figure 7.2b).

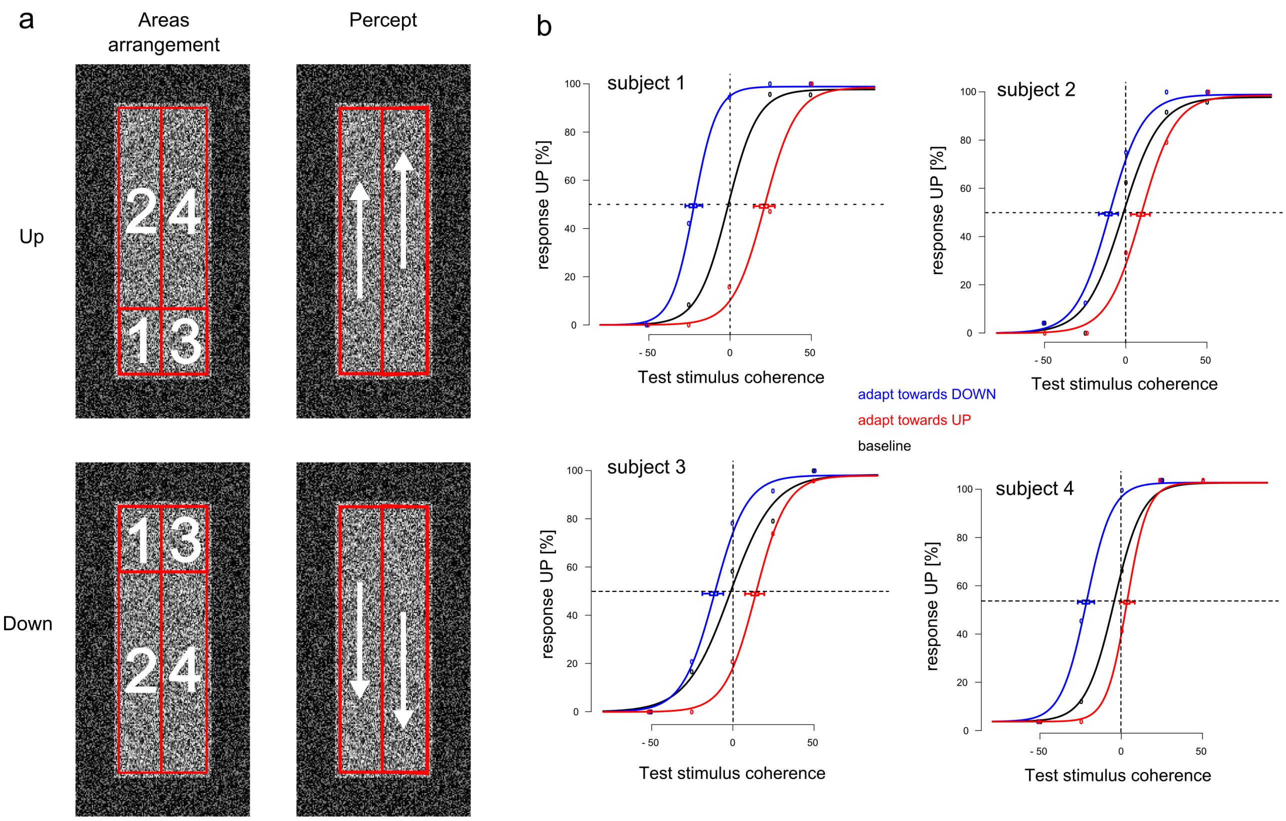

Figure 7.2: Experiment 4 stimuli and results: (a) Depiction of the TAM sequence for upwards and downward motion.. (b) Psychophysical curves showing the transformational motion after-effect, in which the percentage of "up" responses are plotted against the coherence of the test stimulus. Negative values correspond to downward motion, while positive values indicate upward movement. Data is shown for four participants. Each datapoint shows the average from 24 trials. Psychometric curves were obtained using PsychFun package (Kuss, Jakel & Wichmann, 2005) running under the R environment for statistical computing. Error bars show approximate Bayesian confidence intervals for the estimate of the mean.

General Discussion

The main finding of these experiments was that both apparent motion and transformational apparent motion were perceived as a coherent event across saccades. This result provides further evidence that our conscious perception of the world continues across saccade rather than always beginning anew with each fixation (for review, see Melcher & Colby, 2008; Melcher, 2010). In the case of the stimuli used in this experiment, the perception of motion bridged the saccade and the participants reported seeing a smooth, continuous path of motion even though the retinal input, by itself, was entirely inconsistent with this interpretation. The finding that TAM, and not just apparent motion, could be perceived across saccades suggests that some three-dimensional shape information is retained across separate glances.

In the second experiment, spatiotopic and retinotopic motion interpretations were pitted against each other. We found that participants strongly preferred the motion in spatial coordinates. Initially, this might seem like a surprising finding, since it suggests that their natural inclination was to ignore the retinally-defined motion signals from low-level detectors that are usually thought to be the foundation of motion perception. In real life, however, it would be important to be able to accurately distinguish between the motion trajectories of separate objects, and link the correct motion to its respective object, even when we move our eyes. This point is illustrated in Figure 8.2, which illustrates the problem at the heart of trans-saccadic motion perception. As shown in the figure, we do not spontaneously integrate a two-frame transformational apparent motion display in retinal coordinates across a saccade (as we are not able to integrate a 2-frame random-dot kinetogram, see (Shiori & Cavanagh, 1989).

Figure 8.2: Illustration of the importance of ignoring irrelevant retinally-defined apparent motion in everyday life. If one shifts the point of gaze between the two red fixation points, the percept is of two different objects rather than of one object in transformational apparent motion. In contrast, a clear motion impression arises if the two stimuli are presented spatiotopically across eye movements.

While the perception of motion during saccades has received a great deal of study, the mechanisms by which we correctly match moving objects across saccades, while at the same time avoiding to incorrectly perceive irrelevant retinally-defined apparent motion, remain less explored. One idea might be that high-level motion, such as second-order or attention-based motion (Cavanagh, Holcombe, & Chou, 2008), involves transforming retinal coordinates into head-centered, object-centered or world-centered coordinates via gain-fields (d'Avossa et al., 2007). A second idea might be that trans-saccadic apparent motion derives from the spatial updating of an object "pointer" (Melcher & Colby, 2008), which is fed back into the motion computation. There is an interesting parallel between trans-saccadic motion perception and TAM perception. In the case of TAM, the percept is defined by higher-order shape information rather than low-level motion detectors. Similarly, trans-saccadic motion perception would seem to require updating of object location in spatial maps, likely those beyond V1 (Melcher & Colby, 2008).

Our results suggest that the spatial maps which are involved in matching the object in the TAM display are spatially updated across saccades, perhaps via the dynamic remapping of receptive fields. It is important to note that many of the stimuli we tested did not involve a change in spatial location, but only in the stimulus shape. Thus, while updating the spatial locus of attention across the saccade is undoubtedly an important aspect of visual stability (Cavanagh et al., 2010), the remapping of "attentional pointers" cannot, by itself, account for the present results. Given that TAM cannot be accounted for a shift in attentional gradients (Tse & Cavanagh, 1995), the present results are more in line with predictions of object pointers, which include links to visual features such as shape (Melcher & Colby, 2008; Melcher, 2009), than attentional pointers (Cavanagh et al., 2010).

The final two experiments allowed us to directly measure the role of shape information in supporting trans-saccadic motion perception. The **second-order phantom TAE** showed that polarity-change defined regions were sufficient to support trans-saccadic motion perception. In addition, this type of stimulus allowed us to measure a MAE which provides further evidence that participants were seeing “real” motion. Different types of motion after-effects has been described throughout the years (Mather, Pavan, Campana, & Casco, 2008), suggesting that more than one neuronal population contribute to the arising of MAE. This new TMAE may have interesting implications for the current debate about motion after-effects, in particular regarding the relationship between TAM and second-order motion stimuli.

Perception of TAM requires a tight interplay between shape information and the extraction of motion signal in order to fill-in the features along the path of perceived motion (Tse & Logothetis, 2002). Motion detection and shape matching have to run in parallel, computing the motion trajectory according to the outcome of shape processing (Tse & Caplovitz, 2006). A functional neuroimaging study of TAM suggested that a number of brain regions were involved, including hMT and LOC (Tse, 2006). Interestingly, these areas have been implicated in the use of extra-retinal coordinates in the processing of motion (d'Avossa et al., 2007) and shape (McKyton & Zohary, 2007). A critical question for future research is how visual areas which process information in retinal coordinates can support the non-retinotopic perception of shape and motion shown here.

In conclusion, our results suggest that our naïve impression of a “stream of consciousness” in visual perception is not an illusion. Our findings suggest that visual stability involves the integration of information about motion and shape across saccades into a single, coherent percept. The units of time underlying event perception, the “moments” of awareness, can bridge saccades and are not strictly tied to individual fixations. Our results provide further evidence that object and spatial information are matched across saccades, perhaps based on specific objects rather than remapping the entire scene (Melcher & Colby, 2008; Prime, Tsotsos, Keith, & Crawford, 2007). In addition, our findings suggest that trans-saccadic TAM, and in particular the second-order TAM, could be a useful tool to measure the object-based matching of features, such as shape, across saccades.

Chapter 3:

The role of spatiotemporal distortions in the peri-saccadic unmasking of targets presented in rapid serial presentation.

Under review as:

The role of spatiotemporal distortions in the peri-saccadic unmasking of targets presented in rapid serial presentation.

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Vision Research

Abstract

Briefly presented targets around the time of a saccade are grossly mislocalized towards the saccadic landing point. This has been taken as evidence for remapping mechanism that accompany each eye movement, helping maintain visual stability across large retinal shifts. Mislocalization can influence metacontrast masking by causing target stimuli in a masking sequence to be perceived as shifted in space towards the saccadic target and thus more easily discriminated (De Pisapia et al, 2010). Spatial mislocalization is greatly diminished when trains of brief stimuli are presented at a high frequency rate (Honda, 2006), which might help to explain why such mislocalizations do not occur in every day viewing. We investigated the influences of saccades on target discrimination when target and masks are presented in a rapid serial visual presentation (RSVP). We found that “unmasking” occurred even without spatial mislocalization of the target or mask, showing the largest effects when the forward mask was presented during the peri-saccadic time period. Moreover, we show evidence for predictive remapping in the same direction as the saccade, but no evidence of a backwards shift in attention against the direction of the saccade. Overall, these results are consistent with an active, spatiotemporal transformation of visual-spatial maps around the time of saccadic eye movements.

Keywords

noise masking, mislocalization, saccades, remapping;

Introduction

Saccadic eye movements are ballistic drifts aimed to reposition the most sensitive area of the retina, the fovea, to receive information about targets of interest. These movements can be voluntary but tend to go unnoticed during daily life. Saccades are accompanied by a large variety of perceptual effects, including suppression of the visual input (Matin et al 1974; Burr et al, 1994), suppression of saccadic target displacement (Deubel et al 1996b), mislocalization of briefly presented targets around the time of the saccade (Ross et al 1997) and even time compression/inversion (Binda et al 2009, Morrone et al 2005).

Neurophysiological studies have reported the existence of neurons that show receptive field shifts around the time of saccades (Duhamel et al, 1992), with the response of retinotopic neurons gradually shifting from the current receptive field (RF) to the future RF (the position in space occupied by the RF after the completion of the eye movement, Kusunoki & Goldberg, 2003). This shift (usually referred as “remapping”) anticipates the start of the actual eye movement and is interpreted as a predictive signal that anticipates the outcome of the incoming eye movement.

Recently it has been shown that briefly presented targets in a metacontrast masking paradigm can be “unmasked” by an intervening saccade, if the targets are presented during the perisaccadic interval (De Pisapia et al 2010). Participants reported the targets as mislocalized towards the future saccadic landing position, rather than at the same position as the subsequent metacontrast mask. Thus, the target identity could be more easily reported, leading to increased performance. These results have been interpreted as reflecting a remapping process accompanying the execution of the eye movement, since discrimination performance increased for targets that were reported as mislocalized compared to non-mislocalized trials (De Pisapia et al, 2010).

Although saccadic mislocalization is a robust laboratory phenomenon, we do not seem to experience peri-saccadic errors in everyday life. Presumably, this is because stimuli are shown for long periods of time, across the saccade, rather than flashing briefly right around the time in which we move our eyes. Consistent with this idea, it has been shown that mislocalization is greatly reduced if brief stimuli are presented in a long train of stimuli rather that in isolation (Honda, 2006). Specifically, spatial mislocalization is reduced by increasing the frequency of stimulus presentation, which might help to integrate the stream of stimuli into a unique event across the saccade (De Pisapia et al., 2010).

In order to link mislocalization to trans-saccadic perception in everyday life, it would be useful to study this transition between stable objects (as in real-world perception) and the type of stimuli used in laboratory studies. This could be visualized as breaking the temporal flow of a stable perceptual object into a series of separate snapshots. If saccadic mislocalization is a manifestation of a more fundamental remapping process that occurs every time we make a saccade, then it may be possible to find effects of saccades even with spatially stable stimuli, without any spatial displacements of the stimuli. In particular, it has been proposed that mislocalization is caused by a spatiotemporal transformation (STT) in receptive fields that occurs around the time of saccades (Binda et al, 2009; Burr & Morrone, 2011). If so, then these transformations should influence visual processing even when the stimuli are not briefly flashed. We developed a novel method to investigate peri-saccadic perception, without spatial mislocalization, by presenting targets and masks in a rapid visual presentation (RSVP) stream. If a spatiotemporal transformation is applied to visual processing in the peri-saccadic time period, then we expected to find evidence for this in the processing of target and mask stimuli presented during that temporal window, with or without mislocalization. The first step was to determine whether discrimination performance for a rapid series of alternating targets and masks increased in the peri-saccadic time period with respect of stable fixation. Then, we further analyzed the temporal pattern of performance, considering the role of the STT on target unmasking around the perisaccadic interval. To this end, we disentangled the increased performance due to the eye movement itself (leading targets and mask to impinge the retina on different positions, thus increasing the likelihood of correctly discriminate target identity), from the role of the STT in unveiling target identity. In the final experiment, we used our paradigm to test the recent proposal that remapping should occur in the direction opposite to the saccadic eye movement (Cavanagh et al, 2010).

