



Review

Buildup of spatial information over time and across eye-movements

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HIGHLIGHTS

- Spatiotopic representations exist in human vision.
- Spatiotopic representations take time to build up.
- Spatiotopic reference-frame serves the stabilization of object positions in visual memory.

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ABSTRACT

To interact rapidly and effectively with our environment, our brain needs access to a neural representation of the spatial layout of the external world. However, the construction of such a map poses major challenges, as the images on our retinæ depend on where the eyes are looking, and shift each time we move our eyes, head and body to explore the world. Research from many laboratories including our own suggests that the visual system does compute spatial maps that are anchored to real-world coordinates. However, the construction of these maps takes time (up to 500 ms) and also attentional resources. We discuss research investigating how retinotopic reference frames are transformed into spatiotopic reference-frames, and how this transformation takes time to complete. These results have implications for theories about visual space coordinates and particularly for the current debate about the existence of spatiotopic representations.

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1. Introduction

Our eyes are constantly moving in a frequent series of small jumps, called saccades, on average about 3 per second. The visual image on the retina is therefore never really stable. However, we almost never experience perceptual instability. The problem of visual stability across saccade eye movements has a long history

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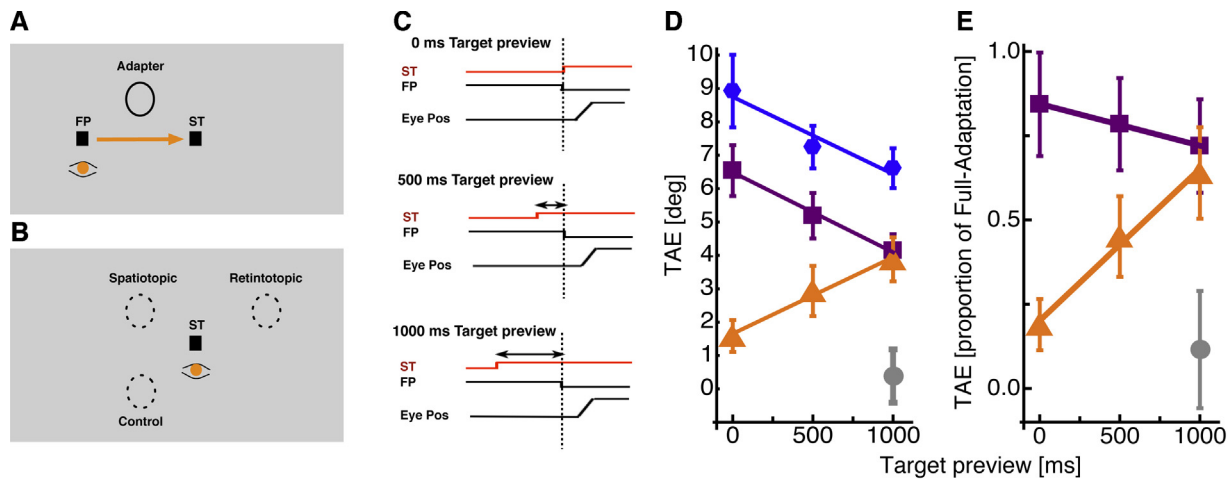


Fig. 1. (A) Graphical illustration of setup used to study spatiotopy with adaptation. Subjects fixated loosely on the fixation point FP for 3000 ms, viewing an adapter grating patch (0.8 c/° , vignettted within Gaussian window of $\sigma = 3.5^\circ$) tilted at 15° or -15° . The saccade target (ST) was then presented, to which subjects saccaded on extinction of the fixation point: either at onset of the saccade target, or 500 or 1000 ms later. (B) The test target came on 300 ms after extinction of the fixation point, always at least 30 ms after the eyes had landed. 300 ms after extinction of fixation point the test patch was presented for 51 ms in the spatiotopic, the retinotopic, or the control position, and subjects indicated the direction of tilt of the test patch. (C) Timecourse of events in a trial for all target preview durations. In the 0 ms target preview duration condition the saccade target appeared simultaneously with fixation point offset. In the other two conditions the saccade target was shown either 500 ms or 1000 ms before fixation point offset. (D) Tilt-aftereffect for the full-adaptation (blue), retinotopic (purple), spatiotopic (orange) and control (gray) conditions, as a function of preview duration of the saccade target, averaged over all subjects. Error bars represent ± 1 SEM. (E) Normalized tilt-aftereffect results for the three eye-movement conditions (color-coding as for B). Aftereffect magnitude was divided by each subject's full-adaptation magnitude, then averaged over subjects. Error bars represent ± 1 SEM. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

and has fascinated many researchers, stretching back to Al Hazen [44], Sherrington [1] and Helmholtz [2] (see [3] for recent review). Helmholtz [2] was the first to suggest a concrete mechanism for the stability, that a copy of the saccade motor command, later termed efference copy [49] or corollary discharge [66] could update the visual system of the upcoming saccade.

