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## Updating spatial working memory in a dynamic visual environment

Boon, P.J.

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# Chapter 6

## Summary & Conclusion

Perceiving and interacting with the visual world around us often seems effortless. Subjectively, we perceive a constant, stable and complete panorama of our surroundings, and we hardly ever experience any problems keeping track of relevant objects while moving through the environment. This is quite intriguing considering the way our visual system is organized. Our brain is not capable to process all information at the same time, so we constantly have to determine which information is the most relevant and should be selected for further processing.

Luckily, we have developed a sophisticated eye movement system. By directing our eyes to the most relevant locations in a scene, they act as the first and foremost filter for visual information. In everyday life we are seldom aware of these rapid movements. Instead of deciding where to move our eyes next, we almost automatically look at the locations containing the most relevant information. But how does the brain decide which locations are the most interesting? And how do we keep track of these locations if while constantly moving our eyes to different locations? Each of these eye movements causes objects in a scene to fall on a different part of the retina, and thus be represented by a different set of neurons. Despite these continuous changes in sensory input we are able to interact with the world around us with impressive accuracy.

In this thesis I studied some of the mechanisms by which the brain keeps track of the most relevant information in the visual environment. In a number of chapters the role of the eye movement system in maintaining spatial information (Chapter 2), the mechanisms underlying the updating of this information during both self-induced (eye) movements (Chapter 3 and 4) and during movement of objects in the world around us (Chapter 5). The main conclusions from my research are summarized below.

### **Motor structures play a crucial role in representation and maintenance of spatial information.**

To be able to efficiently navigate through our environment it is crucial to temporarily store information about the positions of relevant objects around us (spatial working memory). Some authors have argued that working memory might be best described as persistent activity in any of the brain areas involved in the translation of sensory information into the most suitable response (Christophel et al., 2017; Postle, 2006; Zimmer, 2008). Depending on the precise requirements of a task, information might be represented at any stage of this sensorimotor continuum (Christophel et al., 2017; Zimmer, 2008). Detailed sensory information

might be represented in the sensory areas (Harrison & Tong, 2009), while the prefrontal cortex may play a role in the maintenance of more abstract information (Freedman, Riesenhuber, Poggio, & Miller, 2001). The research described in this thesis contributes to the body of evidence demonstrating that the ability to maintain spatial information over short periods of time relies to a large extent on the same mechanisms used to plan and execute actions (Belopolsky, 2015; Theeuwes et al., 2005). The location of an object is memorized by maintaining the motor plan that will eventually be used to act upon it. This way, the motor plan acts as a pointer towards the most relevant objects in our environment. Such prospective motor coding is the most efficient way to represent the location of an object.

This prospective motor coding idea is in line with theories describing the intricate relationship between attention and the eye movement system, like the premotor theory (Klein, 1980; Rizzolatti, Riggio, Dascola, & Umiltá, 1987) or Visual Attention Model (VAM; Deubel & Schneider, 1996; Schneider, 1995). The premotor theory for example, posits that covert attention is in fact a consequence of the preparation of an eye movement. To test the functional coupling between eye movement preparation and covert attention a number of studies have used the *eye abduction* paradigm. It was shown that the physical inability to move the eye to a stimulus resulted in reduced performance in perceptual tasks. In **Chapter 2** I demonstrated that this manipulation also affects how strong a visual stimulus is represented by the oculomotor system. When the eye abduction procedure rendered eye movements to a stimulus impossible, this stimulus also evoked less activation in the oculomotor system, resulting in a decrease in competition with a saccade target.

A question that remains is to what extent the oculomotor system has a privileged role in the maintenance of spatial information. Note that the premotor theory posits that covert attention is an emergent property of movement planning, which is not per se limited to the eye movement system. Locations can be represented in any effector system, depending on the task or goal of the observer (Rizzolatti & Craighero, 1998; Rizzolatti et al., 1994). In line with this, several parietal regions are involved in the transformation of sensory input into maps that code for action intention of different effector systems (Duhamel, Colby, & Goldberg, 1998; Ferraina et al., 1997; Murata et al., 2000).