Experiment 1: Unmasking the Target on RSVP

Material and Methods

Subjects

Four participants took part in experiment 1. All subjects had normal or corrected-to-normal vision. Informed consent was obtained from all subjects and the study was approved by the local ethics committee. Participants received a monetary reimbursement for their time.

Experimental setup

Observers sat in a dimly lit room and viewed the computer screen at a distance of 57 cm with their head resting on a chin rest. Right eye movements were measured using an EyeLink 1000 Desktop Mount (SR Research, Ontario, Canada) sampling at 1 kHz. Software implemented in MATLAB (MathWorks, Natick, Massachusetts, USA) controlled stimulus display and response collection using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997) and EyeLink toolbox (Cornellissen, 2002). Stimuli sequences were presented on a Iiyama CRT 1900 monitor (1280 columns x 1024 lines, refresh rate: 100 Hz) on a uniformly gray background with an average luminance of 8.8 cd/m^2 (CIE coordinates: x = 0.28; y = 0.31).

Stimuli

Three different shapes were adopted as stimuli in all of the experiments (Fig. 1.3), a circle, (diameter ~ 2.82 deg / visual angle, area ~ 6.26 (deg / visual angle)^2), a square (side ~ 2.5 deg /

visual angle, area ~ 6.25 (deg / visual angle)^2), and a diamond (the square rotated by 45°). on the other stimuli used were noise masks (side ~ 4.4 deg / visual angle) made up of black (CIE coordinates: x = 0.35, y = 0.37; luminance = 0.25 cd/m^2) and white (CIE coordinates: x = 0.28; y = 0.30, luminance: 80 cd/m^2) squares (0.058 deg / visual angle each).

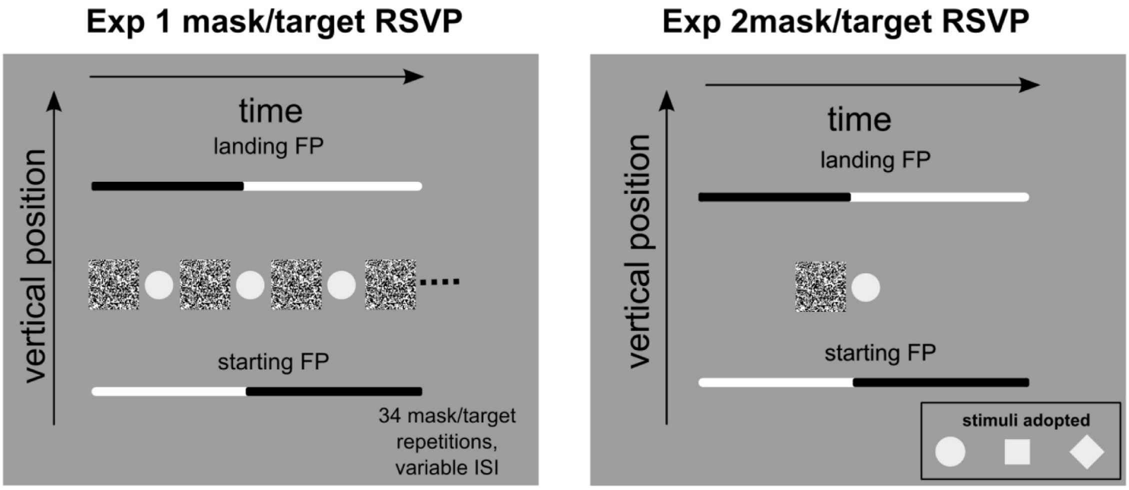

Figure 1.3: Illustration of the masking sequences adopted in the three experiments, including the different stimulus shapes used in the three-alternative forced choice (3AFC) task. The masking sequences were always presented in the centre of the screen. On saccade blocks participants were instructed to perform an eye movement from the initial to the final landing fixation point (FP) as soon as the two fixation points inverted their colors (turned from green to red and vice – versa, shown here as black and white in the figure). In the second experiment short masking sequences were presented jittered in time around saccade onset time in order to map discrimination performance during the peri-saccadic interval. For clarity purposes the stimulus contrast is increased in the figure compared to the real experiment.

Eye movements

Before each session, a five point calibration routine was run and drift correction was applied. Throughout the session (each block in the experiments comprised 50 trials), drift correction was run 5 times. Prior to the analysis of the behavioral performance in the target discrimination task, the saccade size and latency were analyzed for each trial. Trials were excluded if the saccade performed was too short (<7 degrees of visual angle), or the latency was greater than 500ms or less than 100ms. With these criteria ~10% of the trials were discarded.

Procedure

Each trial began with two fixation points (0.29 deg/visual angle diameter) placed 5 degrees of visual angle to the right and to the left of the screen, one red (CIE coordinates: x = 0.41, y = 0.22; luminance = 5.4 cd/m^2) and one green (CIE coordinates: x = 0.23, y = 0.46; luminance = 5.5 cd/m^2), the color order was randomized on each trial (Figure 1.3A). Participants were instructed to fixate the green fixation point and press a button when ready to start the trial. After the button press, a rapid serial visual presentation (RSVP) of target and random masks were presented at a variable alternation rate.

On each trial the RSVP consisted of 34 mask + target repetitions. During the first 6 repetitions, target contrast increased linearly, starting at 1% contrast and increasing by 1% contrast each cycle until reaching the test level of 7% contrast. The cycle was then presented for 22 repetitions at the 7% contrast level and then ended with last 6 targets presentation dropping linearly in contrast (from 6 % till 1 % contrast). The linear increase and decrease of target contrast avoided a sudden onset or offset that might have artificially boosted identification of the target (Beaudot, 2002; Dakin & Bex 2002).

Each RSVP started and ended with the presentation of a noise mask. Each target or mask stimulus remained on the screen for 20 ms (2 flips) and the alternation rate was changed by varying the ISI between target and mask (Cavanagh, Holcombe & Chou, 2008).

After 17 repetitions of the mask and target, the colors of the fixation points were exchanged. On saccade blocks, this signaled participants to perform a saccade towards the new green fixation point.

Instead, on no saccade blocks, participants were required to maintain fixation on the initial fixation point even after the color change. The order of the two different saccade conditions was interleaved between blocks and counterbalanced across subjects.

The six levels of the ISI (20 ms, 40 ms, 60 ms, 100 ms, 150ms and 180ms) were randomly presented across trials within each block. After each trial the screen was blanked for 500ms and then subjects were requested to report the identity of the presented target.

Responses were given using keys 1, 2 and 3 on a keypad (“circle”, “diamond” and “square”, respectively, 3AFC task). A reminder of the key mapping was presented after each trial. Participants had unlimited time to provide a response after the trial.

Data Analysis

Data were analyzed as psychometric functions, plotting the discrimination performance for each ISI level on the two viewing condition: “saccade” and “fixation”, (Fig. 2.3). Psychometric curves were obtained using an approximate Bayesian inference method (Kuss et al, 2005) fitting a Gumbel function to the data and plotting ISI level on a logarithmic scale. As a lapse rate prior we used a beta distribution with □ = 2 and □ = 50. For the location parameter we chose a Gamma distribution with □ = 3 and □ = 1, whereas as prior for the width parameter we choose a log normal distribution with □ = 1 and □ = 1. Acceptance rates for 2500 MCMC (Markov Chain Monte Carlo) generated parameters across subjects ranged from 65% to 84%. Four participants were presented with 24 blocks of 12 trials each, for a total of 288 trials. Participants were tested in two non-consecutive days.

There was also an additional control experiment in which participants were required to maintain fixation during trial presentation. The masking sequence was made up of only two images: a single target and a single mask. On different trials, these stimuli were presented using either forward masking (mask followed by target) or backward masking (target followed by mask). In this control study two different ISI values (30 and 40 ms) were used, giving a 2 X 2 experimental design with masking type (forward or backward) and ISI (30 or 40 ms) as variables. Two separate blocks of 100 trials each were run for each participants, giving 200 trials overall, 50 trial for each condition. As in the main experiment, mean discrimination performance for each participant in each condition was computed (Fig. 2.3).

Results

The main result of the first experiment is that participants were more accurate at discriminating the target stimulus on saccade trials compared to trials with maintained fixation. Discrimination thresholds under the saccade condition were lower than at fixation condition, meaning that participants could correctly discriminate stimuli identity when the ISI between target stimuli and the mask was consistently lower than on fixation condition (Figure 2.3).

Threshold levels (estimated performance at 66%) on the saccade condition span between ~25 ms and ~53 ms, whereas when participants were required to maintain fixation the threshold range was between ~50 ms and 61 ms, estimates of participants precision (width of the curve) were stable within participants, ranging from ~50 ms for participant AF till ~170 ms for participant LP.

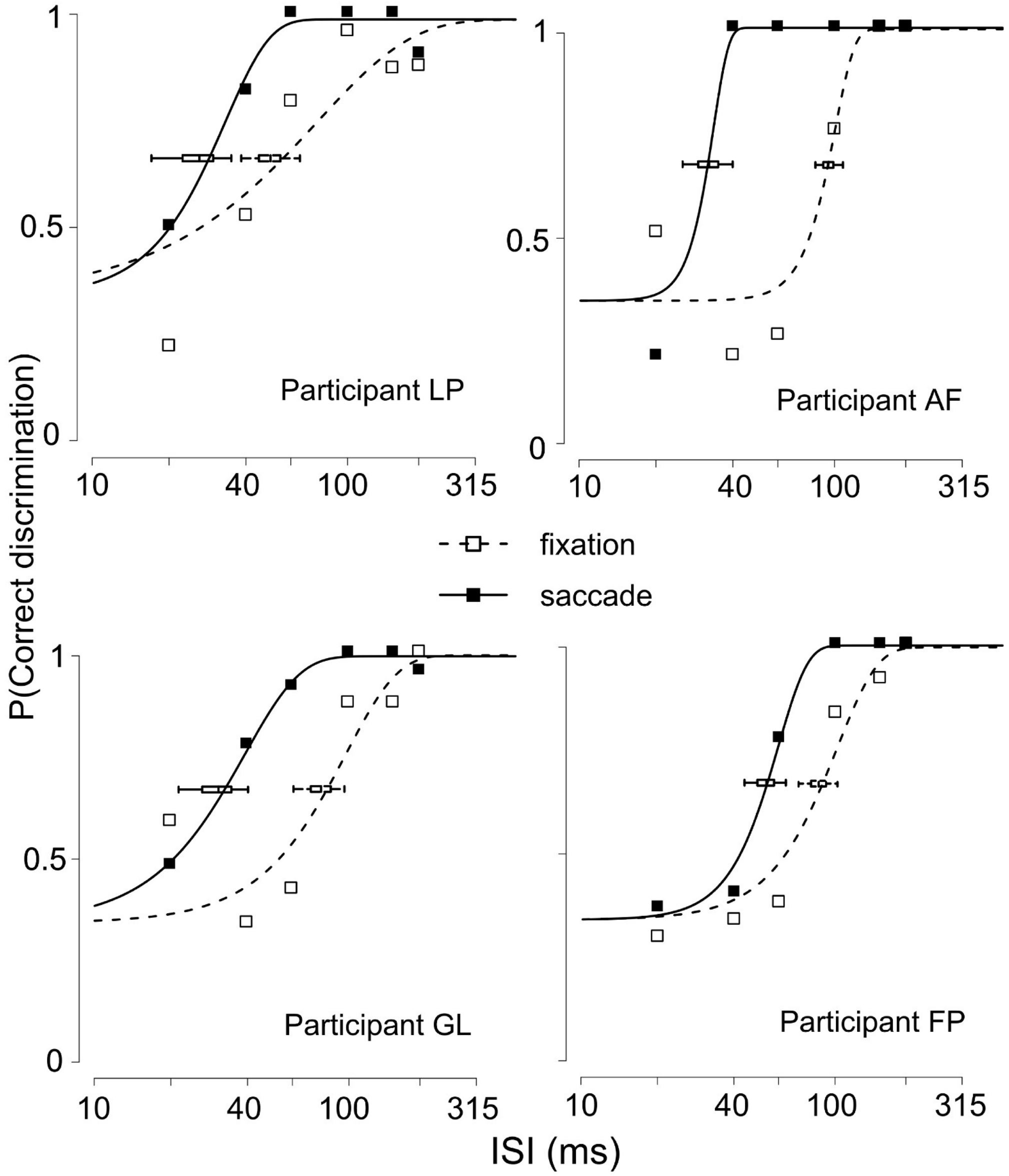

Figure 2.3: Performance in discriminating the target shape on saccade and fixation trials. When required to perform a saccade, participants were able to discriminate accurately the target at higher mask presentation rates (lower ISI between targets and masks) than when asked to maintain stable fixation during the RSVP presentation. Data is shown for four participants. Error bars show 95% confidence interval of the threshold parameter, based on 2500 MCMC bootstrapping repetitions.

The role of forward and backward masking

To better understand the role of the saccade in reducing RSVP masking we ran a control condition to examine the strength of the forward and backward masking components. The most effective masking effect was found with the forward noise mask with a 30 ms ISI (Figure 3.3). This finding was confirmed by the ISI x masking type interaction (logistic multilevel generalized linear model with participants as random factor, $z = -4.762$, $p<0.001$).

