Visual stability: Spatiotopic maps or transsaccadic remapping?

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The movements of our eyes and body result in large displacements of the image on our retina. Still we perceive the world to be visually stable. Two theories have been proposed to explain visual stability; (1) the existence of spatiotopic maps independent of gaze position which are constantly updated and (2) remapping of the information of salient objects around the time of the saccade. Psychophysical and fMRI evidence for both theories is discussed. Evidence exists for both theories, although remapping seems more plausible. Possible mechanisms behind remapping are discussed and the discrimination between the two theories of visual stability is questioned.

1. Introduction

Despite the many movements of our head, body and eyes, the world is perceived to be visually stable. When we enter a new environment, many saccades (rapid eye-movements) are made to explore the area and locate important objects. Saccades are an important instrument to examine new visual environments because they focus on objects of interest by bringing their projection on the high-resolution fovea.

Another mechanism to focus on an object is visual attention, where visual processing is enhanced at a specific location. Attention shifts can be independent of gaze (covert attention) or coupled with eye movements (ouvert attention). The exact relationship between attention and gaze is still unclear but it is known that eye movement and attention shifts are closely related. The regions in the brain activated by covert attention shifts, for example are almost the same as the regions activated by eye-movements (Corbetta *et al.*, 1998).

Unlike covert attention, saccades result in a large displacement of the image on our retina. Nevertheless, we are still able to keep track of salient objects and we seem to have a continuous visual perception during those eye movements.

Even tough multiple studies investigated the problem of visual stability there are a lot of contradictory results and a lack of a generally accepted theory.

Two major theories have been proposed to explain the mechanisms that facilitate visual stability. One possibility is the existence of spatiotopic maps. According to this theory visual information is processed in world-centred coordinates that are independent of gaze and body position.

The other mechanism thought to underlie visual stability is remapping, stating that information of important objects is transferred across saccades (rapid eye movements).

While remapping implies that trans-saccadic integration only occurs around the time of the saccade and only for objects of interest, spatiotopy predicts that the brain is constantly updating a spatiotopic representation of the world around us, a so called spatiotopic map.

To examine the mechanism facilitating visual stability, this review will discuss the two conventional theories.

First the theory of spatiotopicity will be reviewed. Evidence from behaviour experiments will be discussed first followed by data from functional anatomy studies. The theory of remapping will be reviewed secondly starting with behaviour and single-cell recording experiments followed by fMRI data.

2. Spatiotopicity

2.1 Psyschophysic studies

2.1.1 Spatotopic and retinotopic after effects

This paragraph will discuss evidence for spatiotopy from different behaviour studies. Since it is impossible to directly demonstrate the presence of spatiotopic maps, psychophysical research has focussed on the reference frames of information processing. A commonly used paradigm is to investigate the reference frames of after effects. After effects occur when an adaptor stimulus alters the perception of a test-stimulus presented at the exact same location even after the adaptor stimulus disappeared. When the subjects' gaze is fixated, the spatiotopic position equals the retinotopic position. Therefore, the subject is instructed to make a saccade between presentation of the adaptor- and test-stimulus. By presenting the test stimulus after the saccade at either the same retinotopic or spatiotopic (i.e. screen positions) position, the after effect is shown to take place in a retinotopic or spatiocopic reference frame respectively (Fig.1).

Visual information processing is spatiotopic for some, but not all aftereffects. A spatiotopic reference frame was found by Melcher, D. (2007) for the TAE (tilt after effect). The adaptor stimulus of the TAE is a briefly presented strongly tilted stimulus. Stimuli presented after the adaptor stimulus are perceived as tilted in the opposite direction. Melcher presented an adaptor stimulus at the fixation point followed by a displacement of the fixation point resulting in a saccade. The test stimulus was presented at different times before or after the saccade at either the same spatial location (initial fixation point) or the retinal location (new fixation point). Just before onset of the saccade (-75ms) TAE decreased at the retinal location and increased at the spatial location implicating a cross-saccadic transfer of information. A second experiment demonstrated a shift in spatial attention alone didn’t account for this transfer showing the transfer to be directly related to the eye-movement itself. The spatiotopic selectivity in combination with the independence of attention supports the hypothesis of spatiotopic maps. The decrease in TAE at the retinal position, on the other side, suggests a dynamical update of a spatial map as predicted by the remapping-theory.