On the other hand, there is also reason to assume that the oculomotor system is special with regard to the representation of spatial information. First, its retinotopic nature allows for a straightforward translation from perceptual

information into action codes. Second, in everyday life most actions are preceded by an eye movement. Try grabbing your cup of coffee standing next to you, and you will notice that even before your hands start moving your eyes have probably already fixated it (Land & Hayhoe, 2001). In line with this, it has been suggested that our eye movements work as *deictic pointers* (Ballard et al., 1997). By indexing the object that has to be acted upon, this strategy frees up resources that would otherwise be necessary to hold things in mind. In this way, perception and motor control can be vastly simplified.

Of course, isolated eye movements are rather rare during normal orienting behavior. Instead, gaze shifts are usually accomplished by combined eye and head movements. Interestingly, both appear to be controlled by the same mechanism. The SC not only codes for eye movements but is also involved in the control of other forms of motor behavior such as head and arm movements (e.g. Freedman, Stanford, & Sparks, 1996; Guitton, Crommelinck, & Roucoux, 1980; Roucoux, Guitton, & Crommelinck, 1980; Stuphorn, Bauswein, & Hoffmann, 2000). In fact, it might be better to get rid of the term oculomotor system and replace it with the more suitable *gaze motor system*. The remaining oculomotor competition in the abducted field in the experiments described in **Chapter 2** might also have resulted from the preparation of a head movement. However, the fact that the strength of this competition is significantly decreased indicates that, at least in the current experimental setup, these forms of movement are not completely interchangeable.

A related question is, if one assumes that attention and spatial working memory are relying on the same oculomotor circuitry, in what way do they differ from each other? My own view is that both concepts are closely intertwined and very much akin. Exogenous attention, endogenous attention, and spatial working memory all rely (at least to a certain degree) on oculomotor mechanisms, and are in some way part of oculomotor behavior. Exogenous attention might, in fact, be best described as an intrinsic part of the oculomotor act itself. Every saccade is accompanied by a presaccadic shift of attention towards the target. The enhanced processing of the future saccade target enables the storage of information about this target in transsaccadic memory (Currie et al., 2000; Irwin & Gordon, 1998). As eye movements are quick but sloppy, this information can then enable swift corrections upon saccade landing (Hollingworth, 2007; Irwin & Zelinsky, 2002; McConkie & Currie, 1996). Endogenous attention and spatial working memory might rely on the same oculomotor architecture, but function in a somewhat different way. It appears that retinotopic oculomotor maps are utilized as some

kind of priority map, in which sustained activity codes for the locations of the most relevant objects in a scene. This way, relevant locations can be maintained as potential future targets for eye movements. Endogenous attention and spatial working memory may very well be two sides of the same coin. Although the function of endogenous attention is not to maintain spatial information but to enhance processing at a location without making an eye movement, it shares most features with spatial working memory (voluntarily, sustained over a longer period of time). However, it is hard to determine its ecological function outside of the psychology lab. As discussed in the Chapter 1, when we want to extract detailed information about a certain object it is much more efficient to move our eyes to that location. Although it has been argued that there is some social function (Laidlaw, Rothwell, & Kingstone, 2016), it might to a large extent be an artifact of the peculiar task instructions of our own experiments.

**Transsaccadic updating relies on a combination of extraretinal and retinal information and the time available to integrate them.**

**Chapter 3** focusses on the question how different sources of positional information contribute to the updating of memorized spatial information across eye movements. Traditionally, there are two dominant views on this topic. The first group of theories emphasizes the role of extraretinal signals that are used to compensate the displacement of retinal image induced by the eye movement (Helmholtz, 1867; Holst & Mittelstaedt, 1950). Consistent with this idea are phenomena like the remapping of neural activity in oculomotor areas (Duhamel et al., 1992) and predictive shifts of visual attention around the time of a saccade (Jonikaitis et al., 2013; Rolfs et al., 2011, see also Chapter 4). Others argue that even though there is quite some empirical evidence for the existence of a cancellation mechanism driven by the extraretinal signals, this information is ordinarily discarded in normal perception. Instead, the visual system relies on the null hypothesis that the visual world is stable across saccades. As long as there is a rough match between pre- and postsaccadic stimulus location and identity, the visual world is realigned with these objects even if large intrasaccadic displacements occur (Deubel, 2004; Deubel et al., 2010; Germeys et al., 2004).