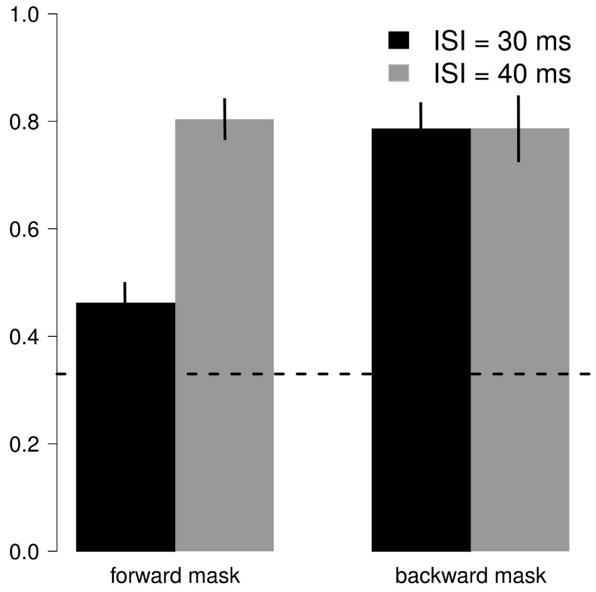

Figure 3.3: Target shape discrimination performance in the control experiment for forward and backward masking. Average results from 4 participants are shown. Error bars indicate one standard error of the mean

Discussion

The main finding of the first experiment was that making a saccade during the RSVP stream led to an “unmasking” of the target. The control experiment demonstrated that the forward mask, preceding the target by 30ms, was more effective than the backward mask. Thus, it would seem that at least some of the unmasking might occur due to the saccade starting in the interval between the forward mask and the target stimulus, leaving only the target and backward mask to be seen after saccade landing. In this way the effect of the forward mask could have been minimized by having forward mask and target in different retinal positions due to the eye movement. Alternatively saccadic remapping might have played an active role on the unmasking effect found on the previous experiment, leading to an increased discrimination performance, even though masks were not perceived as mislocalized towards saccade landing position given the high presentation rate and the extended duration of the RSVP before and after the eye movement. The aim of the second experiment was to discriminate between these two possible explanations of the unmasking effect.

Experiment 2: Spatial displacement of the mask

In the second experiment we tested whether the saccade might have interfered specifically with the efficacy of the forward mask. Specifically, the aim was to disentangle the roles of retinal displacement (the retinotopic location of the pre-saccadic and post-saccadic stimulus differs by 10 deg/visual angle) and peri-saccadic changes in visual processing.

Methods

Subjects

Five observers participated in experiment 2. All subjects had normal or corrected-to-normal vision. Informed consent was obtained from all subjects and the study was approved by the local ethics committee. Participants received a monetary reimbursement for their time.

Procedure

The trial procedure was similar to the first experiment with the following differences. First, only one masking sequence was adopted, namely forward masking (Figure 1). Second, after each trial two different questions were asked to the participant. Participants were asked to report both the identity of the stimuli presented (if perceived or to guess otherwise) and also to report the perceived location of the mask with respect to the target stimuli using keys 1, 2 and 3 on a keypad (“left to the target”, “same location as the target”, “right to the target”). Participants were instructed to respond “same location as the target” when they could not discriminate target stimuli.

Three different conditions were run with different masking parameters. In the first condition (experiment 2.1, Figure 4) ISI was set to 30 ms and both noise mask and the stimuli remained on the screen for 20 ms (2 flips). Each participant performed a variable number of 50 trial blocks, for a total number of trials per participant that ranged from 400 to 600 trials.

For the second condition (experiment 2.2, Fig 5.A) ISI was set to 10 ms and both noise mask and the stimuli remained on the screen for 10 ms (1 flip). Again, five participants took part in the second version, each performed a variable number of 50 trials blocks, for a total number of trials that ranged from 450 to 600.

In the third and last version (experiment 2.3, Fig 5.C) ISI was set to 0 ms (no ISI was employed) and both noise mask and the stimuli remained on the screen for 10 ms (1 flip), presented subsequently one after the other. Four participants took part in the experiment, each performed a variable number of 50 trials blocks, for a total number of trials that ranged from 400 to 600.

Data analysis

Masks were coded as mislocalized on those trials in which the reported location of the mask with respect to the target stimuli was congruent with saccade direction (e.g. saccade requested to the left, mask perceived to the left of the target stimuli), consistent with previous reports of mislocalization of briefly flashed targets presented along the saccade trajectory (Honda, 1989; Lappe et al. 2000; Matin & Pearce, 1965; Morrone et al. 1997; Ross et al, 1997; Ross et al. 2001).

For analysis purposes, the trials were sorted post hoc based on the saccade offset time. On experiment 3.1, the analysis of mislocalization reports was based on 30ms bins starting from 150ms before saccade onset till 90 ms after saccade onset (Fig. 4). For discrimination performance, trials were sorted into 30 ms bins starting from 90 before saccade onset till 150 ms after saccade onset. In a separate analysis, we focused on the perisaccadic interval examining discrimination performance on mis-localized trials and veridical trials using 20 ms bins ranging from 40ms before saccade onset till 60 ms after the saccade onset.

Before each session, a five point calibration routine was run and drift correction was applied. Prior to the analysis of the behavioral performance in the target discrimination task, the saccade size and latency were analyzed for each trial. Trials were excluded if the saccade performed was too short (<7 degrees of visual angle), or the latency was greater than 500ms or less than 100ms. With these criteria ~15% of the trials were discarded.

Results

Discrimination accuracy was highly dependent on the timing of the forward mask with respect to saccade onset (Figure 4.3). Figure 4.3A depict the timecourse of both mislocalization reports and discrimination accuracy around the perisaccadic interval for experiment 3.1 (masks and target stimuli remained on the screen 20 ms, ISI was set to 30 ms). When the mask was presented near the saccade onset time, participants reported seeing the mask in the wrong location, shifted towards the saccadic landing position. The proportion of mislocalization reports (triangles on Figure 4.3A) was greatest around saccade onset and rapidly decreased approaching baseline around 60 ms after the saccade onset.

Discrimination performance followed a similar pattern but the time course was delayed with respect to the mislocalization time course. The estimated delay between the two time courses derived from fitting a smooth spline on 1000 boootstrapped samples of the dataset is ~55ms, close to the SOA between forward mask and target stimuli set for the experiment (50ms).

Figure 4.C shows discrimination performance in the perisaccadic interval (20ms bins, from 40 ms before saccade onset till 60 ms after saccade onset) for mislocalized vs non-mislocalized trials. A multilevel logistic regression analysis with stimuli onset time and reported mislocalization as main variables and participants as a random factor revealed a main effect of stimuli onset time ($z = 7.750$, $p<0.001$) and a significant interaction between the two ($z = 2.269$, $p<0.05$). Post-hoc comparisons showed that a significant difference between mislocalized and non-mislocalized trials can be found for target stimuli presented right after saccade onset time (time interval: (0ms , 20ms], $z= 2.691$, $p<0.05$, with discrimination performance increasing from 50% till 75%), which would correspond to a mask presentation during the peri-saccadic time period. In contrast, if the improvement in performance had resulted from a change in retinal coordinates between the mask and the target, one would expect the largest benefit for trials in which the target was shown after the saccade offset.

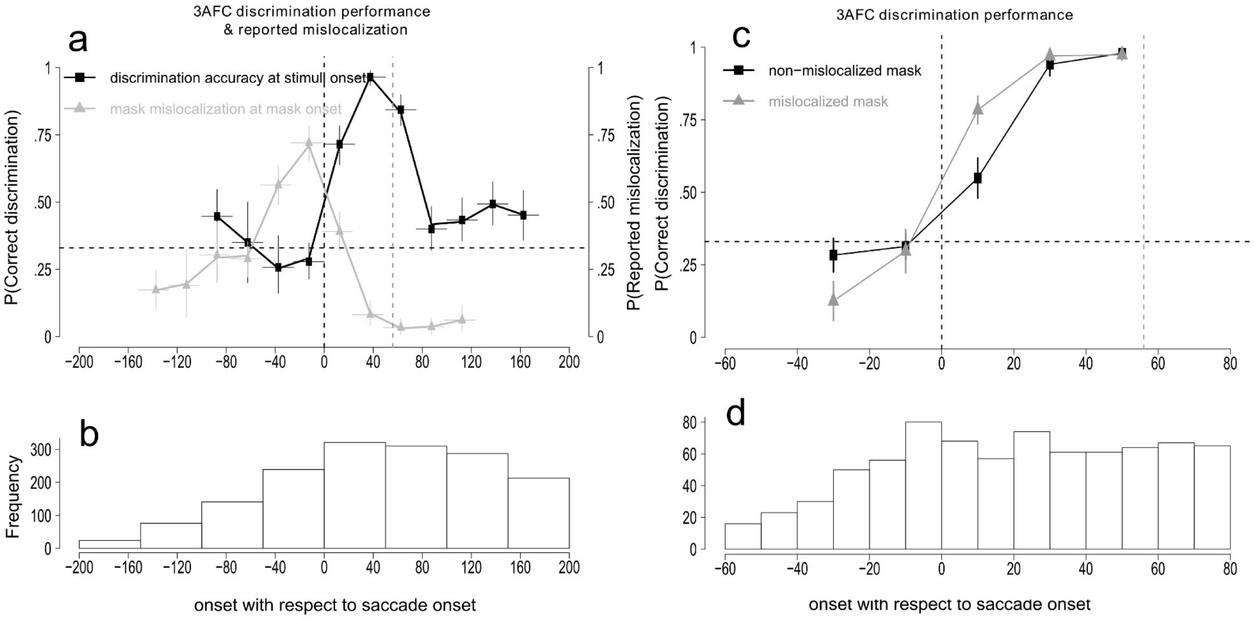

Figure 4.3: Results of the first condition of the second experiment, in which there was an ISI of 30 ms between the mask and target. A Shape discrimination performance and proportion of reported mask mislocalization around the perisaccadic interval. Vertical bars represent 95% confidence intervals based on 1000 bootstrapping technique (with replacement). B frequency histogram indicating the number of trials for each time interval around saccade onset time. C discrimination performance for stimuli presented around the perisaccadic interval separated for trials in which the preceding mask was reported as mislocalized (dark gray triangles) VS trials in which it was not (black squares). For the interval between 0 and 20ms after saccade onset time mislocalized trials yielded a better performance than non-mislocalized trials. D frequency histogram indicating the number of trials for each time interval around saccade onset time.

In order to more closely investigate the peri-saccadic time period, in the remaining two conditions the forward mask and target stimuli duration were reduced to 10 ms and the ISI was reduced to either 10 ms or 0 ms (no ISI between the stimuli), respectively. Again, discrimination performance started to increase around saccade onset time and reached a peak around 20 to 40 ms after the saccade, whereas mislocalization reports were greatest around saccade onset. Analysis of the 10ms ISI masking sequence revealed a significant difference in discrimination between mislocalized and non-mislocalized mask trials (multilevel logistic regression, z = -3.690, p<0.001, figure 5.3A) and a significant interaction between stimuli onset time and mislocalization reports ($z = 8.032$, $p<0.001$).

When the mask was reported as mislocalized, stimuli presented right after the eyes started to move were reported with an higher accuracy then for non-mislocalized masks (between 0 and 20 ms after saccade onset, post hoc contrast $z=6.851$, $p<0.001$). Moreover the difference is maintained also for stimuli presented after saccadic onset, when both mask and target stimuli were presented after saccade onset (between 20 and 40 ms after saccade onset, post hoc contrast $z=4.146$, $p<0.001$, and between 40 and 60 ms after saccade onset, post hoc contrast $z=4.123$, $p<0.001$).

These results were replicated also for the 0 ISI condition (figure 5.3C), in which case the difference in performance between trials with mislocalization and the other trials was particularly dramatic, since performance was at chance on all trials except for the time periods. Again, mislocalization reports started to increase right before saccade onset time and peaked when eyes started to move.

An analysis of the frequency of mislocalization revealed a main effect of stimuli onset time (multilevel logistic regression model, $z=2.035$, $p<0.05$) and a significant interaction between reported mislocalization and stimuli onset time with respect to saccade onset ($z=2.878$, $p<0.05$), Post-hoc comparisons shown that a significant difference between mislocalized and non-mislocalized trials can be found on those target stimuli presented on a time interval between 0 and 20 ms after saccade onset time ($z= 8.088$, $p<0.001$) and between 20 till 40 ms after saccade onset ($z = 6.909$, $p<0.001$).

To summarize, the different retinal positions occupied by the mask and the target due to the intervening saccade cannot explain why performance increased on those trials in which the mask was reported as mislocalized. The eye movement by itself can explain departures from chance level for targets reported as non-mislocalized (for example experiment 2.2, Fig 5.3A), but this is not the case, in general, for the mislocalized versus non-mislocalized difference along the perisaccadic time course.

