Seen in a flash: spatial and temporal aspects in movement related (mis)localization

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Chapter 1

General introduction

It is amazing how our brain functions; even the simplest signal processes that we can think of are very complex. Luckily, we are not aware of all the processes that must be going on in our brain. In this thesis I will focus on how the brain combines self movement related signals from the different sensory organs of our body. This will be done from a behavioral perspective: by investigating human perception (the ability to detect structures (patterns) and events in the surrounding) while making fast eye movements or arm movements.

Eye movements

Once light falls on our retina, the light signals are processed in several brain areas to be able to construct a percept of the visual scene. When we are looking at the picture of the girl in figure 1 (Yarbus, 1967), we are not able to perceive the whole image of the girl at once. Rather there is only a small area of the picture that we can see sharply. So in order to perceive this whole picture we have to make eye movements to build an image in our head. A map can be made of the path of the eyes when a person is looking at this picture (figure 1). The map shows that the eye fixates at specific locations and makes many jumps from one location to another. In this thesis most chapters will only focus on this kind of eye movements: saccades.

Figure 1. *A photo of a little girl and a map of the path of fixations and saccadic jumps of one subject for three minutes (Yarbus, 1967).*

It is known that we make up to three saccades a second and that the peak velocity of those saccades depends on saccade amplitude. For saccades of 10 degrees of visual angle (1 deg ≈ 1 cm when the scene is about 60 cm distance from your eye) the peak velocity is about 300 deg/s (Collewijn, Erkelens, & Steinman, 1988). One can imagine that it is hard to describe the visual content of the scene when our eyes are moving at a velocity of about 300 deg/s. Our eyes move so fast that we are not aware of the saccades we make. We think that the visual scene at which we are looking is continuously visible. It can be compared to watching television; we don't perceive the 50 images per second, we think it is a continuous (changing) image.

This suppression of vision during saccades (e.g. Burr, Morrone, & Ross, 1994; Campbell & Wurtz, 1978; Ross, Morrone, Goldberg, & Burr, 2001; Watson & Krekelberg, 2009; Wurtz, 2008) could also be explained by the following example. When we look into the mirror we are not able to see our own eyes moving, however when someone else looks across our shoulder he or she will be able to see your eyes moving. The fact that you don't perceive your own eye moving suggests that vision is suppressed during saccades.

Experiments have shown that not all vision is suppressed during the saccade. Objects that are briefly presented during the saccade can be perceived. However, the location at which they are perceived is systematically misjudged when they are presented near the time of the saccade (Mateeff, 1978; Matin, Matin, & Pola, 1970; Matin & Pearce, 1965; figure 2). This phenomenon is called peri-saccadic mislocalization, and it is the phenomenon that is mainly studied in this thesis.

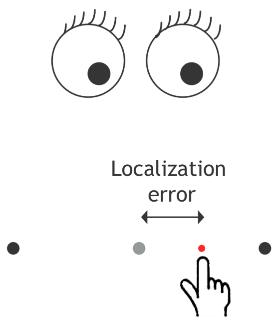

***Figure 2**. One trial of a saccadic localization task. The subject makes a saccade from the left black dot to the right black dot. Near the time that the eye starts to move a gray dot is flashed for a short time. Afterwards, the subject indicates the perceived location of the flash (red dot). The difference between the perceived location and the true location of the flashed target is the localization error.*

Peri-saccadic mislocalization

The perceived location of an object that is flashed near the time of a saccade depends on many factors. The first reports of systematic localization errors demonstrated that for experiments that were performed in a completely dark room the localization errors are independent of the flash location, which is referred to as a transient shift (Bischof & Kramer, 1968; Honda, 1989, 1990, 1991, 1993; Mateeff, 1978; Matin et al., 1970; Matin & Pearce, 1965). The apparent position of the flash was found to change less than 100 ms before saccade onset with a maximum error at saccade onset. Figure 3A shows an example of the time course of the mislocalization pattern with a transient shift.