Knapen *et al*. (2010) failed to replicate the results found by Melcher, D. (2007). The experiment of Melcher was duplicated as closely as possible but no spatiotopic TAE was found. Several experiments were conducted to investigate the different results of both studies. Even when the position of the adaptor-stimulus, attention, gaze angle and head position was varied, significant after effects were only found for retinotopic reference frames.

In contrast with the TAE, the MAE (motion after effect) was found to be retinotopic, rather than spatiotopic. The adaptor stimulus used by Knapen *et al*. (2009) consisted of an array of dots all moving in a different direction but with a horizontally right or left net movement. After a delay, a similar test-stimulus but with a net movement of 0 was presented. Subjects had to report the direction of motion of the test stimulus. Besides the spatiotopic and retinotopic condition, a full and a nonspecific condition were introduced. In the full condition, the gaze returned to the original fixation point and the test-stimulus was presented at the same location as the adaptor stimulus (and therefore at the same retinal an spatial location). The nonspecific condition was introduced to control for general adaptor-induced motion after effects by presenting the test-stimulus at neither the retinotopic nor the spatiotopic location. MAE was equal for both the retinotopic and full condition and equally close to zero for the spatiotopic and nonspecific condition. These findings lead to the conclusion that the reference frame of the MAE is retinotopic rather than spatiotopic.

The motion and tilt after effect were shown to occur in different reference frames. Since higher visual areas (MT, motion) are known to be more spatiotopic than lower visual areas (Crespi *et al*., 2011) one would expect the MAE to be spatiotopic and the TAE to be retinotopic. This is in direct contrast with the results of both studies.

Although the spatiotopic reference frame of the tilt aftereffect supports the hypotheses of spatiotopic maps, it does not prove the constant updating and continuous existence of these maps. These temporal aspects are hard to determine, since measurements are only made around the time of the saccade.

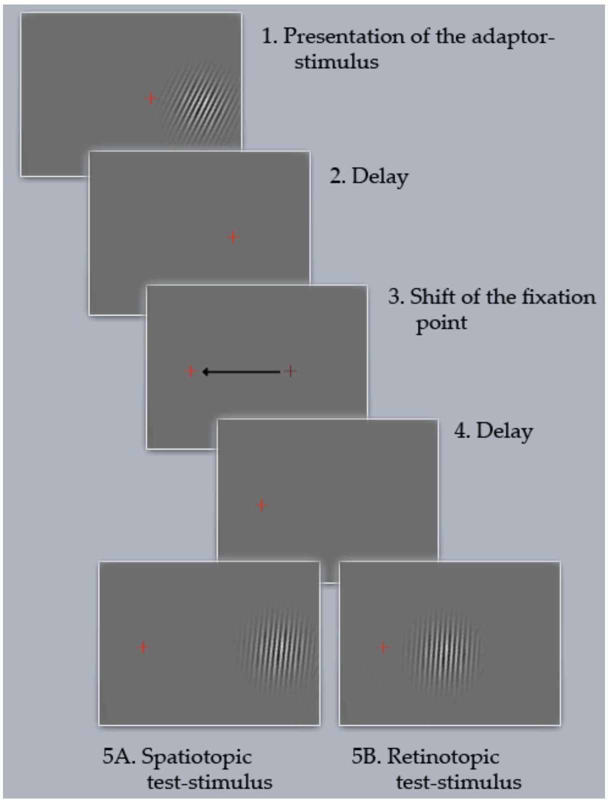


Figure 1. *An example of an after effect paradigm.*
The adoptor stimulus (in this case the heavily tilted gabor in 1.) causes the test-stimulus (in this case slightly tilted gabor in 5.) to be perceived differently (in this case as tilted leftward).
The test-stimulus is in 5. is at the same screen position in the spatoptopic condition (5A) and at the same location with respect to the fixation point in the retinotopic condition (5B).

2.1.2 Spatiotopic guidance of saccades and attention

The reference frame for the coordination of the saccades themselves is spatiotopic as well. Zimmerman *et al*. (2011) instructed subjects to make two consecutive saccades to two remembered targets just after they disappeared. During the second saccade the target stimulus was displaced giving false visual feedback. After about 100 trials the second saccade was corrected in the direction of the displacement. Once adaptation occurred the real experiment was conducted. The adaptation experiment was repeated with four slightly different conditions. The initial fixation point and the targets were presented at the exact same locations in the full adaption condition. In the spatiotopic condition, the two targets remained in the same position as well, but the initial fixation point was shifted. In the retinotopic condition, all three points were shifted but the relative distance remained constant. In the control condition, all three points were shifted and the relative distance was the same as in the spatiotopic condition. As expected, adaptation occurred in the full adaptation condition, which was the same as the first experiment. The only other condition in which adaptation occurred was the spatiotopic condition. Since adaptation occurred in an equal amount in the spatiotopic and full adaptation condition, all adaptation was due to spatiotopic visual feedback. The results of Zimmermann suggest that saccadic coordination is guided by a spatiotopic visual map.