Two groundbreaking electrophysiological studies identified areas which might deliver signals of this type. First, Duhamel et al. [4] found that in lateral intraparietal cortex, neurons respond shortly before a saccade to stimuli presented to positions that will fall in the receptive field after the saccade is made (thereby “anticipating” the effect of the saccade). These *receptive-field shifts* are a likely candidate for the mechanism that transfers visual information from the pre- to the post-saccade position, thereby facilitating visual stability. How exactly the shift – in the same direction of the saccade – facilitates stability is not that obvious, but goes beyond the scope of this review. The reader is referred to Burr and Morrone [45] for a discussion of how the important aspect of the shift in receptive fields may be the return to resting state, allowing a transient spatiotopy. Another ground-breaking discover came from Sommer and Wurtz [5], who reported evidence showing that the efference copy signal may be carried along the pathway ascending from the brainstem through the thalamus to the frontal eye fields. This efference copy signal may in principle be sufficient to create a spatiotopic representation from the retinotopic visual input, along the lines suggested by Burr and Morrone [45]. A spatiotopic representation maintains visual space in gaze-invariant coordinates – at least transiently – thereby compensating for the retinal displacement during each saccade.

If the effects of saccades are compensated for “on-line” by a mechanism that effectively annuls to image motion created by the saccade, as argued above, is there any need for any other form of spatiotopic representation, one that remains solid in external rather than retinal coordinates? Many researchers (e.g. [3,6]) have argued that this form of representation may not be necessary, that all that is needed is a locally updated retinotopic representation. However, whether or not they are theoretically necessary, there is much evidence from various sources for the existence of spatiotopic representations within the human visual system.

In this review we use the term “spatiotopic representation” when we speak about encoding of object positions invariant to retinal displacements induced by saccades. In principle, a spatiotopic representation can encode object positions in a head-centered, a body-centered or an external world-centered reference frame. The experiments we describe in most cases do not distinguish between the various supra-retinal reference frames (except that of Fig. 2). We therefore mostly use “spatiotopic” to refer to every representation that survives the retinal shifting of a saccade.

We discuss evidence for long-term spatiotopic representations in the human brain, and go on to describe how these are built up slowly over time. As the build-up renders these mechanisms too slow to bridge the perisaccadic gap, it is unlikely they are involved in on-line stability. It would seem more likely that their purpose may be to encode objects in external space coordinates for a longer-lasting representation of the world, probably necessary to allow interactions with the world. The novel aspect that we stress in this review is that this long-term spatiotopy does not happen immediately, but takes time, and probably also attentional resources, to build up.

2. Trans-saccadic visual adaptation

Visual adaptation has proven to be a powerful method to study trans-saccadic spatiotopic representations in humans [54]. Adaptation produces visual aftereffects, which can remain for some seconds after adaptation, sufficient to interpose an eye-movement and study the reference frame of their selectivity. For example, after subjects inspect a tilted adapter stimulus for some seconds, the tilt of a subsequently presented probe stimulus will appear shifted away from that of the adapter stimulus. The trick of trans-saccadic adaptation is to adapt tilt in a specific position in external space (see Fig. 1A), and then require the subject to make a saccade before presenting the test: this dissociates the spatiotopic position of the adapter stimulus from its retinotopic position (see Fig. 1B).

David Melcher has pioneered this kind of method and used several visual features including contrast, tilt, form and faces [54]. He found that the spatiotopic aftereffect strength increased with the complexity of the visual feature tested: there was very