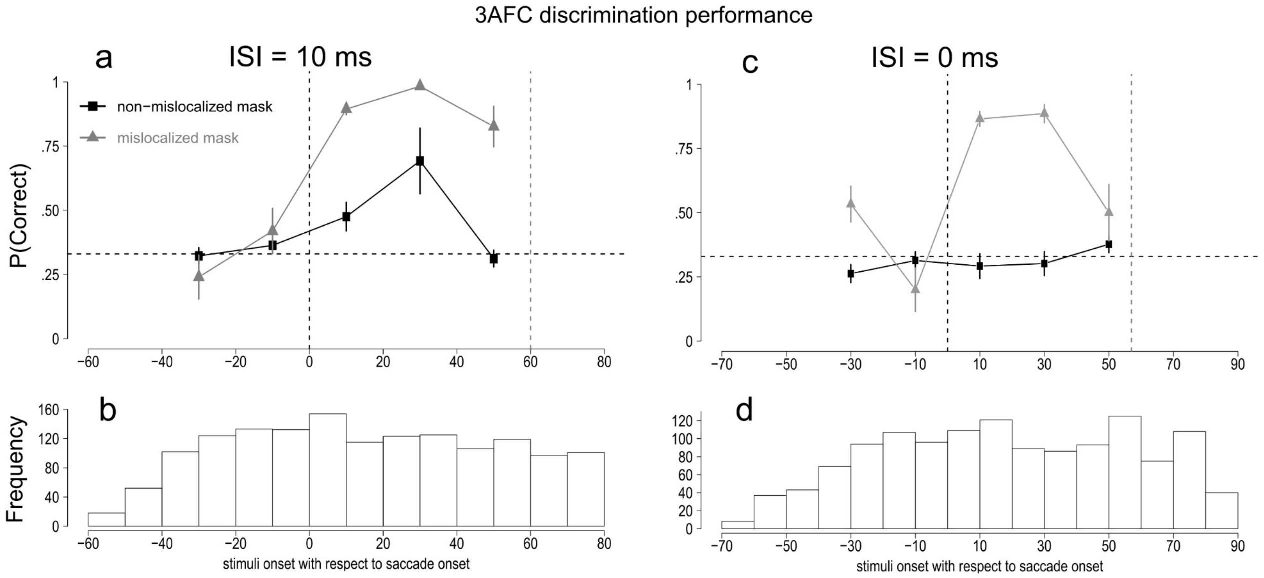

Figure 5.3: A Discrimination performance for stimuli presented around the perisaccadic interval for trials in which the preceding mask was either reported as mislocalized (dark gray triangles) or in which it was not (black squares). In this condition, ISI was set to 10 ms. B Frequency histogram indicating the number of trials for each time interval around saccade onset time. C Discrimination performance for stimuli presented around the perisaccadic interval separated for trials in which the preceding mask was reported as mislocalized (dark gray triangles) versus trials in which it was not (black squares), when ISI was set to 0 ms. D frequency histogram indicating the number of trials for each time interval around saccade onset time.

Experiment 3: Future versus Backward Remapping

In a recent theoretical proposal (Cavanagh et al, 2010) it has been argued that remapping activity is caused by shift of attentional pointers towards retinotopic coordinates that will cover the expected retinal post-saccadic location of the target (that is on the opposite direction of the impending eye movement). Here we test this proposal, referred to as the backward remapping hypothesis, figure 6.3, panels A and C). In contrast, other models of remapping have been based on shifts in receptive fields, such as increased sensitivity at the future receptive field (Hall & Colby, 2011) or compression towards the saccadic target (Hamker et al., 2011). Results of a recent study using backward noise masking has been interpreted as evidence in favor of the backwards remapping view (Hunt & Cavanagh, 2011). Specifically, they reported that masking increased during the perisaccadic interval for target stimuli shown above the landing fixation point when the backward noise mask was shown above the starting fixation point.

The authors of that study interpreted this finding as evidence that the target-related activity shifted towards a retinal position where there was a mask immediately before the impending saccade, that is the retinal location that the target will occupy after saccade completion, decreasing participants ability to report target identity. However both intracranial recordings on alert monkeys and human psychophysics suggest an opposite direction of the remapped activity following an eye-movement. Transient distortions of retinotopic receptive fields reported for stimuli presented during the perisaccadic interval are found along the direction of the eye movement (Kusunoki and Goldberg, 2003), consistent with the subjective experience of mislocalization along the direction of the eye movement (Ross et al. 2001).

In our experiment we report discrimination accuracy as a dependent variable, the interpretation of Hunt and Cavanagh (2011) could have also been biased by the nature of the dependent variable adopted in their experiment. The masking effect measure (their figure 4 on page 5) could suggest misleading interpretations, given that on different experimental conditions the baseline to obtain the resulting measure differs considerably.

As in our first two experiments, reported above, the mislocalization of the mask towards the direction of the impending eye movement (future remapping hypothesis) was taken as an index of remapping.

Following the logic of backward remapping, we implement the same design used by Hunt and Cavanagh (2011) with a forward noise masking sequence. As in their study, we presented the mask and target either on the same spatial location or in different spatial positions.

This would allow us to make specific predictions about the results based on future and backward remapping hypotheses in order to test the different proposals.

Based on the future remapping hypothesis, we would expect to replicate our previous experiments when mask and stimuli are presented on the same spatial position, namely higher discrimination accuracy for those trials when mask was presented during the perisaccadic interval, and would expect that the best performance would be found when the mask was reported as mislocalized along the direction of the eye movement.

If, on the other hand, backward remapping would occur, then we would also expect higher discrimination accuracy for perisaccadic presented masks on the same spatial position of the target. However, this higher accuracy should be found irrespective of whether the mask was reported as mislocalized or not. Moreover we would expect a selective drop on discrimination accuracy on trials in which the masks were presented above the saccadic landing position and the target was presented above the initial fixation point. This condition is the critical test of the backwards remapping hypothesis (Cavanagh et al., 2010; Hunt & Cavanagh, 2011). Since the mask is presented in the same post saccadic retinal coordinates as the subsequent target, and then should, according to the backward remapping hypothesis, decrease participants ability to discriminate target identity (Figure 6.3).

Importantly, the use of a forward, rather than backward, masking procedure avoids one of the potential confounds of the Hunt and Cavanagh study. The finding of reduced performance for targets presented near the future fixation position in their study may have been caused by the occurrence, typically reported in experiments with a flashed target such as theirs (Sogo & Osaka, 2001), that the target presented first would be mislocalized along the saccade direction and thus be further away from fixation and harder to see. Since participants were not asked to report the location of the target or mask on each trial in their study, we explicitly measured mislocalization on each trial to see if it would indeed occur under those experimental conditions.

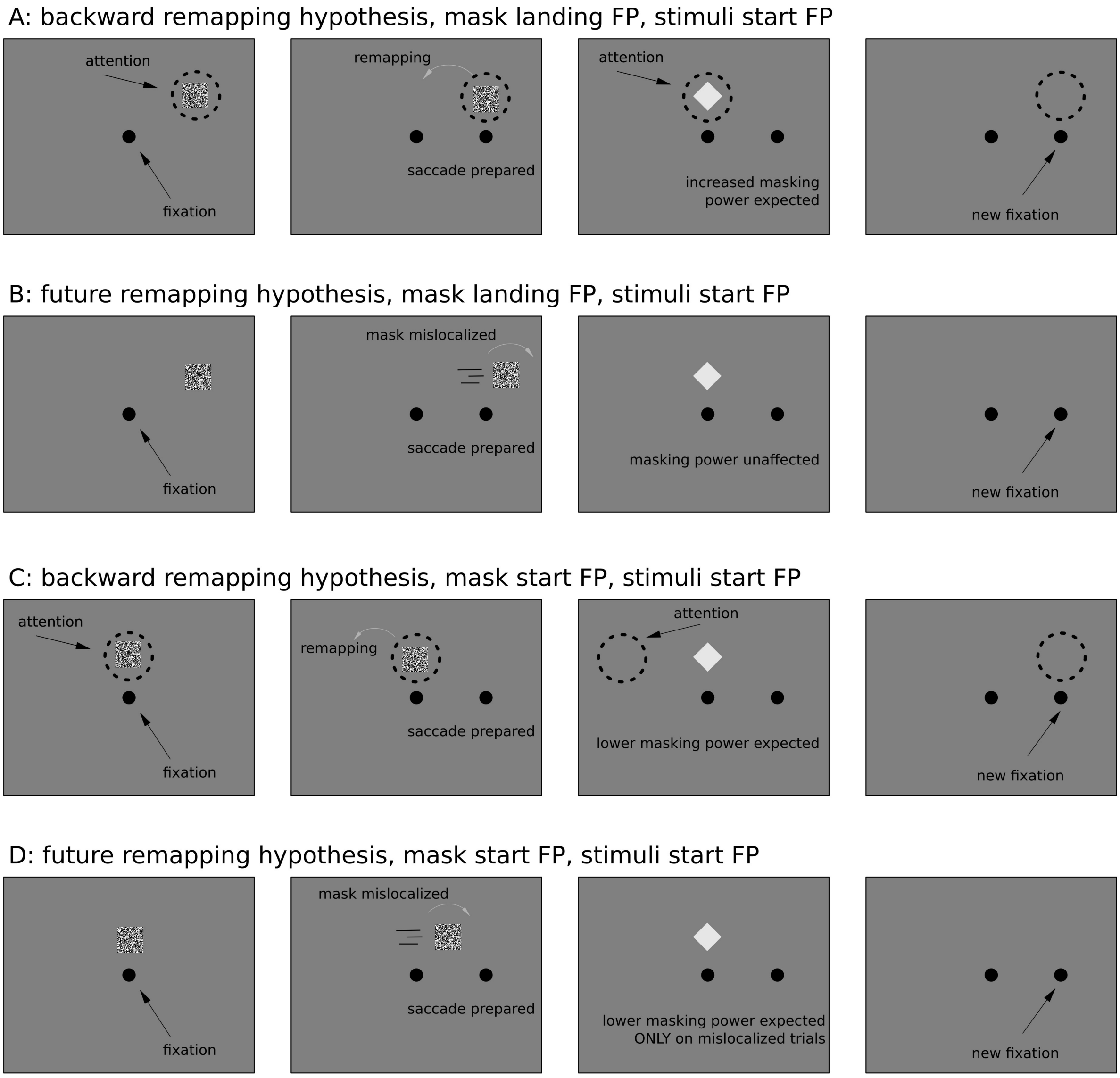

Figure 6.3: Future versus backward remapping hypothesis for different mask / stimuli spatial arrangements. A backward remapping hypothesis for mask at saccade landing position and stimuli at saccade starting position, masks presented during the perisaccadic interval are expected to be backward remapped towards mask post-saccadic retinotopic location, increasing masking power. B future remapping hypothesis for mask at saccade landing position and stimuli at saccade starting position, no masking effect is expected here since masks could be mislocalized along the direction of the eye movement, away from target stimuli. C backward remapping hypothesis for mask and stimuli at saccade starting position, unmasking of the target is expected in this condition, irrespective of whether mask is reported as mislocalized or not. D future remapping hypothesis for mask and stimuli at saccade starting position, unmasking of the target specific for mislocalized masks trials. Figure adapted from Hunt & Cavanagh, 2011.

Methods

Subjects

Five observers participated in experiment 3. All subjects had normal or corrected-to-normal vision. Informed consent was obtained from all subjects.

Procedure

The trial procedure was similar to experiment 2.1 except that the spatial arrangement of mask and targets could be presented in 4 different conditions: (1) both target and mask presented at the same spatial position 1.5 deg/visual angle above starting fixation point, (2) both presented at the same spatial position 1.5 deg/visual angle above landing fixation point, (3) the mask presented above the starting fixation point while the target was presented above the landing fixation point, or (4) the mask shown above the landing fixation point and the target presented above the starting fixation point. As with the previous experiment participants were asked to report both the identity of the stimuli presented (if perceived or to guess otherwise) and also to report the perceived location of the mask with respect to the target stimuli using keys 1, 2 and 3 on a keypad (“left to the target”, “same location as the target”, “right to the target”).

Data analysis

For analysis purposes, the trials were sorted post hoc based on the saccade onset time with respect to mask onset time. The analysis of discrimination performance was based on 50ms bins starting from 150ms before saccade onset till 50 ms before saccade onset for the four conditions (Fig. 8.3). For each of the four conditions a Bonferroni corrected single one-way within participants ANOVA was run with mask onset time as a linear predictor of subject performance. In a separate analysis, we examined discrimination performance on mislocalized versus non-mislocalized trials in the 100 ms bin ranging from 100 ms before saccade onset till saccade onset. Discrimination performance for mislocalized vs non-mislocalized trials were computed for each participant and the difference between the two conditions tested via a two sample paired t-test.

Results

Discrimination performance increased during the perisaccadic interval when both the stimuli and the mask were presented on the same spatial position (mask and stimuli above the starting fixation point: within subjects anova with mask onset time with respect to saccade onset time as linear predictor, $F(1,4)=27.25$, $p<0.001$; mask and stimuli above the landing fixation point: $F(1,4)=10.16$, $p<0.05$). Crucially, in these conditions accuracy increased selectively on trials where the mask was reported as mislocalized with respect to non mislocalized, consistent with the future remapping hypotheses (two-samples paired t-test, $t(4)=7.951$, $p<0.05$, figure 7.3).