The guidance of covert attention, which is functionally closely related to saccade control (Corbetta *et al*., 1998), was reported to be spatiotopic as well. Pertzov *et al*. (2010) used the inhibition of return effect to examine the reference frame of attention. When a cue is presented, stimulus detection at the cue location will be enhanced at first, but is followed by impaired stimulus detection. This impaired discrimination at the cue location is called the IOR (inhibition of return). After presentation of the cue Pertzov *et al*. instructed subjects to make a saccade. Next, a target stimulus was shown at either the same spatial or retinal location. Reaction time of these stimuli was measured and compared with those of a control location, which was not cued, to calculate IOR magnitude. IOR was maximal in the spatiotopic condition. Directly after landing of the saccade (10 ms) IOR was maximal and decreased rapidly with time. Because of the rapid saccadic transfer of the IOR effect attention was shown to be either remapped rapidly or coded in spatiotopic reference frames.

2.2 Functional imaging studies

Spatiotopic selectivity varies between different brain areas and be dependent of attention. Crespi *et al*. 2010 used fMRI to examine the reference frame for different brain areas. Subjects were shown the same stimuli of moving dots while fixating at different points. The difference in BOLD response for the different fixation positions was used to calculate a spatiotopy-index ranging from retinotopic to spatiotopic. The experiment was conducted twice with one condition where subjects were allowed to focus on the stimuli and one condition were subjects had to perform a distracting task. Higher visual areas V4,V6 and MT showed spatiotopic selectivity but only when subject were attending the stimulus. When attention was at the distractor task, these areas showed retinotopic selectivity. Spatiotopic coding was shown to depend on spatial attention but to exist at least under some conditions.

The finding that area MT is only spatiotopic when stimuli could easily be attended might be expected to explain the lack of spatiotopy of the MAE in the study of Knapen *et al*. This study did however account for the effect of attention by adding a secondary stimulus related task, which ensured attention was at the adaptor-stimulus location. Crespi *et al*. used a demanding task to distract attention from the stimulus while Knapen *et al*. used a task to direct attention to the stimulus. The different results might therefore be explained by the nature of the attentive task. Apart from methodical differences it is concluded that different aspects of motion are processed in different reference frames.

2.3 Conclusion

The previously discussed studies have proved spatiotopic reference frames to exist. This is however no conclusive evidence for the existence of continuously updated spatiotopic maps. The mechanisms that guide saccade movement and attention seem to be fully spatiotopic.

3. Remapping

Predictive remapping was first described by Duhamel *et al*. (1992) who examined the effect of saccades on neuronal firing in monkeys. LIP, a high visual area accociated with attention, was examined using single cell recording. A stimulus was presented and at the same time the fixation point moved, instructing the monkeys to make a saccade. Some of the cells whose receptive field would be at the same location as the stimulus after the saccade, started firing before onset of the saccade. These cells fired even when the stimulus disappeared before landing of the saccade and therefore never was in the receptive field. Since receptive fields seemed to be remapped to their future location this phenomenon was called predictive remapping.

3.1 Psychophysic studies

The possibility of remapping is not excluded by the evidence for spatiotopic reference frames in paragraph 2. In fact, this evidence is in favour of remapping, since the reference frame of remapping is spatiotopic as well. The difference with spatiotopic maps is that remapping only occurs around the time of the saccade and for specific objects. The selection of objects and object features to be remapped is thought to mediated by attention. Hence, psychophysic studies focus on the effect of attention on trans-saccadic perception.