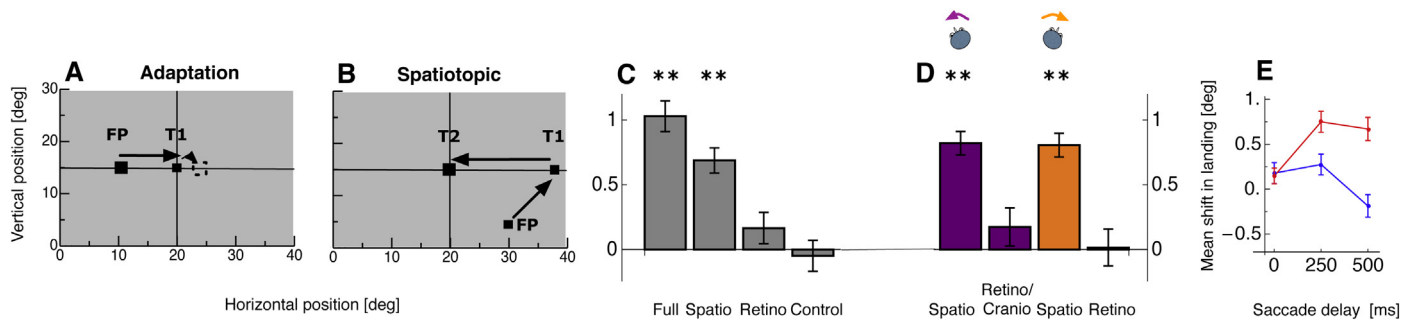


Fig. 2. (A) Positions of the fixation point (FP) and the saccade target (T1) for the adaptation procedure. During execution of the saccade, the saccade target jumped in the outward direction. (B) Positions of the fixation point and the saccade targets (T1 and T2) in the “spatiotopic condition.” Subjects fixated on the fixation point until saccade target T1 appeared and then made a saccade to T1. From T1 they had to initiate a saccade to T2. (C) Effect of adaptation on the amplitude of the horizontal saccadic vector of the second saccade in the double-step sequence, expressed as the difference in average amplitude before and after adaptation. Error bars represent the standard error of the sample mean. Adaptation occurs in the spatiotopic (and full) conditions, but not in the retinotopic conditions. (D) Effect of head-turn on adaptation-induced horizontal saccade amplitude changes of the second saccade in the double-step sequence. Horizontal saccades were adapted with the head facing the screen center, and test trials were collected with the head turned 9° leftward (purple) or rightward (orange). The adaptation remained spatiotopic with head turns. Error bars represent the standard error of the sample mean. (E) Mean shift in saccade landing position for the 3 overlap durations during adaptation in the spatiotopic condition. Shifts of saccades performed to targets presented for 50 ms are shown in blue, and shifts of saccades performed to targets presented for 500 ms are shown in red. Error bars represent SE. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

little spatiotopy for contrast (thought to be mediated primarily in V1); intermediate effects for orientation (probably reflecting V4 activity); and strong effects for face adaptation (presumably IT). However, others failed to replicate these results [7,8,53]. The reasons for the failure to replicate are far from clear.

We have recently confirmed and extended Melcher’s work by showing that the spatiotopic tilt adaptation takes time to build up [9–11]. We presented the saccade target but asked subjects to delay saccade initiation until the fixation point disappeared (see Fig. 2C). In this way we systematically varied the viewing duration of the saccade target before saccade execution. We found that the magnitude of spatiotopic aftereffect increased as a function of the saccade target preview duration. Whereas the magnitude of both the retinotopic and full aftereffect decrease with preview duration (reflecting the fact that aftereffects decline over time), the magnitude of the spatiotopic aftereffect increases with preview (Fig. 2D). When we normalize the magnitude of the retinotopic and spatiotopic effects to the full-adaptation effects (factoring out the effect of aftereffect decay), we see that the magnitude of the spatiotopic aftereffect increases greatly with target preview, by a factor of about three (Fig. 2E).

Trans-saccadic spatiotopic aftereffects have also been revealed with other adaptation techniques, such as adaptation to motion. However, not all motion adaptation studies show spatiotopy. For example, Wenderoth and Wiese [12] and Knapen et al. [67] reported that the classic motion aftereffect is purely retinotopic, agreeing with the original description by that the effect “moves with the eyes” so the adjacent rocks (not in correspondence with the waterfall) are seen to move upwards. Turi and Burr [13] confirmed that the classical motion aftereffect is selective in retinotopic coordinates, but went on to test the *positional motion aftereffect* (PMAE), the change in apparent position after adaptation to motion. They argued that this aftereffect is a more likely candidate for spatiotopic coding, as it seems to be processed at higher levels of the cortical hierarchy after color and luminance motion signals are combined [14]. They showed that the positional motion aftereffect is indeed coded almost entirely in spatiotopic coordinates. This is interesting, as it suggests that the spatiotopic map that can be disrupted by motion adaptation is one that represents the position of the moving object, rather than just the velocity.

The adaptation technique has also evidenced spatiotopic selectivity for the perception of duration. Adaptation to fast-moving grating causes a subsequently displayed stimulus appear to be of shorter duration [15], even when the change in apparent speed is

compensated for. By interspersing a saccade between the adaptation and test, we have shown that this adaptation too, is almost entirely spatiotopic [57]. Orientation, motion and duration are all encoded in maps anchored in real-world coordinates.