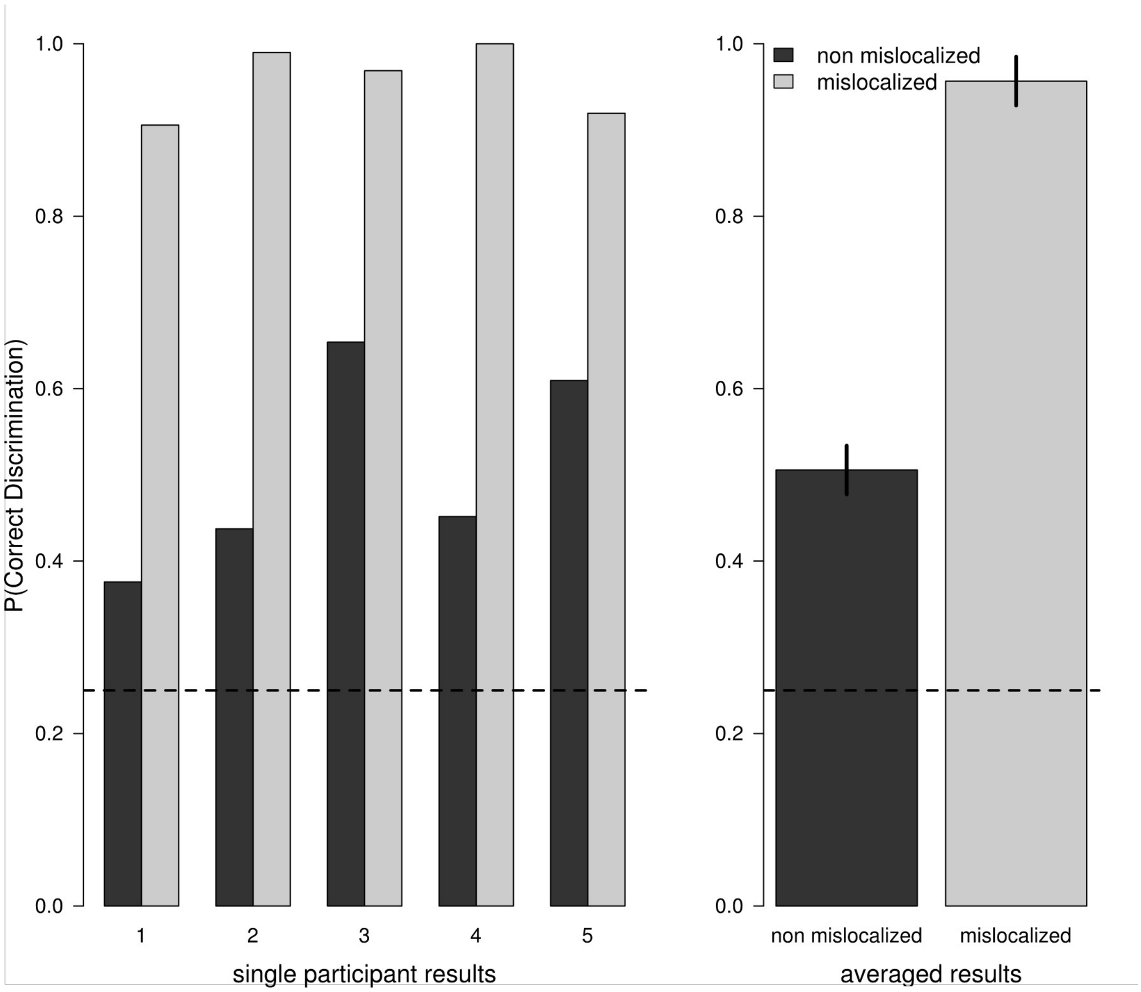

Figure 7.3: Discrimination accuracy for trials where masks was presented [-100, 0] with respect to saccade onset. Left panel, single subjects results for mislocalized VS non-mislocalized trials. Right panel, averaged results, 2 SEM after between-subject variability correction (Loftus & Masson, 1994) are reported.

Contrary to the backwards remapping hypothesis, the ability to discriminate target identity did not change significantly (F(1,4)=2.208, n.s.) in the crucial condition where the mask was presented right before saccade onset above the saccadic landing position and the target stimuli right above the starting position. Thus, the report of backward remapping reported under similar experimental conditions with a backward masking paradigm was not replicated here with a forward masking paradigm.

Perhaps most interesting was the finding that discrimination accuracy decreased in the final condition (Figure 8.3, where the mask was presented above the starting fixation point and stimuli above saccadic landing position (F(1,4)=31.94, p<0.05). This finding is consistent with various models and neurophysiological reports of future remapping (Hall & Colby, 2011; Hamker et al., 2011) but would not be predicted by the backward remapping proposal.

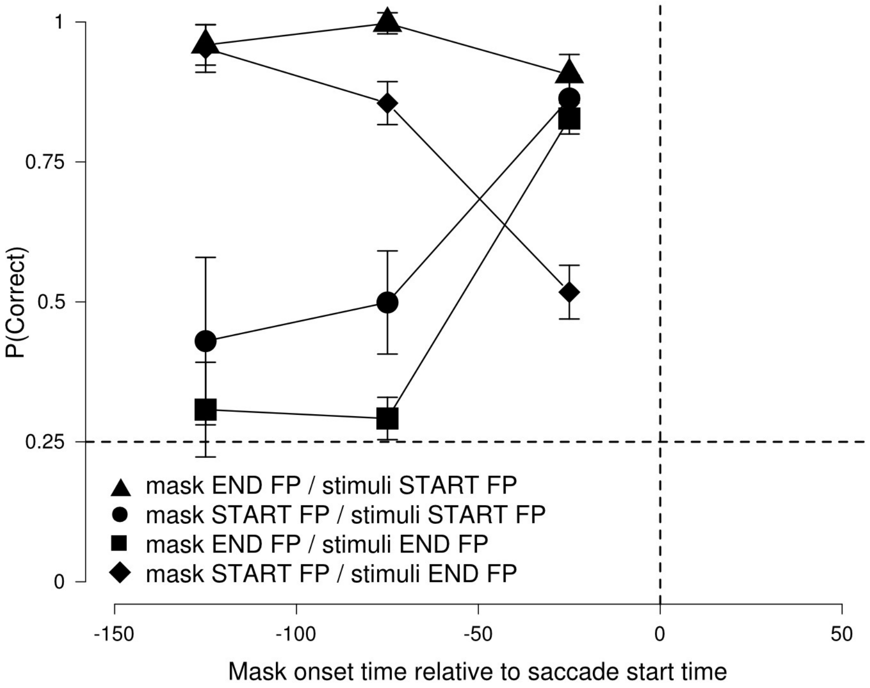

Figure 8.3: Results of the third experiment for each experimental condition based on the four possible ways to match mask and target locations. When mask and target stimuli were presented at the same spatial position (circles and squares), discrimination accuracy increased for perisaccadically presented masks. Performance did not drop when mask was presented above landing fixation point and stimuli above starting fixation point (triangles), as would have been predicted by the backward remapping hypothesis. 2 SEM after between-subject variability correction (Loftus & Masson, 1994) are reported.

Discussion

The results of the third experiment corroborated the future remapping hypothesis but found no evidence for the the backward remapping hypothesis. We replicated our previous results, showing that when mask and stimuli were presented on the same spatial position discrimination accuracy increased specifically for those trials in which the mask was reported as mislocalized whereas remained unchanged on non-mislocalized trials. Masks were considered as mislocalized if reported as shifted along the direction of the eye movement. Mislocalizing mask led to around ceiling target discrimination performance.

Considering the backward remapping hypothesis, we had expected to find decreased performance on those trials where the mask was presented above saccadic landing position but this was not the case and performance did not changed consistently along the perisaccadic interval. The intriguing finding of increased masking in the condition in which future remapping effects might occur cannot be explained by a simple drop in performance for targets presented around the time of saccades, since performance increased (there was “unmasking”) for targets presented in the exact same location (the saccade end point) in another condition (both mask and target at the saccade end point). Overall, the results support future rather than backward remapping.

General Discussion

We measured the influence of a 10°/visual angle horizontal saccadic eye movement on target discrimination performance on various conditions of a noise masking paradigm. In the first experiment, we found that performing a saccade while presented with a train of rapid alternating masks and target lead to improved discrimination with respect to stable fixation, even though participants did not report perceptual mislocalization. The goal of the second experiment was to further investigate the timing of this effect with respect to the peri-saccadic time window. In this case participants were requested to report both target identity and the relative position of target and mask after each trial. When a relatively long ISI was adopted (30 ms) we found higher discrimination performance for mislocalized rather than non-mislocalized masks around the time of eye movements, consistent with De Pisapia et al (2010). We further decreased the ISI between noise masks and targets and found that under these conditions the influence of the saccade timing became even more dramatic. In particular, when the ISI was set to 0, non-mislocalized trials around the perisaccadic interval never departed from chance level, whereas discrimination accuracy for mislocalized masks reached ~80%. Overall, the pattern of results reported here is consistent with an active spatiotemporal transformation in visual processing around the time of saccades (Binda et al., 2009) that is present even under conditions in which we do not notice any mislocalization. Building on these ideas, we provide evidence for these spatiotemporal transformations when when there is no perceived mislocalization.

One advantage of the unmasking paradigm is that it avoids the potential confound of previous studies which have used saccade-induced reductions in performance as the measure, such as in the saccadic suppression of displacement paradigm (Deubel et al, 1996) or recent reports of saccadic remapping of masking (Hunt and Cavanagh, 2011). It is difficult to interpret whether worse performance around the time of saccades in those tasks was actually caused by remapping itself or instead results from factors such as the addition of a second task (the need to shift attention and resources to perform a saccade), failure to align the pre-saccadic and post-saccadic information or even suppression of visual processing (Burr et al, 1994). Here we report that the saccade can dramatically increase target discrimination performance. In the case of the ISI of zero, we found that only in the peri-saccadic time period participants were able to perform above chance (around 80% correct in a 3AFC task).

One recent contribution on the relation between backward noise masking and saccade execution (Hunt and Cavanagh, 2011) reports a form of predictive retinotopic masking when a mask was presented on a location overlapping to the future retinotopic location of the target. This data is consistent with a remapping proposal in which activity shift right before the impending saccade on the retinal location that will be occupied by the object after the eye movement (Cavanagh et al. 2010). This idea, though intriguing, has been criticized both in terms of the nature of the remapped activity (Melcher, 2010) and also because it is not entirely consistent with the existing neurophysiological data (Mayo & Sommer, 2010). Transient distortions of retinotopic receptive fields reported for stimuli presented during the perisaccadic interval are found along the direction of the eye movement (Kusunoki and Goldberg, 2003), consistent with the subjective experience of mislocalization along the direction of the eye movement (Ross et al. 2001). Moreover, it has also been repeatedly shown that attentional benefits anticipating the execution of an eye movement are also in the direction of the intended action (Mathot & Theeuwes, 2011). In fact, target stimuli presented at the saccade landing position are better discriminated than in other locations (Kowler & Blaser, 1995; Bridgeman & Schneider, 1996a).

In the third experiment we selectively tested the backward remapping proposal employing our forward noise masking paradigm. First, we wound that when the mask was reported as mislocalized, then discrimination performance was considerably higher than for non-non mislocalized masks. Moreover, in the crucial condition identified as indicative of backward mapping (Cavanagh et al., 2010; Hunt & Cavanagh, 2011), discrimination accuracy remained constant during the perisaccadic interval.

The current results add further evidence to the basic question of how visual stability is achieved across saccadic eye movements (for review, see Melcher, 2011). Potential mechanisms include non-retinotopic receptive fields (allocentric or head-centered RFs), remapping of the spatiotemporal sensitivity of neurons via dynamic receptive fields (Duhamel et al, 1992; Kusunoky & Goldberg, 2003) or shifts in attention pointers with static RFs (Cavanagh et al, 2010).

Although there have been numerous reports of non-retinotopic receptive fields (d'Avossa et al, 2007; Duhamel et al. 1997), most of the relevant neurophysiological data, since the fundamental work of Duhamel et al. (1992), has been collected to characterize the behavior of retinotopic neurons around the time of the saccades. Those studies have shown that a consistent proportion of neurons in various visual and oculomotor areas of primate brain lose their fixed retinotopy right before the initiation of the eye movement, starting to respond to locations that will be occupied by the actual receptive field only after the completion of the saccadic eye movement, a phenomenon usually referred to as “remapping”.

Remapping has been shown in neurons in many visual areas both with neurophysiological studies on primate brain as well as humans using fMRI (Hall & Colby, 2011; Merriam et al. 2003, 2007). The proportion of cells (or voxels) showing remapping behavior increases as we move along the visual hierarchy, with the peak of remapping activity found mostly in LIP and FEF (Nakamura and Colby, 2000).

Kusunoki and Goldberg (2003) in particular studied the response of lateral intraparietal neurons (LIP) to stimuli briefly flashed around the onset of the eye movement and showed that the response shifted transiently as if the receptive field moved ahead of the actual saccadic movement.

Moreover this shift spreads over time decreasing the response for the actual (current) receptive field and increasing the response for the future RF as the saccade onset approached. This lead to the crucial finding that for a short time window right before the saccade, on average, the neuron responded more to the “future” than to the “current” receptive field. We believe that this neurophysiological evidence can be linked to our behavioural behavioural data since in our second experiment the same pre-saccadic event (the onset of the noise mask) resulted in substantially different percepts depending on whether the pre-saccadic mask was perceived as mislocalized or not. When mislocalization occurred, the target was almost always visible and when there was no mislocalization the target and mask were perceptually fused. It is important to note that the increased performance for mislocalized versus non-mislocalized reported masks in the second experiment was not limited only to those masks and targets presented right around the onset of the eye movement. Masks presented right after the onset of the saccade, and reported as mislocalized, also lead to clearly better discrimination performance than non-mislocalized ones. This latter finding underlies the transient nature of the remapping process which starts well before the initiation of the movement but develops continuously even while the eyes are moving.

It might be argued that the retinal displacement introduced by the eye in motion could explain this increased performance for masks presented after saccadic onset time. However an account based solely on the different retinal positions occupied by the mask and the target would not explain why performance increased only on those trials in which the mask was reported as mislocalized. At most, the relatively small increase in accuracy found for non-mislocalized trials (experiment 2.2, Fig 5.3A) could potentially be accounted by the eye movement in itself. But this is not the case, in general, for the overall trend in performance for mislocalized versus non-mislocalized trials which was found along the perisaccadic performance time course.