The amount of trans-saccadic aftereffects is affected by attention. Melcher, D. (2009) investigated the TAE under different attentional conditions. In his study, two adaptor-stimuli were shown simultaneously. After a delay, a test-stimulus was shown at one of the two locations. Subjects were instructed to attend either both, or one of the two stimuli. The experiment was repeated with a saccade instruction between the presentation of the adaptor- and test-stimulus. The test-stimulus was presented after completion of the saccade at the same retinotopic location. An effect was found for both attention and the presence of a saccade. TAE was maximal when the correct stimulus was attended, decreased when both stimuli were attended, and was minimal when the wrong stimulus was attended. The presence of a saccade decreased TAE for all attentive conditions, and was found to be independent of attention. The additive and independent effects of both attention and saccades suggest that trans-saccadic perception depends on the allocation of attention. The progressive effect of attention suggest that attention determines the importance of remapping per object, rather than selecting one object which perceptual properties are remapped. This conclusion is consistent with the theory of attention-mediated remapping.

Even tough saccades were made, Melcher, D. only investigated the influence of attention on TAE for retinotopic conditions, resulting in a more reliable comparison between saccade and fixation experiments. The use of spatiotopic TAE on the other hand, would have been more similar to the conditions of remapping and therefore more meaningfull.

Attention itself is spatially remapped as well. Predictive remapping of attention was demonstrated by Rolfs *et al*. (2010). Subjects had to make two consecutive saccades. Stimulus discrimination was measured at different times before the saccade and at different spatial positions including a control condition, the first saccade target, the second saccade target and it's remapped position. Before onset of the first saccade, the remapped position didn't match the spatial or retinal location of the second saccade target. Only after completion of the first saccade, the remapped position corresponded to the retinal postion of the second saccade target. Discrimination performance increased just before onset of the saccade for both the first and second saccade target, indicating an increase in attention. The same increase was found for the remapped location, consistent with predictive remapping. Moreover, a successful stimulus discrimination at the first saccade target and the remapped location were associated with speeded execution of the first and second saccade respectively.

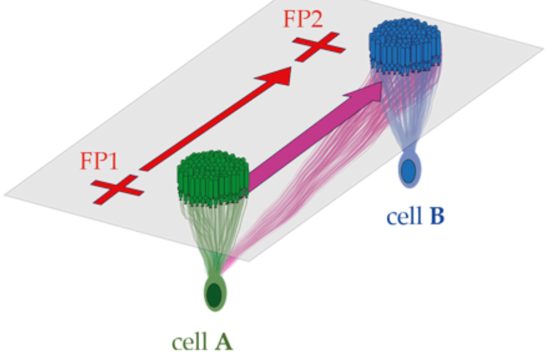
The increase of attention at the remapped position provides direct evidence for remapping.

3.2 Functional imaging studies

Remapping is also known to occur between to hemispheres. Merriam *et al*. (2003) used fMRI to examine contralateral stimulus remapping. Subjects had to fixate to either the right or the left side of the screen while a stimulus was presented at the screen centre. After 2 seconds the stimulus disappeared and a saccade was made to the opposite side of the screen. Due to the saccade, the location of the (extinguished) stimulus was now in the opposite visual field. BOLD-responses in the same regions of the parietal cortex (where higher visual areas involved in attention are located) were recorded for both hemispheres.

As expected, a visual response in the hemisphere contralateral to the stimulus was found. A remapped response in the other hemisphere was found after a delay of 2 seconds. Control experiments revealed that either the saccade or the stimulus alone were not sufficient to evoke a remapped response. A control experiment in which the stimulus stayed on screen, elicited a response with the same shape as the remapped response, but with a bigger magnitude. All together, these results show that stimulus evoked activation is dynamically remapped between hemispheres and suggest the representation of space in human cortex is remapped dynamically rather than continuously, as would be the case considering spatiotopy.

a. Shifting of receptive fields



b. Remapping of activation

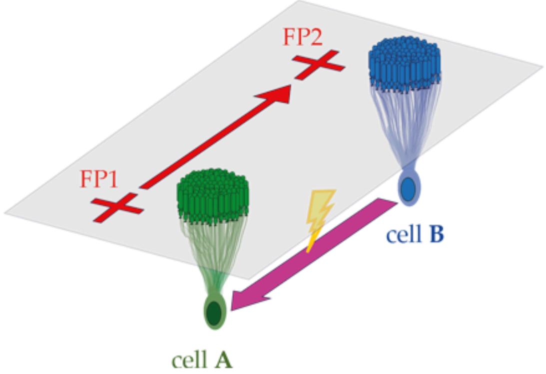


Figure 2. *Two possible mechanisms behind remapping.*
When a saccade is made from one fixation point (FP1) to another (FP2). The cell A becomes receptive for it's future receptive field, that of cell B, just before onset of the saccade. This can be due to **(a)** a shift of receptive fields (as shown in purple, the receptive field of A shifts to that of B) or **(b)** to a transfer of activation (receptive fields don't shift, but cell B transfers its activitiy to cell A)

3.3 Possible mechanisms

The mechanism originally believed to underlie predictive remapping, as proposed by Duhamel *et al.*, was the shifting of receptive fields just before onset of the saccade (Fig. 2a). As seen in fig. 2a, all neurons in a low visual area should have connections to all possible receptive fields in the retina, according to this theory.