Other evidence for spatiotopic maps for motion come from a different technique, called “motion priming”. Under certain conditions viewing motion the after-effects of viewing motion can be position, causing the direction of subsequently viewed motion stimuli to be biased in the *same* rather than *opposite* direction. These effects are typically referred to as “priming”, and are thought to occur at higher levels than the negative adaptation aftereffects. Ong et al. [16] have shown that these motion-priming effects, unlike the motion aftereffect, are spatiotopic. Yoshimoto et al. [17] performed a more extensive study, where they manipulated the stimuli to produce either positive priming or negative aftereffects, in the same experimental conditions. They confirmed Ong et al. [16] in showing that positive priming was strongly spatiotopic, while negative aftereffects were observed in retinotopic coordinates. Importantly, however, Yoshimoto et al. [17] measured the timecourse of the buildup of the effects, and showed that the spatiotopic effect occurred only when the period between adapter and test stimulus was delayed more than 600 ms, proving strong confirmation for the idea that the spatiotopic representation takes time to build up.

The evidence for a long-term spatiotopic map is very compelling. These maps are not static snapshots, but rich with information about position, motion and time.

3. Functional magnetic resonance imaging studies

Other techniques besides psychophysics have demonstrated spatiotopy in primate cortex. Back in 1993, Galetti, Battaglini and Fattori [47] described a small proportion of neurons in area V6 of the monkey with a craniotopic spatial selectivity. Duhamel and Bremmer [46] later reported a similar craniotopic selectivity in area VIP of the monkey. Spatiotopic representation (particularly of motion) in humans has recently also received strong support from neuroimaging studies. D’Avossa et al. [55] showed that the BOLD response of cortical area MT was selective in spatiotopic rather than retinotopic coordinates, and Crespi et al. [58] went on to show spatiotopy not only in MT, but much of parietal cortex, including MST, LO, V6 and even V4.

Perhaps the most interesting aspect is that the spatiotopic response depends very strongly on subjects paying attention to the

stimuli [61]. When subjects were required to perform an attentionally demanding task at the center of screen (the origin of the retinotopic coordinate system), rather than being free to attend to the stimuli, the spatiotopic response reverted to a retinotopic response. Areas of the dorsal stream (MT, MST, LO and V6), which were clearly spatiotopic in passive viewing, became clearly retinotopic when attention was directed to fovea. This agrees well with work by Gardner et al. [18], who also reported retinotopic BOLD responses for the entire visual cortex when attention was directed to the fovea.

These results show that not only does spatiotopy take time to build up, it requires attentional resources to do so. Much evidence suggests that attention is allocated in spatiotopic coordinates [19–21,42]. However, the research has been controversial. Mathôt and Theeuwes [52] reported evidence for the initial coding of inhibition of return to be retinotopic, becoming spatiotopic over time, which also finds support in Golomb et al. [22,23]. However, while Pertzov et al. [20] and Hilchey et al. [24] presented evidence for spatiotopic IOR at much shorter post-saccadic intervals than were tested by Mathôt and Theeuwes [52]. This raises the fascinating possibility of an important link between attention and the creation of spatiotopy. It is possible that attention is necessary for the buildup of spatiotopy, and how long it takes to build up depends critically on the attentional resources available. It may be that attention anticipates spatiotopy in some sense, before the spatiotopic representation is well formed. As it is well-known that there exists a close link between attention and eye movements, it is not unreasonable that the two should work together to produce spatial maps.

That BOLD responses are selective in external coordinates does not in itself prove that those areas have a functional spatiotopic selectivity. The origin of the BOLD signal is not well understood, and the possibility that it reflects modulatory feedback from higher areas, rather than the primary response of neurones in the area being scanned, cannot be ruled out. It is therefore imperative that the imaging studies be backed up by solid psychophysics showing that observers can integrate information across saccades, and use this to improve performance.

We have also investigated the buildup of spatiotopic maps with an fMRI-adaptation paradigm [25], which takes advantage of the fact that the repeated presentation of a stimulus results in a reduction in the BOLD amplitude responding to that stimulus [26,27]. We placed the adaptor to the right of fixation (as in Fig. 2A), which will stimulate only the left visual cortex. After adaptation, subjects made a rightward saccade to the saccade target, so a probe stimulus presented at the same spatiotopic position should activate the right visual cortex. Although the adaptor and probe stimulate different cortices, we found clear fMRI-adaptation to a probe shown in the spatiotopic location as the adaptor in visual areas V1–V4. We suggest that the remapping signal, originating in lateral intraparietal cortex [4], transports the feature information from the adaptor activity across the hemispheres.