Instead of relying on a single source, it has been argued that updating might be driven by a combination of extraretinal and retinal signals. The relative contribution of these sources of positional information is modified depending on the reliability and precision of both signals. The visual system optimally integrates sensory and motor information attain the most reliable estimate of the postsaccadic locations of objects (Byrne & Crawford, 2010; Niemeier et al., 2003).

The results described in **Chapter 3** of this thesis are in line with this idea. Neither extraretinal nor retinal information is dominant when calibrating the postsaccadic location of a memorized object. More importantly, the results show that timing might be a very important factor in determining their relative contribution. Although retinal information is more precise it takes considerable time to integrate new input upon saccade landing. Only if behaviour does not necessitate a fast response do these signals influence subsequent action. This is illustrated by the work described in **Chapter 5**, which involves updating a memorized location on a moving object. In this case, extraretinal signals are not available, and a perceiver has to rely on visual input in updating the location. This resulted in a more gradual updating of oculomotor competition.

### **Endogenously maintained information is rapidly updated across saccades.**

The results described in **Chapter 3** and **4** demonstrate that endogenously maintained information can be rapidly updated across saccades. Shortly after an eye movement, oculomotor competition resulting from the maintenance of a location in memory is represented in spatiotopic coordinates. This resembles the timecourse of updating oculomotor activity elicited by simply showing a salient distractor (Jonikaitis & Belopolsky, 2014). It seems unlikely that both processes rely on separate updating mechanisms. Instead, both processes appear to be driven by a similar remapping mechanism.

Remapping was initially thought to underlie the maintenance of visual stability across saccades by compensating for the displacement of the retinal image. However, given the sparse nature of conscious visual perception, the necessity of such a mechanism is highly questionable (O'Regan & Noë, 2001). Instead, remapping might serve the transsaccadic maintenance of a set of prioritized locations. An influential idea is that brain areas involved in oculomotor control, like the IPS, FEF, and the SC, serve as priority maps (Awh et al., 2012; Belopolsky, 2015; Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Ipata et al., 2009; Serences & Yantis, 2006; Zelinsky & Bisley, 2015). These maps contain dynamic representations of space, in which the saliency of objects in the environment and the goals of the observer are thought to be amalgamated into one priority landscape, in which activity tags the locations in the environment that are behaviourally most relevant. These locations, which are agnostic to the actual visual content they indicate, have also been dubbed 'attentional pointers' (Cavanagh et al., 2010).

It has been argued that maintaining these spatial representations across saccades is especially important for action control (Bays & Husain, 2007). For a purely perceptual task it is not necessary to have a precise prediction of the post-saccadic location of a continuously present object because its features are stored in transsaccadic memory and it can easily be relocated upon saccade landing. However, in order to interact with objects and to avoid obstacles, fast updating of potential movement goals is crucial. A gradual updating mechanism would render most tasks impossible. The predictive nature of extraretinal signals enables such rapid updating of action goals. It is therefore not surprising that the compensation mechanisms driven by these signals have mainly been identified within (oculo)motor regions.

**Saccade curvature provides an ideal tool for measuring spatial representations in the brain.**

Finally, Saccade curvature provides an ideal tool for measuring spatial representations in the brain. Where most researchers used perceptual discrimination tasks to investigate the updating of memorized content, measuring saccade trajectories in **Chapter 2, 4 and 5** allowed us to directly and unobtrusively tap into the oculomotor system. This might also to some extent explain the discrepancies in timing between ours and earlier studies. The efference copy is likely to be generated in the SC, one of the latest stages along the sensorimotor continuum, and subsequently fed back to cortical areas through the thalamus. Neurophysiological studies suggest that the earlier in the visual pathway, the later relative to saccade onset activity is remapped, so it is not unlikely that there is some delay between the updating of oculomotor competition within the SC and the emergence of perceptual enhancement at the corresponding location.

In sum, spatial information is likely to be represented in the effector systems that facilitate a suitable response towards the object they indicate, and most prominently in the eye movement system. Activity in these areas is likely to act as pointers towards the most relevant objects in our environment. These pointers are continuously updated as we move through our dynamic environment and move our eyes to locations of interest. Luckily, the oculomotor system already contains the mechanisms for efficient updating. Remapping of neural activity allows action plans to be available shortly after intervening eye movements. Retinal information also plays a role in keeping track of the objects around us, but only if there is sufficient time to integrate it.