Another possibility is the transfer of activation, proposed by Wurtz. Where the receptive field of a neuron A doesn't shift, but where neuron A gets activated by neuron B with a receptive field at the location where the receptive field of neuron A will be after the saccade (Fig 2b).

The hypothetical connectivity are the same for both theories, they only differ in the level of the brain where the transfer takes place. While, according to the theory of shifting receptive fields, activation is remapped at the level of the lowest visual areas, activation is transferred in higher visual areas according to the theory of remapping of activation. Activation might even be remapped in areas involved in attention as proposed by Cavanagh *et al*. (2010). Cavanagh *et al*.(2010) formulated this theory as the remapping of attention pointers.

The pre-saccadic remapping of attention found by Rolfs *et al*. (2010) supports the theory of remapping of attention pointers but isn't exclusive evidence to the theory of shifting receptive fields.

3.4 Conclusion

The dynamics of attention around the time of the saccade are supportive to the theory of remapping.

As for the mechanism some evidence supports the theory of shifting attentive pointers, but shifting receptive fields is still a possible alternative.

4. Discussion

Some visual perception takes place in spatiotopic reference frames. Although this is supportive for the theory of spatioticipy, it does not necessarily prove the existence of spatiotopic maps which are continuously updated and object-unspecific. The continuous updating of spatiotopic representations has been hard to prove, since meaningfull measurements are only made around the time of the saccade.

The updating of spatiotopic maps should be unselective for specific objects as well. Properties and locations of all objects should be transferred across a saccade. Little about this is examined in the studies discussed. The finding of Melcher, D. (2009) that less information was transferred for two stimuli than for one suggests object-selective remapping. The evidence discussed is therefore insufficient to prove the existence of spatiotopic maps.

The spatiotopic reference frames in visual processing demonstrate the transfer of perceptual information across saccades and can therefore be viewed in the light of remapping as well. As discussed, the temporal aspect of remapping was hard to determine but object selectivity has been shown by Melcher, D. (2009). His study demonstrated how remapping was altered by attention. Attention itself was found to be remapped as well, especially to saccade targets and around time of the saccade. These dynamics of attention support the dynamic remapping theory rather than spatiotopic maps. Since spatiotopic evidence supports both remapping as the spatiotopicity, attentional evidence is additional and more in favour of remapping. Current evidence is not sufficient to reject the hypothesis of spatopicity, though.

It remains unclear what mechanism controls this remapping. According to the reviewed studies, attention might be the control mechanism for dynamic remapping. This is supported by the dynamics of attention as described by Rolfs *et al*. (2011) and the finding that attention has to be at the saccade target at onset of the saccade (Deubel, H., 2008). The high overlap in brain areas involved in the guidance of attention and eye-movements (Corbetta, M., 2008) is consistent with this theory as well.

In order to remap correctly, the mechanism that remaps has to be aware of object positions in world-centred coordinates at all times, as supported by the spatiotopic reference frames of saccade (Zimmerman *et al*.,2001) and attention control (Pertzov *et al*., 2010). Since spatiotopicity for all objecs raises the problems earlier discussed, the remapping-mechanism might contain spatiotopic maps only for salient objects. In order to calculate these maps, oculomotor information has to be combined with visual information.

The mechanism of shifting attentive pointers leads to an elegant hypothesis of how this information might be combined. If oculomotor signals arrive in a brain area where large receptive fields receive high (i.e. abstract, object-related) visual input, this system would be self learning. When a saccade would be made, oculomotor-signals would arrive and just a moment later activity of visual (object) cells would shift. Since the oculomotor signal will always be followed by a change in visual input these two will be associated automatically, assuming hebian learning. Note that this is just a theory which has not been proven.

It is made clear that remapping and spatiopicity do describe the same process and their predictions are very much alike. To avoid confusion and communicate clearly, researchers should focus on the temporal aspects and object selectivity of spatiotopic reference frames in perception in order to make a more objective discrimination between spatiotopicity and remapping.

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