4. Spatiotopic saccade adaptation

One important function of a long-term spatiotopic map may be for the planning of saccades. In saccade sequences the oculomotor system needs to know where the first saccade went, in order to perform the second saccade accurately. Adaptation, which we have seen is such an efficient tool for studying visual perception, can also be used to modify saccade vectors. Systematic displacements of the saccade target during execution of the saccade leads to an adaptive change in saccade amplitudes ([59,51]). Either inward or outward adaptation can be induced, depending on the direction of the target displacement. However, the two types of adaptation are quite

different in several respects [28]. Only outward adaptation transfers to pointing movements [48] and to visual perception [29,30]. Semmlow et al. [31] showed that with outward adaptation spatial positions were adaptable irrespective of the amplitude of saccades to these locations.

We have investigated the coordinate system of saccadic adaptation with a memory-guided, double-saccade task [32], following previous studies of eye position effects [32,33,43]. Subjects observed two saccade targets (see Fig. 2A and B), and were required to memorize the position of the second saccade target T2, which was extinguished before initiation of the saccade sequence. Then they made a two-saccade sequence: the first to the visible target T1, then to target T2 only when the target T1 disappeared. The interleaved first saccade to the visible target T1 served to dissociate the spatiotopic from the retinotopic location of saccade target T2. These trials were tested after saccades had been adapted either in inward or in outward direction. Significant adaptation was found in the full-adaptation condition, where the targets were shown in the same position as during induction of adaptation (left-most bar of Fig. 2C). If adaptation is linked to the position in external space, adaptation should occur also in the spatiotopic condition. This was indeed the case. Adaptation was observed only in the spatiotopic, but not in the retinotopic nor in the neutral control condition. A neural representation of visual space, not referenced to retinal coordinates, could in principle be encoded in head-centered coordinates or indeed in external space. We have tested the possible involvement of head-centered coordinates by changing the head rotation of the subjects in between the adaptation and the test phase. In this experiment no adaptation was found in the condition that would have proven a head-centered coding of visual space. Again, only the spatiotopic condition yielded significant adaptation (see Fig. 2D).

In a follow-up study, one of us investigated the time-course of the build-up of this spatiotopic representation [34], using a very similar paradigm: the saccade target T2 was presented either for 50 or 500 ms. Subjects were again instructed to perform the saccade to target T2 when the target T1 disappeared, which could be either immediately with appearance of target T2 (0 ms) or 250 ms or 500 ms later. For targets presented for 500 ms, the spatiotopic adaptation strength increased as a function of saccade delay duration (Fig. 2E, red symbols and lines). However, for targets presented for 50 ms, no spatiotopic adaptation was observed (shown in blue color). Spatiotopic buildup thus again depends on presentation duration of the target. It occurred only when overlap saccades (considered voluntary saccades) were adapted. This is consistent with previous evidence for separate adaptability of reactive and voluntary saccades [28], and may be part of an explanation for the involvement of different neural mechanisms. The spatiotopic coding of the saccade target was seen only for outward adaptation, which—as mentioned above—transfers to visual perception. We therefore suggest that the spatiotopic representation is a visual phenomenon, rather than residing in the motor system.

Levy-Bencheton et al. [35] recently replicated these results and showed that multiple reference frames are involved in saccade adaptation. They tested different saccade types in either complete darkness or in darkness but with an LED-simulation of the monitor frame. Double-step memory guided saccades showed spatiotopic adaptation only when the LED-frame was visible. Adaptation of double-step memory guided saccades therefore seems to be coded in allocentric coordinates, relative to an external reference object. Single-step memory-guided saccades showed spatiotopic adaptation irrespective of the presence of the LED-frame. Visually-guided single-step saccades did not show any spatiotopic adaptation at all. This latter finding suggests that the standard reference frame for visually-guided saccades is retinotopic. Spatiotopic effects emerge when sequence planning or memory guidance is involved in saccade generation. This further strengthens the hypothesis that the