Overall, our findings are consistent with a spatiotemporal transformation (STT) across saccadic eye movements. Indeed, it has been shown that saccades can also grossly influence temporal judgments for perisaccadic presented stimuli (Morrone et al, 2005)

Binda et al (2009) reported how spatial mislocalization and temporal judgments around the perisaccadic interval are tightly coupled, showing high correlated temporal dynamics. This tight relationship suggests that stimuli presented around the saccade undergo a strong spatiotemporal distortion that presumably accounts for the remapping process in individual neurons.

These authors developed a model that simulates the perisaccadic distortion by orienting the spatial receptive field and their temporal latencies of neurons towards the future receptive field (the region of space that will be covered by the receptive field after the completion of the saccade).

A spatiotemporal transformation across saccades would change the subjective perception of space and time for briefly presented peri-saccadic stimuli, causing them to deviate away from the actual temporal and spatial parameters of the computer display. These changes would be expected to influence the masking paradigm used in our first experiment. Specifically, the STT would not only shift the spatial position of the mask with respect to the target, but also distort the temporal ISI at which stimuli were flashed. Indeed, such a model of the STT could explain the higher discrimination accuracy –in the RSVP task, as shown in Figure 9.3.

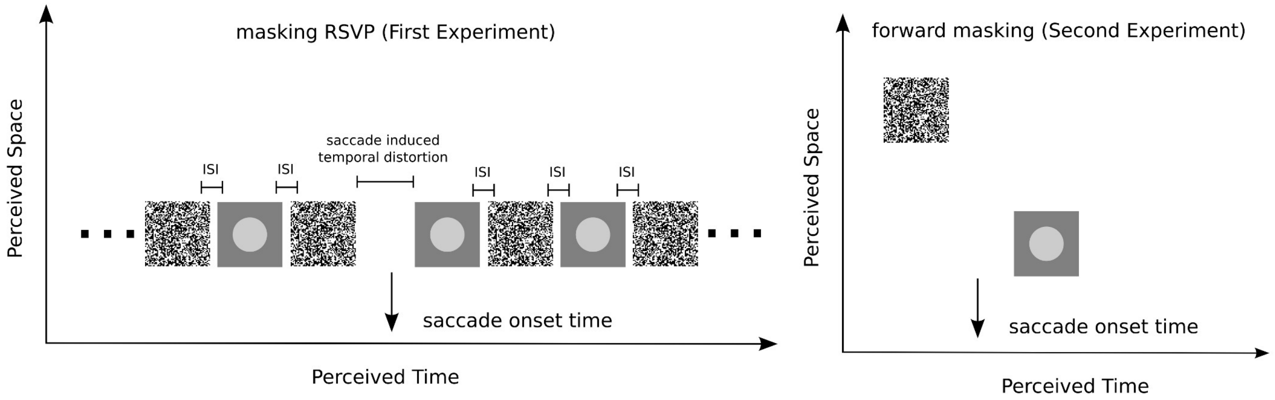

Figure 9.3: Illustration of a spatio-temporal transformation and how it might affect discrimination performance in our masking experiments. During RSVP presentation, the perceived spatial alignment of the train of stimuli would be maintained due to the extended stimulation in time which crosses over the duration of the eye movement. However, perceived time could still be influenced by the incoming eye movement, leading to a temporal distortion (distorted ISI) that leads to a better discrimination performance when required to perform the eye movement. During simple forward masking, without RSVP stimuli to anchor the stimulus in space, the spatial position of the mask would be expected to be mislocalized and participants would then reports masks as mislocalized towards saccade direction.

In conclusion our study characterizes the time course of mislocalization pattern across the eye movement with a novel paradigm using forward noise mask sequences. This method allowed us to report an objective behavioral measure that remarks the transient nature of the remapping process accompanying saccades.

Moreover we disentangled between two possible explanations of perisaccadic unmasking. Our results strongly support an active remapping process that involves a receptive fields shift (a "future remapping" hypothesis) rather than a backwards shift in an attentional pointer (backward remapping hypothesis).

Chapter 4

Remapping of the line motion illusion across eye movements

Under review as:

Remapping of the line motion illusion across eye movements

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Experimental Brain Research

Abstract

Although motion processing in the brain has been classically studied in terms of retinotopically-defined receptive fields, recent evidence suggests that motion perception goes beyond the limits imposed by a retinotopic reference frame. At present it is unclear whether non-retinotopic motion effects involve a transient remapping of retinotopic receptive fields, craniotopic or spatiotopic receptive fields, or are created by top-down attentional mechanisms. In this study we take advantage of a well known visual illusion (the line motion illusion, LMI), in which a straight line briefly shown after an high contrast stimulus (inducer) is perceived as expanding away from the inducer position. This illusion provides an interesting test of spatiotopic motion because the neural correlates of this phenomenon have been found early in the visual cortex and the effect is largely independent of attention. We measured the strength of LMI both with stable fixation and when participants were asked to perform a 10° saccade during the blank ISI between the inducer and line.

A strong motion illusion was found across saccades in spatiotopic coordinates. We varied the ISI between the inducer and the saccade cue in order to investigate the influence of saccade programming on the effect. When the inducer was presented near in time to the saccade cue, saccade latencies were longer, saccade amplitudes were shorter and the strength of reported LMI was consistently reduced. Together, these results suggest that motion perceived in non-retinotopic coordinates depends on an active, saccade-dependent remapping process.

Keywords

Remapping, line motion illusion, visual stability, eye movements;

Introduction

One of the major challenges for the visual system is to distinguish whether a motion signal on the retina was caused by motion of an object in the world, or rather by self-motion. An example is our ability to avoid moving obstacles while walking down the street. This capacity for visual stability is all the more mysterious given that the visual system encodes information in retinal coordinates (for review: see Melcher & Colby, 2008; Melcher, 2011). How do we successfully perceive motion in allocentric coordinates? There is recent psychophysical and fMRI evidence both for (Melcher & Morrone, 2003; d'Avossa et al. 2007; Ezzati et al. 2008; Ong et al. 2009; Fracasso et al. 2010; Zhang & Li, 2010) and against (Wenderoth & Weise, 2008; Knapen et al. 2009, Gardner et al. 2008) allocentric/spatiotopic motion processing. One hypothesis is that spatiotopic motion involves remapping in the specialized processing areas in the brain, such as V5/MT and MST, which are normally used to process motion in retinal coordinates (Melcher & Morrone, 2003;

Fracasso et al. 2010; Melcher, 2011; Biber & Ilg, 2011). An alternative hypothesis is that spatiotopic motion reflects a high-level attentional gradient moving through space (Cavanagh et al. 2010).

The line motion illusion (LMI) provides an interesting test of the nature of spatiotopic motion perception. This illusion occurs when a static line, shown shortly after an inducer (flashed stimulus) appears to radiate away from the location where the inducer had been presented (Figure 1.4A&B). This illusion is interesting for our purposes for three reasons. First, neural correlates of this illusion have been found in early visual cortex (Jancke et al. 2004). Cortical responses to the LMI, as measured by optical imaging in the cat, were found to move through cortex just like real motion stimuli. However, the feed-forward neural processing mechanisms hypothesized to underlie the LMI are found earlier in the visual system than spatiotopic effects have previously been reported (for review, see: Melcher & Colby, 2008; Berman & Colby, 2009). Second, the LMI cannot be explained by an attention gradient, since the illusion occurs even without selective attention to the inducer (Von Grunau, Dube & Kwas, 1996; Fuller & Carrasco, 2006; Blanco & Soto, 2009; Markwick & Corballis, 2010). Third, the LMI is an example of an event which unfolds over time (Eagleman & Sejnowski, 2003). Thus, it tests the role of trans-saccadic perception in supporting coherent event perception across gaze shifts (De Pisapia et al. 2010; Fracasso et al. 2010; Melcher & Colby, 2008).

To investigate the spatiotopic LMI, we measured the strength of the illusion, as a function of the inducer’s contrast, for trials in which the eye was stationary or in which a horizontal saccade was made during the ISI between the inducer and the presentation of the line (Figure 1.4C&D). We varied the timing of the stimuli with respect to the saccade to test whether the LMI effect was influenced by saccade timing, as would be predicted by a remapping explanation for spatiotopic motion perception.

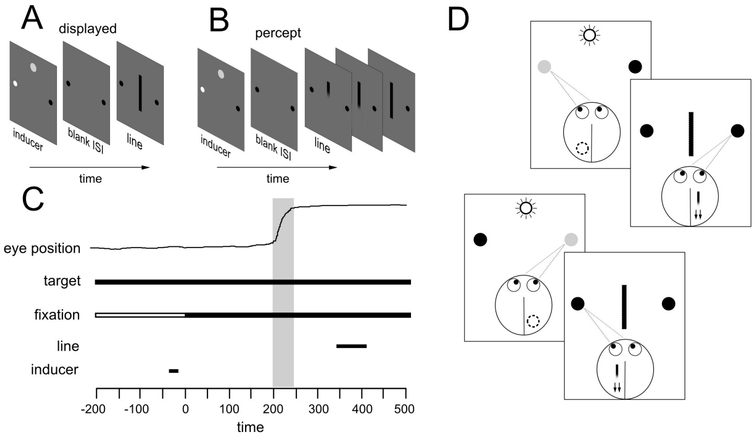

Figure 1.4: A. Illustration of the order of events in a sample trial. Fixation points are shown in white and black, with white indicating where the subject should fixate at the beginning of each trial and black showing the potential saccade target (during the experiment fixation points were green and blue, see Methods). On fixation trials, subjects maintained fixation on one point throughout the trial but on saccade trials were cued by a change in the color of the fixation point to make a horizontal eye movement during the ISI. B. Illustration of the line motion illusion. C. Timing of events during a saccade condition trial, along with a typical eye position trace. D. Sequence of events during a rightward saccade (up) and leftward saccade (down) trial, the inducer is shown before the initiation of the eye movement and appears in the opposite hemifield than the subsequent line, presented after eye movement completion.

Materials and Methods

Subjects

Twenty-two participants (19–32 years of age, 8 Females) participated in the experiments: the same eight participants took part in experiments 1a and 2, five (one author and four naïve subjects) in experiment 1b and ten in experiment 3. All subjects had normal or corrected to normal vision. They were all naive as to the purpose of the experiment and were paid for participation, except one author, AF, who participated in experiment 1a and 1b. Informed consent was obtained from all subjects before participation in the study, which was approved by the local ethics committee.

Experimental setup

Stimuli were presented on a gamma corrected Iiyama CRT 1900 monitor running at 85 hz (resolution: 1280 x 1024), except for experiment 1b where monitor refresh rate was set to 160hz at a resolution of 800 x 600. Subjects sat in front of the monitor at a distance of 57 cm, with their head fixed by means of a chinrest. Experiments were performed in a dimly lit room. Right eye movements were measured using an EyeLink 1000 Desktop Mount (SR Research, Ontario, Canada) sampling at 1 kHz. Software implemented in MATLAB controlled the stimulus display and response collection using Psychophysics toolbox (Brainard, 1997; Pelli, 1997) and EyeLink toolbox (Cornelissen, Peters & Palmer, 2002).

Data analysis

Data were analyzed with multilevel logistic regression (Jager, 2008; Baayen et al. 2008) implemented in the statistical software R which allows to fit categorical outcome variables accounting for random subject effects, and standard generalized logistic regression. For experiment 1b we fit logistic curves to obtain the point of subjective equivalence (PSE, point at which participants could not discriminate motion direction) on each condition, 95% confidence intervals of the threshold parameter were obtained by means of 1000 bootstrapped samples with replacement.

Procedure

Experiment 1a

All stimuli were presented on a uniformly gray background with an average luminance of 8.8 cd/m^2 (CIE coordinates: $x = 0.28$; $y = 0.31$). Each trial started with the presentation of two fixation dots 5° right and left of screen center (0.4° in diameter; one blue and one green; luminance, 13 cd/m^2, CIE coordinates: x = 0.18; y = 0.13 and x = 0.28; y = 0.58, respectively). Subjects were instructed to direct their gaze towards the green fixation dot (presentation side randomized across trials) and to press a button when ready. After acquiring a stable position for 500 ms (defined as the average detected eye position inside an area of 2x2 °/visual angle, around the initial fixation point), the trial started with a variable delay (between 500 - 1200 ms), at which point a small white disk, the *inducer* (0.8 °/visual angle diameter) was flashed for 2 frames (23ms) at a location 2.7 degrees of visual angle either above or below (randomized across trials) the center of the screen. The contrast of the inducer was chosen among 5 different levels (2%, 4%, 8%, 16%, 32%), randomized across trials. After a constant delay of 23 ms (2 frames) from the offset of the inducer stimulus, the color of the starting fixation point abruptly changed from green to blue. On fixation blocks, participants were requested to maintain fixation on the initial fixation point ignoring the change, while on saccade blocks participants were requested to perform an eye movement towards the opposite fixation point (10 °/visual angle amplitude) as soon as the starting fixation point changed color.

After 340 ms (29 frames), a black vertical line (0.27 x 4.86 °/visual angle, luminance = 0.25 cd/m^2) was presented at the center of the screen for 70ms (6 frames). Participants were then requested to report the perceived direction of the line motion (expanding towards up or towards down), if any, or to guess otherwise. Responses were re-coded for later analysis in 2 different categories, responses coherent or opposite with the line motion direction induced by the rapid flash. For each participant and condition the overall proportion of responses coherent with LMI were computed and analyzed.

After each trial the eye position for 150ms preceding the onset of the inducer and 50ms preceding the onset of the line was checked against the expected experimental conditions to ensure that the subject had followed the directions of that trial. After trials in which eye position was not within 2 degrees of visual angle of the correct fixation position, negative feedback was given to the participant and the trial was repeated at the end of the experimental block. Four blocks of 75 trials each (2 blocks for each viewing condition) were run for each subject. Before each block, a 5 point calibration sequence was performed and drift correction was applied after every 5 trials. During offline analysis, a trial was considered valid if the saccade reaction time was less than 300ms and the saccade amplitude was larger than 7 °/visual angle. Based on this criterion, 12% of trials were excluded from the subsequent analysis.