Some decades later Ross and colleagues (1997) found a different pattern for each flash location when the experiment was performed in a normally lit room. When the flash was presented beyond the saccade target the perceived flash location was in the direction of the saccade target: we refer to this as a transient compression. Compression has also been found by others (e.g. Lappe, Awater, & Krekelberg, 2000; Maij, Brenner, & Smeets, 2009; Ostendorf, Fischer, Finke, & Ploner, 2007). All these studies showed slightly different patterns. It appeared that a transient shift was found when performing the experiment totally in the dark, whereas once visual references were visible after the saccade a transient compression was found (Lappe et al., 2000). Lappe and colleagues defined two measures to compare the mislocalization across subjects and conditions. The shift index was defined as the mean over the flash locations and the compression index was defined by the standard deviation of the flash locations. In the *Chapters 2, 3* and *8* we will also look at the compression and shift.

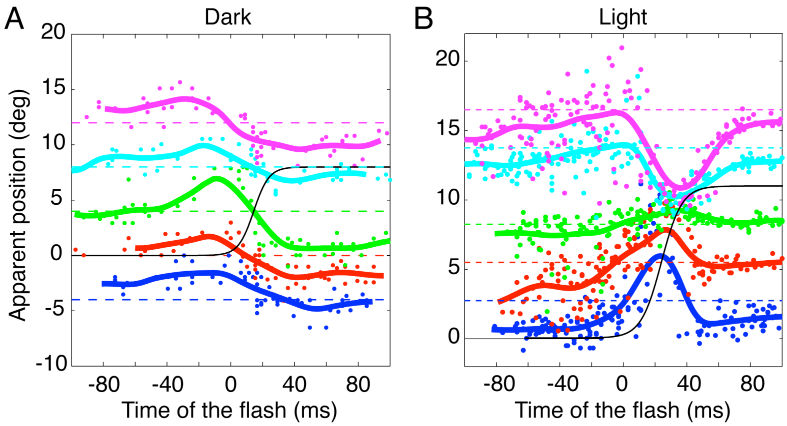

Figure 3. *Localization errors for each time of the flash relative to saccade onset in two studies: Honda (1991) (**A**), Maij et al. (2011a) (**B**). Each color represents a flash location (dashed horizontal lines). Dots represent the indicated positions on single trials. The colored curves through the data points are smoothed Gaussian averages of the data. The black line is a minimum jerk movement simulating the eye position (Flash & Hogan, 1985). Note that different flash locations and saccade amplitudes were used in the different studies and note the differences in the localization pattern.*

Recently, more studies revealed that slight variations in the experimental setup change the amount of transient compression and shift. For instance stimulus contrast (Michels & Lappe, 2004), stimulus luminance (Georg, Hamker, & Lappe, 2008), saccade amplitude (Lavergne, Vergilino-Perez, Lappe, & Dore-Mazars, 2010) and so on all influence the mislocalization. All these findings make it hard to understand what is going on. With this thesis I hope to convince you that (despite the variations in the experimental setup that I add) there is a way to reach some consensus on why people mislocalize briefly presented objects near the time of a saccade.

The chapters of the thesis are not presented in chronological order, but they are organized thematically. I have grouped the Chapters in two parts. The first three chapters will focus on the *spatial aspects* of mislocalization and the last four chapters will focus on the *temporal aspects* of mislocalization. The next sections will introduce these aspects.

Spatial aspects

As was mentioned earlier, visual references play a role when localizing flashes presented near the time of saccades. In *Chapter 2* we are interested in the role of the saccade target. It has been shown that during the saccade people do not perceive a jump of the saccade target of up to one third of the saccade amplitude (Bridgeman, Hendry, & Stark, 1975). Therefore we are interested in whether people localized flashes with respect to the new saccade target location as if the saccade target is used as a visual reference. We found that changing the location of the saccade target during the saccade resulted in a change in the perceived location of the flash; that is, flashes were perceived in accordance with their position relative to the saccade target. Furthermore, we demonstrated that the manipulation of the duration that the saccade target remained on the screen influenced the perceived location of the flash before and after the saccade.

When looking at an image we make many eye movements in unpredictable directions (figure 1). However, in many studies localization errors are investigated by asking subjects to make the same saccade over and over again. In *Chapter 3* we investigate the role of the predictability of the location of the saccade target by comparing the localization errors of random direction saccades and the same horizontal saccade over and over again. We did not find an effect of the predictability of the saccade target on the localization errors.

On page 9 I discussed that in order to perceive a stable world, perception is suppressed during saccades. In *Chapter 4* we study the origin of this saccadic suppression by changing the luminance contrasts in the background. We showed that people were not able to perceive a flashed bar during the saccade when there was a high luminance contrast between segments in the background. However when the luminance contrast was absent, people were able to perceive the flashed bar. This suggests that masking by moving luminance contrasts plays an important role in saccadic suppression. In addition we showed that the borders between the colored regions are used as a visual reference just before and after the saccade to localize the flash.