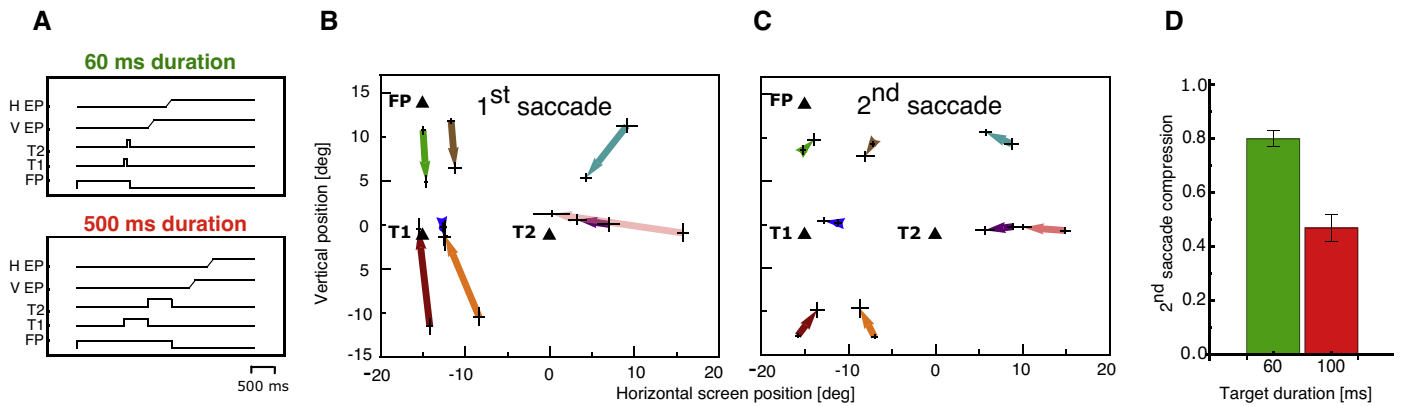


Fig. 3. (A) Timecourse of events in the orthogonal double step task where the saccade targets T1 and T2 were presented either for 60 ms (upper panel) or 500 ms (lower panel). (B) Mislocalization of probe dots at onset of first saccade. The start of each arrow represents baseline localization from 100 ms before onset of the first saccade. The arrowhead indicates peak mislocalization at first saccade onset. Error bars indicate the horizontal and vertical SEM of the baseline and the peak mislocalization. (C) Spatial distribution of mislocalization at second saccade onset. Same conventions as (B). (D) Average compression magnitude (0 is maximum, 1 minimum) in trials with different presentation duration of the saccade targets T1 and T2 (between 60 and 500 ms). Data were averaged across subjects and trials. Errors are SE of the mean.

spatiotopic component is connected to a visual representation rather than the motor system.

5. Compression

Trans-saccadic visual stability is frequently studied by probing visual perception shortly before, during or shortly after the execution of saccade eye movements. In this line of research, visual stimuli are presented for only a few milliseconds around the time of saccade initiation, and subjects indicate the apparent position of the probe stimulus after the saccade is finished. Studies conducted in complete darkness found that probe stimuli presented in the perisaccadic range were mislocalized in the direction of the saccade (e.g. [50,60]). This shift has been taken as evidence for a remapping process, which transports visual information to the post-saccadic fixation location [61]. However, when visual references are available, perisaccadic stimuli are perceived compressed towards the saccade target ([36,37,62]).

We recently confirmed the visual influence on compression by asking subjects to perform saccades onto an empty screen, thus eliminating all visual references close to the saccade landing position [25]. In this condition compression magnitude was greatly reduced compared with normal saccades to a visual target. We then tested compression in a double-step paradigm, to investigate the reference frame of the memory representation, which stores the visual target [63]. In the classical double-step paradigm, two saccade targets are shown briefly, and subjects are required to sequentially perform saccades to the two targets [38,39]. Unlike in saccade adaptation, where the second target step starts contingently to saccade execution, all saccade targets are switched off before the first saccade is executed. The oculomotor system thus must rely on a memory representation of the targets to perform the saccades correctly, particularly the second saccade, as the retinal image will have moved by then. We tested perisaccadic mislocalization in a double-step paradigm, where subjects first had to execute a vertical and then a horizontal saccade. We presented the saccade targets either for 60 ms or for 500 ms. In both cases subjects were allowed to initiate the saccade sequence only once the targets had disappeared (see Fig. 3A).

Perisaccadic compression magnitude at the time of the first saccade is symbolized by the length of the arrows in Fig. 3B. The saccade was performed vertically from the fixation point (FP) to the saccade target (T1). There was strong compression parallel to the saccade path but also a component of orthogonal compression. Surprisingly, at the time of the second saccade, no compression was

observed. It therefore seems that the very short target presentation duration of 60 ms was not sufficient long enough to store the visual signal of the second target in a format which is updated at the time of the second saccade. When we repeated the task with a saccade-target duration of 500 ms, compression was much stronger at the time of the second saccade. We calculated a compression index (where zero means total compression, one means none) to compare mislocalization magnitude for the 60 ms and the 500 ms target presentation duration (Fig. 3D). Compression obviously is stronger with 500 ms target duration than 60 ms. Consistent with the results from the spatiotopic saccade adaptation experiments, these results suggest that a spatiotopic component is involved in the memory of the second saccade target.