Experiment 1b

The procedure was similar to experiment 1a with the following exceptions: (1) we maintained a fixed inducer contrast (32%); (2) we introduced real line motion rather than only presenting a static line on all trials (see Fuller & Carrasco, 2009). On each trial, the line could be shown either all at once or divided into 5 or 8 increasing segments in order to replicate the percept of an expanding line (Fuller & Carrasco, 2009). Thus, there were 5 total conditions (-8, -5, 0, 5, 8), where 0 represents the whole line being presented in a single frame, the sign represents the direction of the expansion, negative towards down, positive towards up. Each frame lasted for 1/160 Hz (~ 6 ms) so, for example, a line that was presented in 8 frames (8 segments) towards up took 48 ms to expand completely from a short segment to the full line. The use of different real line motions allowed us to fit psychometric curves to estimate the point of subjective equivalence (PSE) between real motion and illusory motion. To generate these psychophysical curves, 10 blocks of 40 trials each (5 blocks for each viewing condition) were run for each subject. The number of leftward and rightward saccades, as well as the inducer position was balanced on each block.

Before each block, a 5 point calibration sequence was performed and drift correction was applied after every 5 trials. During offline analysis, a trial was considered valid if the saccade reaction time was less than 300ms and the saccade amplitude was larger than 7 °/visual angle. Based on this criterion, 7% of trials were excluded from the subsequent analysis.

Experiment 2

Procedures for the second experiment were identical to experiment 1a except for the following points: (1) only saccade blocks were run; (2) there was only one inducer contrast level, 32%; (3) two inducers were presented for 2 frames (23ms) on each trial prior to saccade execution. One of the two inducers was presented 2.7 degrees of visual angle either above or below (randomized across trials) the center of the screen, as in the previous experiments, while the second inducer was aligned with the line in retinotopic coordinates. Importantly, the vertical position of the spatiotopic inducer was always opposite to the retinotopic inducer (e.g. if the spatiotopic inducer was presented 2.7 deg/visual angle above the center, then the retinotopic inducer was presented 2.7 deg/visual angle below the center, and vice-versa, see Figure 2.4). In this way, based on subject response on each trial, we could disentangle between a spatiotopic and a retinotopic influence of the inducer on the illusorily line direction.

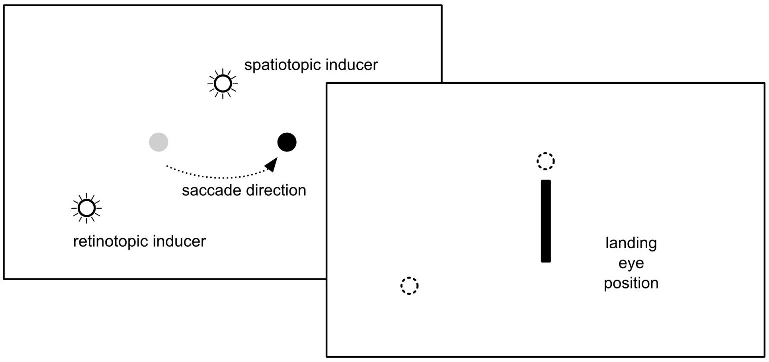

Figure 2.4: Illustration of the order of events in a sample trial (rightward saccade case) in the second experiment. On each trial, two inducers were presented in opposite positions (upper and lower part of the screen). After participants performed the eye movement and reached the landing eye position, the line stimulus was presented. The line was spatially aligned with the spatiotopic inducer and retinotopically aligned with the retinotopic inducer (that is, the retinal position stimulated by the retinotopic inducer is aligned with the bar after the completion of the saccade).

Experiment 3

Procedures for the third experiment were identical to experiment 1a except for the following points: (1) only saccade blocks were run; (2) there were only two inducer contrast levels, 2% and 32% (3) the ISI between the inducer onset and the request saccade signal was varied to be either 23 ms or 105 ms; and (4) the ISI between saccade offset and the onset of the line stimulus was varied, using gaze contingent displays, to be either 23 ms or 105 ms. Given that our design required controlling the ISI between saccade offset and line onset, we had to change the gaze contingent procedure in this experiment. When saccade onset was detected (velocity criterion of 30 °/second) a constant delay was added of ~60 ms (5 frames) to allow the eyes to complete the movement along the requested trajectory and then, after either 23 ms or 105 ms (according to the condition), the black vertical line (0.27 x 4.86 °/visual angle, luminance = 0.25 cd/m^2) was presented on the center of the screen for 7 frames.

There were 6 blocks of 32 trials each, with a 5 point calibration sequence at the beginning of each block and drift correction performed every 5 trials. During offline analysis a trial was considered valid if saccade reaction time did not exceed 300ms and saccade amplitude was larger than 7 °/visual angle. With this criterion, a mean of 15% of trials were excluded from the subsequent analysis.

Results

Experiment 1a tested the perception of the LMI as a function of the contrast of the inducer, for both fixation and saccade trials. As expected, the proportion of trials in which the participants perceived the motion illusion increased for higher contrast inducers (multilevel logistic regression, $z = 6.783$, $p < 0.001$, Figure 3.4A). On saccade trials, the overall proportion of illusory line motion perception was less than in fixation trials (multilevel logistic regression, $z = -4.110$, $p < 0.001$, Figure 3.4A). Viewing condition (saccade or fixation trials) interacted with inducer contrast ($z = -2.627$, $p < 0.05$). Post-hoc analyses revealed that fixation trials significantly differed from saccade trials for the lower inducer contrast levels of 4%, 8% and 16% ($z > 3$ for the three contrast values, $p < 0.05$). Given the variability in saccadic reaction time (saccade onset: Figure 3.4F), psychophysical data is plotted based on a median split based on saccade reaction time (median saccade reaction time = 185 ms), together with fixation condition results (Figure 3.4B). The proportion of trials with Illusory line motion perception was larger for fast saccade RTs trials than for slow RTs trials (logistic regression, $z = 2.730$, $p < 0.05$). With high contrast inducers and fast saccade RTs, the proportion of trials in which the LMI was perceived was similar for saccade and fixation trials (Figure 3.4B).

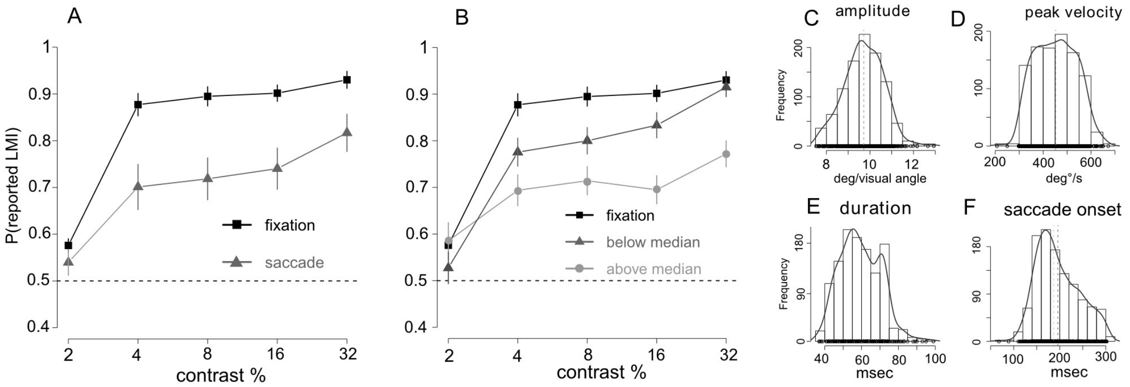

Figure 3.4: Proportion of trials showing the line motion illusion for fixation and eye movement trials in Experiment 1a, along with eye movement parameters. A. Reports of the LMI plotted as a function of inducer contrast, perception of the LMI increased with higher contrast inducers when participants were asked to perform a saccade between inducer and line presentation (triangles) as well as when they were asked to maintain fixation (squares). B. Median split of saccade condition trials based on saccade reaction time, showing that illusory motion perception was stronger on trials with faster saccades (triangles), whereas weaker LMI was found for slower saccades (circles), reported LMI from fixation condition re-plotted from panel a (squares). C-F. Eye movement parameters for the trials included in the analysis. Average data is shown for 8 participants. Error bars indicate 1 SE.

Experiment 1b measured psychophysically the strength of the inducer in the LMI in single fixation and saccadic conditions. Figure 4.4 shows the averaged data for five participants together with the 95% confidence interval of PSE estimate for each curve, based on a bootstrap procedure with 1000 samples with replacement. LMI strength was calculated as the mean between the estimates for the two inducer positions (upward and downward). The main result was that the LMI was found in both viewing conditions but was stronger at fixation than when participants were asked to perform a saccade during the ISI between inducer and line (mean estimate PSE fixation = 28.6 ms, mean estimate PSE saccade = 10.6 ms). This suggests that the perceived LMI was weaker, or perhaps slower, across saccades, consistent with the predictions of an active trans-saccadic remapping process.

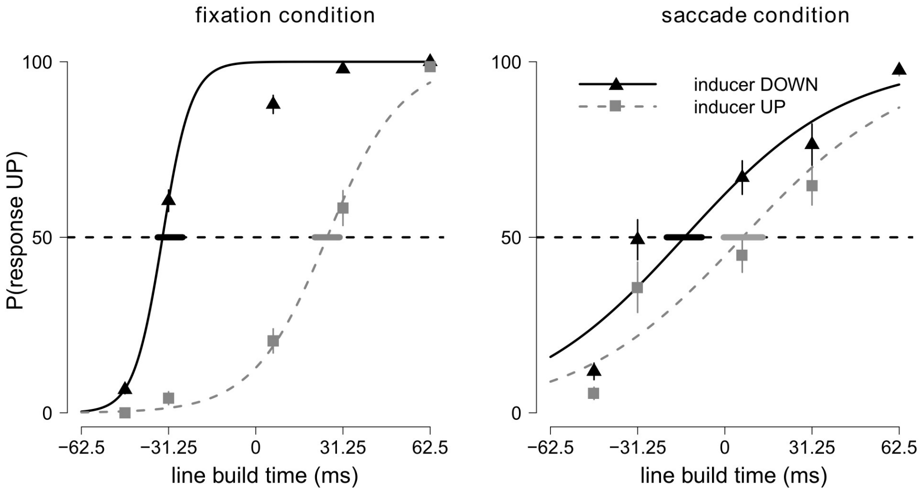

Figure 4.4: Experiment 1b results. When participants were asked to perform an eye movement (saccade condition panel) during the ISI between the inducer and the line presentation strength of inducer greatly diminished compared to a condition where participants maintained a fixed eye position while presented with LMI (fixation condition panel). 95% confidence intervals of PSE estimates based on 1000 bootstrapped samples are reported on each curve.

The second experiment indirectly tested whether participants preferred a spatiotopic or a retinotopic interpretation of LMI by showing two inducers on each trial which were compatible with different motion directions (see Fracasso et al. 2010 for a similar approach with apparent rotation motion). One inducer was *spatially* aligned with the line whereas the second was *retinotopically* aligned with the line (that is, the retinal position stimulated by the inducer was aligned with the subsequent line presentation after the saccade, see Figure 2.4). Since the two inducers were in opposite positions, they would trigger the illusion in opposite directions. Based on responses we could then derive an index of spatiotopic preference, based on the proportion of subject responses that followed the line direction triggered by the spatiotopic inducer.

Overall, participants tended to interpret the LMI according to the direction primed by the spatiotopic inducer (one sample t-test against chance level, t(7) = 2.519, p<0.05). Based on the observations of the influence of saccade RT in experiment 1a, we divided the data in two based on a median split (median onset time = 176 ms) and then computed the proportion of spatiotopic interpretation the fast and slow saccade reaction times. Results (Figure 5.4) shows how proportion of trials with spatiotopic line motion perception was larger for shorter saccade RTs trials than for longer RTs trials (t(7) = 2.4587, p < 0.05).

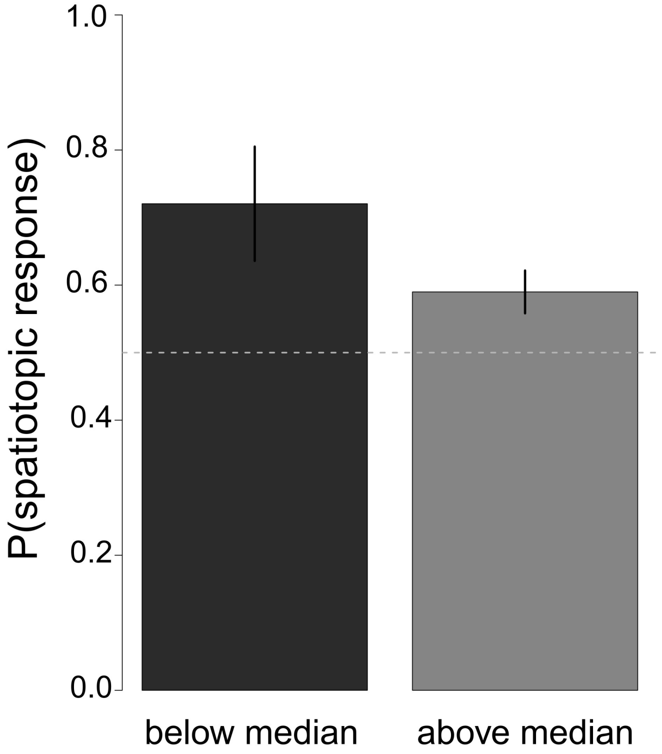

Figure 5.4: Experiment 2 results. Participants systematically reported line motion illusion direction towards the direction primed by the spatiotopic rather than the retinotopic inducer. The effect is magnified for shorter saccade RTs compared to longer saccade latencies (latency split based on a median split across participants, median onset time = 176ms) . Error bars indicate 1 SE.