Temporal aspects

In the second part of my thesis I will focus on the temporal aspects of mislocalization. Before introducing the experiments, I will illustrate the importance of timing by an example. When I look out of the window of my room at the VU University there are many birds on a rail above my window. This time I see and hear a bird. It is quite amazing that I can perceive the sound of the tweet and I see the bird making the tweet at the same time, especially given the fact that auditory and visual information are processed with different time delays. So in order to perceive multiple sensory signals as originating from one event our brain needs to cope with different time delays of signals that are combined (e.g. the combination of the retinal and the extra-retinal information, or like in *Chapter 4* the tactile and proprioceptive information).

We propose that temporal uncertainty about the time of a flash underlies many of the peri-saccadic errors in localization. This proposal is further investigated in the chapters described in the following paragraphs.

If temporal uncertainty about the time of the flash underlies peri-saccadic mislocalization errors then people should also mislocalize objects that are briefly presented in other modalities, such as in the haptic modality. And indeed, this is what has been found before; people mislocalize stimuli that are presented in the haptic domain (Dassonville, 1995; Watanabe, Nakatani, Ando, & Tachi, 2009). So far, all studies that have investigated localization errors were performed in a laboratory setting. That is, in visual localization tasks a flash was presented on a screen (e.g. Lappe et al., 2000; Morrone, Ross, & Burr, 2005;

Ostendorf et al., 2007; Ross et al., 1997) and in haptic localization tasks people stimulated the finger with use of a small vibrator (Dassonville, 1995; Watanabe et al., 2009). All these stimuli are artificial, and in this chapter we wondered whether people would also mislocalize objects that they will touch themselves when making an arm movement. This can be compared to more natural conditions like for instance finding a light switch when you enter a dark room. When making arm movements across the wall, your hand is already at another location once you realize that you felt the light switch and you need to go back to the felt location of the switch. We will show that, indeed, people make localization errors under more natural conditions.

If the theory that uncertainty about the time of the flash underlies peri-saccadic mislocalization is correct, then it should be possible to influence the mislocalization by influencing the perceived time of the flash by additional sensory information, such as an irrelevant tone. We call the tone 'irrelevant' because the subjects were not instructed to do anything with this tone. The effect that the tone can alter the perceived time of a visual stimulus has been shown before (Morein-Zamir, Soto-Faraco, & Kingstone, 2003; Vroomen & de Gelder, 2004). If the tone and the flash are perceived as originating from one event, we expect the time of that event to be a weighted average of the times of the tone and the flash (Ernst & Bülthoff, 2004). In *Chapter 6* we study the effects of the tone on the localization errors. We found indeed that the tone caused the mislocalization curves to shift in time: the subjects mislocalized the flash as if the flash was presented closer in time to the tone. This demonstrates that additional temporal information (e.g. the tone) is taken into consideration when combining sensory information streams for localization.

The results of the two experiments discussed above stressed the importance of temporal aspects, but what happens if you combine spatial aspects (such as visual references in the background; e.g. a red and green segmented background) with those temporal aspects. Would it be possible that people perceive a flash that is presented on a red segment to have been presented on a green segment on the background? If people are uncertain about the time of the flash then people should perceive the flash to be presented on another segment, whereas if people use deformed spatial relationships (e.g. Ross et al., 1997) they would always perceive the flash on the segment on which it is presented. We found in *Chapter 7* that people readily perceived the flash on the wrong color of the segment. This shows that subjects don't use the color of the background in order to localize the flash. We created a model that explains the localization errors with the use of a temporal uncertainty about the time of the flash and a bias to believe that the flash was presented at the position at which our eye is looking.

This model is expanded in *Chapter 8* by showing the effect of changing the parameters on the localization errors (the width of the temporal uncertainty and the spatial prior to believe that the flash was presented at the location where the eye was looking). We also demonstrate that the saccade amplitude, and therefore also its duration, influences the localization pattern. With this model we are able to explain both the differences in the transient compression and shift across experiments.

Summary

The here described studies gained insight in the temporal and spatial aspects of localization near the time of eye (i.e. saccades) or arm movements. Taken together, these studies further enhance the knowledge of how the brain combines different sensori-motor signals.

Spatial Aspects