6. Suppression of displacement

A classical test of visual stability across saccade eye movements is the saccadic suppression of displacement paradigm (SSD) [40,41]. In that paradigm subjects are asked to perform a saccade, and while the saccade is still in flight, the saccade target is shifted slightly to the left or to the right. Since motion perception sensitivity is degraded at the time of saccades [56], subjects cannot rely on the motion signal to judge the displacement direction. Subjects perform poorly in this task, with displacements up to 30% of the saccade amplitude size going undetected. However, blanking the saccade target during the saccade and presenting it 250 ms after saccade end in a displaced position leads to a massive improvement in displacement detection [41]. These findings largely motivated the formulation of the “reference object theory”, which states that a particular object is selected as the saccade target and perceives preferential perceptual processing. After the saccade is finished this object will be sought by the system. If an object matching the selected one is found it will become the reference object and the system maintains the visual stability assumption.

We have tested the idea of the spatiotopic build up duration with the SSD paradigm. Subjects fixated on a fixation point, which was extinguished after 100 ms to remove visual references. After a fixation period the saccade target was shown but subjects were instructed to wait with saccade initiation until an acoustic go-signal. The time between saccade target presentation and appearance of the go-signal was systematically varied to investigate the proposed build up duration. During saccade execution the saccade target was displaced and subjects reported the direction after performance of the saccade. We also tested this task in a condition where subjects fixated throughout the entire trial.

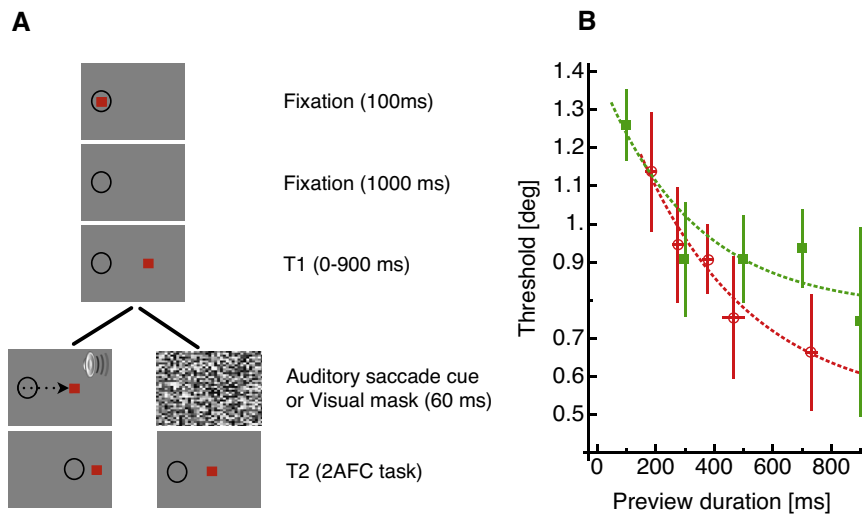


Fig. 4. (A) Experimental setup for saccade and fixation trials. The black circles indicates eye position. The red squares indicate targets for fixation or saccades. A trial started with subjects directing gaze to a fixation point. After 100 ms, the fixation point was turned off and subjects continued to maintain fixation on the blank screen. The saccade target T1 appeared 1000 ms later. In the saccade trials subjects saccaded to the target on auditory cue 0–500 ms after saccade target onset. As soon as the saccade was detected, the saccade target was displaced either leftwards or rightwards (T2). At the end of the trial, the subject indicated the direction of the target displacement by key press. In the fixation trials subjects maintained fixation at the position of the fixation point for the entire trial. T1 was displayed for 0–900 ms, and followed by 60 ms of high-contrast mask (simulating the masking effect of the saccade). T2 was then displayed leftwards or rightwards of its original position and subjects reported the direction of the shift by key press. (B) Displacement thresholds (geometric mean of thresholds, calculated separately for all subjects) for the saccade (shown in red) and the fixation (shown in green) condition as a function of presentation duration. Saccade latencies were measured for all trials, and target presentation time binned into 100 ms bins. Error bars represent standard error across subjects. The continuous curves show exponential fits to the data. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

In this condition the masking effects of the saccade was replaced by a whole-field visual texture, which was presented for 50 ms. Immediately after the disappearance of the mask the target was shown displaced and subjects again reported the displacement. Fig. 4B shows the perceptual thresholds of the target displacement performance against preview duration of the saccade target. In both conditions, in saccades (shown in red) and in fixation (shown in green), performance increased, i.e. perceptual thresholds decreased, as a function of the duration the saccade target was seen before saccade initiation.

The results suggest that the visual system is well able to store precise position information across saccades as long as a certain amount of time is available to process the target position before saccade initiation.