In the third experiment, we further investigated the role of saccade timing on the trans-saccadic LMI to see whether the slow saccades resulted from interference from the flashed inducer on saccadic programming, such as might be expected based on the remote distractor effect (RDE: Walker et al. 1997; Bompas & Sumner, 2010), or rather that fast saccades allowed for more time, after the saccade, for remapping of the inducer to occur prior to the onset of the line (see, e.g. Mathôt & Theeuwes, 2010). On a given trial, the inducer was shown either outside of the typical RDE time window (105 ms before the saccade cue) or within the time window in which the RDE has been reported (23 ms before the saccade cue). Likewise, the timing of the appearance of the line after the saccade was varied, using a gaze-contingent display (see Methods) so that it was shown either just after (ISI = 23 ms) or well after (ISI = 105 ms) the saccade offset.

Consistent with the first hypothesis (RDE interference with saccadic programming), participants tended to see the LMI more consistently when the flash was presented well before the saccade cue (multilevel logistic regression z = 4.118, $p < 0.001$, Fig. 6.4 A). Moreover, flashing the inducer just 23ms before the saccade cue lead to slower saccades (two-tailed paired t test, t(9) = 5.77, $p < 0.001$, Figure 6.4B) and smaller saccade amplitudes (two-tailed paired t test, t(9) = 4.716, $p < 0.05$) compared to trials in which the inducer was shown 105 ms before saccade cue. No differences were found between inducer levels for peak velocity or duration of the saccade (t(9) = 1.451, ns and t(9) = -1.023, ns, respectively). The timing of the line with respect to the saccade offset did not significantly influence the LMI percept (multilevel logistic regression z = 0.98, *ns*). As in the previous experiment, inducer contrast had a significant influence of on the proportion of perceived LMI (multilevel logistic regression z = 4.639, $p < 0.001$).

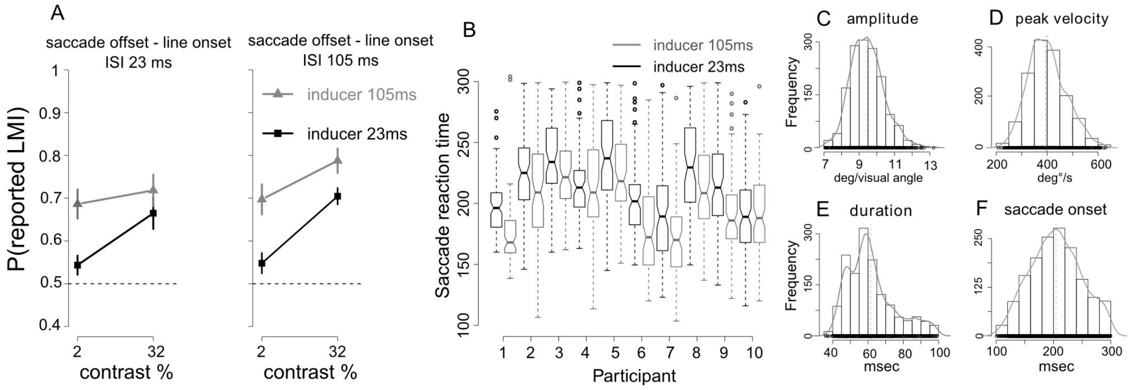

Figure 6.4: Proportion of trials showing the LMI as a function of inducer contrast, inducer ISI and line onset ISI, along with eye movement parameters for Experiment 2. A. Reports of the LMI increased as a function of inducer contrast and inducer ISI (interval between the inducer and the saccade cue), while the timing of line stimulus presentation after the saccade did not influence significantly the reports. B. Boxplot of saccade RTs for each participant on each inducer ISI condition. Saccade RTs were faster when the inducer preceded the saccade cue by 105 ms rather than only 23 ms. C-F Eye movement parameters for the trials included in the analysis. Average data is shown for 10 participants. Error bars indicate 1 SE

Discussion

Motion processing in the brain has been historically defined in terms of retinotopically-defined receptive fields. The line motion illusion, for example, has previously been shown only when the inducer and line were closely matched in both retinal and spatial coordinates (Kawahara et al. 1996; von Grunau, Dube & Kwas, 1996). In contrast, our normal experience of objects moving in the real world typically takes place while we are also moving our gaze and body. Although there has been recent debate over the existence of spatiotopic motion, it is important to note that the psychophysical evidence that motion perception can occur also in external coordinates is quite compelling (Rock & Ebenholtz, 1962) and easy to demonstrate using animated demos (see, e.g. Fracasso et al. 2010, Figure 1: http://www.journalofvision.org/content/10/13/14/media-2.medium.mov).

The current results show that the line motion illusion is seen in spatiotopic coordinates when a horizontal saccade causes the line to be shown in a different visual hemifield with respect of the inducer. The results cannot be accounted solely by the prior expectation about direction of motion given by the inducer position. In experiment 1b we measured trans-saccadic LMI with a cancellation method similar to the one implemented by Fuller and Carrasco (2009). Participants were able to correctly discriminate the physical line motion direction, and the effect of the LMI was additive to this perception of motion. Moreover, when participants were asked choose between a spatiotopic or retinotopic interpretation of LMI on the same trial we found a systematic preference for the former type of response. This preference was closely linked with saccade RTs, with shorter saccades RTs yielding larger proportion of spatiotopic responses than longer saccades RTs. This result speaks in favor of a spatially-constrained mechanism for LMI generation, where inducer and subsequent line need to be aligned and close in space to give a reliable motion impression (Kawahara et al. 1996; von Grunau, Dube & Kwas, 1996; Fuller & Carrasco, 2009).

The pattern of results suggests that an active remapping mechanism, which is closely linked to oculomotor programming, underlies the trans-saccadic LMI. Slower and smaller saccades resulted when the inducer and saccade cue were presented near to each other in time, consistent with the temporal dynamics of the remote distracter effect (RDE: Walker et al. 1995, 1997). The influence of the RDE on the saccade should disappear when the flashed stimulus is more than about 80 ms before the cue (Bompas & Sumner, 2010), as confirmed in our second experiment. It is interesting to note that previous studies have shown that the competition between potential saccade targets, such as occurs with the RDE, reduces the saccade-related signal in the superior colliculus (Munoz, Waitzman & Wurtz, 1996). Our results suggest that the RDE might also influence the degree to which the copy of the saccade command (efference copy) from the superior colliculus is used for saccadic remapping.

Although the LMI was initially described in terms of attention and high-level perception (Hikosaka et al, 1993), a number of subsequent studies have demonstrated that attention is not necessary for the effect (Von Grunau, Dube & Kwas, 1996). For example, masked inducers, which do not attract attention, still evoke the LMI (Blanco and Soto, 2009) and the illusion occurs even when multiple inducers are presented (Fuller & Carrasco, 2009). Likewise, inducers placed in the compromised hemifield of neglect patients induce the LMI (Markwick & Corballis, 2010). Also, the measure of the neural correlate of the LMI by Jancke and colleagues (2004), described above, was recorded in anaesthetized cats, precluding a strong role for top-down attention. Rangan and colleagues developed a model of V1 showing an LMI effect, without the need of top-down feedback (2005). Although a shift in attention to the saccade target would occur prior to the saccade (Kowler et al. 1995; Deubel et al. 1996), previous studies have shown that attention to the inducer is not required for the LMI to occur. Thus, it seems unlikely that our main effects were caused by attention to the saccade cue interfering with the LMI. The finding that the LMI was relatively independent of the timing of the presentation of the line after the saccade suggests a role for predictive remapping. A slow, post-saccadic mechanism, such as been suggested in some studies of attention (see, for review: Mathôt & Theeuwes, 2010) should have resulted in a weaker LMI when the line was presented just 23 ms after the saccade offset. Instead, our results are consistent with other recent studies showing a strong perceptual effect before, or immediately after, saccade onset (Melcher, 2007; Mathôt & Theeuwes, 2010; Pertzov, Zohary & Avidan, 2010). What neural mechanisms might underlie this predictive change in motion processing? A corollary discharge (efference copy) of the motor plan would seem to be required to explain predictive remapping (for reviews, see Crapse & Sommer, 2008; Sommer & Wurtz, 2006, 2008; Wurtz, Joiner & Berman, 2011). Recent evidence suggests a role for a corollary discharge pathway, going from superior colliculus to the medial dorsal nucleus of the thalamus to the cortical frontal eye fields, in the double-step saccade task (Sommer & Wurtz 2002, 2004). Another pathway from the superior colliculus through the pulvinar to areas of visual cortex, including MT/V5, might be more directly related to motion processing (Berman & Wurtz, 2008; Wurtz et al. 2011). At present, much more is currently known about saccadic suppression of motion than on saccadic remapping of motion (see, e.g. Bremmer et al. 2009). There is some recent work, however, showing that saccades qualitatively alter activity in MT and MST rather than just reducing it (Bakola et al. 2007; Ibbotson et al. 2008; Cloherty et al. 2010).

In conclusion, we demonstrate that the line motion illusion is remapped across saccades. In other words, the perception of the line stimulus shown after the saccade is influenced by the presentation of an inducer dot flashed prior to the saccade in the same spatial location (but different visual hemifield). These results challenge the notion that motion processing in areas such as V5/MT is strictly retinotopic. The LMI is a robust, easy to measure phenomenon which would lend itself to further study of the neurophysiological correlates of trans-saccadic motion perception.

General Summary

In this thesis I investigated the processes underlying mechanisms of visual stability in the visual system, by devising visual and visuo-motor tasks that required spatial updating and remapping across eye movements, the questions are whether and how the visual system maintain visual stability across eye movements.

First, if visual stability were just a perceptual illusion, then the vast majority of perceptual tasks should be severely impaired by performing saccades during performance, however this does not seem to happen in our everyday life in which we are constantly executing eye movements but nonetheless we are also efficiently moving in the environment, avoiding obstacles and performing goal-directed movements in a noisy environment, this observation leads to the second aspect: if eye movements were taken into account by the visual system in order to maintain visual stability, then the parameters of the movements can tells us something about the mechanisms and the strategies that the system employs to correct and update visual information across saccades. A related question pertain how the system takes into account this reafferent information. It could be that images from subesequent fixations are compared and matched in order to obtain the flow of continuity that is common in our daily perception, or information from subsequent fixations are integrated into a coherent percept. In this thesis I studied (1) the behavioral evidence that shows the actual cost (or lack of it) of spatially updating a visual stimuli across eye movements, (2) whether there are parameters in the saccade metrics that can correlate with that cost, linking directly participant performance on saccade properties and (3) the possible link between saccadic updating and pre-saccadic remapping.

In Chapter 2 I studied the trans-saccadic integration hypothesis by employing a novel paradigm, using a peculiar type of apparent motion sequence, namely transformational apparent motion (TAM, Tse et al, 1998). In order to perceive motion with this particular form of apparent motion sequence the system needs to parse and match elements from the two frames in order to integrate them into a coherent moving percept. We showed that this compelling form of apparent motion is relatively unaffected by performing an eye movement between the two subsequent frames, indicating that the process on integration of subsequent snapshots takes place also without a matching in retinal coordinates of visual stimuli.

The purpose of Chapter 3 was to study the relation between saccadic mislocalization and saccadic updating. The spatiotemporal transformation that takes place whenever we perform an eye movement (Binda et al, 2009) affects our perception also in the absence of saccadic mislocalization, moreover, in classical case of perisaccadic mislocalization studies, masking sequences has been proven to be easily unmasked by performing an eye movement. The time course of this phenomenon closely resembles the peri-saccadic shifts found in neurophysiology (from neurons in the frontal eye fields or lateral intraparietal sulcus). We took advantage of the stochastic nature of the mislocalization phenomenon by showing how target stimuli were easily discriminated on those trials when the mask was perceived as mislocalized. This situation changed consistently when the masks was not perceived as mislocalized, in this case participants performance departed only slightly from chance, indicating an actual integration of mask and target-stimuli into a single entity, even though presented in completely different retinal coordinates.

In Chapter 4 another apparent motion stimuli, the Line Motion Illusion (LMI) in which a straight line is perceived as expanding rapidly from a transient flash that temporally preceded the line. Again participants were tested either in the classical condition when the flash and the stimuli were aligned in spatial and retinal coordinates, as well as a condition in which they were aligned only in spatial but not retinal coordinates, by asking participants to perform an eye movement between the flash and the line onset. In this case an actual cost of the eye movement in the subjective reports was found, and this cost has been linked directly to the saccade reaction time. This effect links the saccadig updating mechanisms to the actual parameters of the eye movement, an index that the visual system takes into account the reafferent information starting from the visuo-motor system that informs the brain about upcoming oriented action.

The cost is evident in figure 4.4 where the psychophysical measure of line motion illusion strength was compared when participants were asked to maintain stable fixation or to make an eye movement between the frames. This decreased strength of the visual illusion across eye movements represents the additional computational effort that the system has to perform in order to integrate information from successive fixations. Neural signature of spatial updating across hemispheres has been studied using fMRI (Merriam et al, 2003), the present behavioral evidence builds upon that finding, showing that not only stimuli are updated across eye movements, but also that this updating influence the subsequent information impinging the retina after eye movement completion, integrating the two sources into a coherent percept.

Overall these studies shed light on the problem of visual stability and suggest that perception does not start anew with each fixation but instead is a continuum of information, updated each time we perform an eye movement. Moreover data suggests that visual stability is obtained by a process that not only matches visual input form subsequent saccades but actually integrates it giving rise to a coherent percept across multiple fixations.

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