7. Concluding thoughts

In this article we have reviewed evidence for the existence of a spatiotopic representation in human vision, which builds up over time. The buildup duration is of the order of 320–1000 ms, depending on the experimental situation. The buildup of the spatiotopic representation occurs when a delay is inserted between saccade initiation and probe presentation, or when the period between saccade end and probe presentation is delayed. This is consistent with other reports in the literature, where spatiotopic memory effects were seen when the probe was shown some hundred milliseconds after saccade execution [17,42]. The long build-up duration, and the finding that the build-up can also be triggered after the saccade is finished, show that the spatiotopic representation we describe here probably has little to do with the classical problem of keeping vision stable on each saccade.

We believe that this slower spatiotopic reference-frame serves the stabilization of object positions in visual memory by creating a longer-lasting scene representation that remains solid with the environment. As the build-up is slow, at least 320 ms, it is likely that the mechanism integrates over several saccades. Its function

therefore may be not to bridge information across saccade, but to store object positions in a gaze-invariant visual memory representation. Our data from the suppression of displacement experiment show that the spatial integration has the same timecourse during fixation and when saccades were performed. This finding suggests that the build-up of this spatiotopic representation does not depend on the imminent execution of a saccade but seems to be created in any case. We therefore link the long build-up duration to a visual memory encoding rather than to a saccade-contingent computation.

Much research has demonstrated that separate visual systems control visually-guided motor actions and cognitive scene representations [64]. These systems code visual space in different coordinate systems: whereas direct motor responses rely on an egocentric reference frame, cognitive object representations are mostly coded in external space coordinates [65,66]. The experiments reviewed in this article demonstrate this dissociation of reference frames for fast and delayed responses. They suggest that retinotopic reference frames are transformed into spatiotopic reference-frames, and that this transformation takes time. These results have implications for theories about visual space coordinates and particularly for the current debate about the existence of spatiotopic representations.

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References

- [1] Sherrington CS. Observations on the sensual role of the proprioceptive nerve supply of the extrinsic ocular muscles. *Brain* 1918;41:332–43.
- [2] Helmholtz HV. *Handbuch der physiologischen Optik*. Hamburg, Germany: Voss; 1867.

- [3] Wurtz RH. Neuronal mechanisms of visual stability? *Vision Res* 2008;48(20):2070–89.
- [4] Duhamel JR, Colby CL, Goldberg ME. The updating of the representation of visual space in parietal cortex by intended eye movements? *Science* 1992;255(5040):90–2.
- [5] Sommer MA, Wurtz RH. A pathway in primate brain for internal monitoring of movements *Science* 2002;296:1480–2.
- [6] Cavanagh P, Hunt AR, Afraz A, Rolfs M. Visual stability based on remapping of attention pointers? *Trends Cogn Sci* 2010;14(4):147–53.
- [7] Afraz A, Cavanagh P. The gender-specific face aftereffect is based in retinotopic not spatiotopic coordinates across several natural image transformations. *J Vis* 2009;9(10):10.1–17.
- [8] Knapen T, Rolfs M, Wexler M, Cavanagh P. The reference frame of the tilt after effect. *J Vis* 2010;10(1):1–13.
- [9] Zimmermann E, Morrone MC, Fink GR, Burr D. Spatiotopic neural representations develop slowly across saccades. *Curr Biol* 2013;23:193–4.
- [10] Zimmermann E, Morrone MC, Burr D. Spatial position information accumulates steadily over time? *J Neurosci* 2013;33(47):18396–401.
- [11] Zimmermann E, Fink G, Cavanagh P. Perifoveal spatial compression. *J Vis* 2013;13(5):21.
- [12] Wenderoth P, Wiese M. Retinotopic encoding of the direction aftereffect? *Vision Res* 2008;48(19):1949–54.
- [13] Turi M, Burr D. Spatiotopic perceptual maps in humans: evidence from motion adaptation. *Proc Biol Sci* 2012;279(1740):3091–7.
- [14] McKeefry DJ, Laviere EG, McGraw PV. The segregation and integration of colour in motion processing revealed by motion after-effects? *Proc Biol Sci* 2006;273(1582):91–9.
- [15] Johnston A, Arnold DH, Nishida S. Spatially localized distortions of event time. *Curr Biol* 2006;16(5):472–9.
- [16] Ong WS, Hooshvar N, Zhang M, Bisley JW. Psychophysical evidence for spatiotopic processing in area MT in a short-term memory for motion task; 2009.
- [17] Yoshimoto S, Uchida-Ota M, Takeuchi T. The reference frame of visual motion priming depends on underlying motion mechanisms. *J Vis* 2014;14(1).
- [18] Gardner JL, Merriam EP, Movshon JA, Heeger DJ. Maps of visual space in human occipital cortex are retinotopic, not spatiotopic. *J Neurosci* 2008;28(15):3988–99.
- [19] Sapir A, Rafal R, Henik A. Attending to the thalamus: inhibition of return and nasal-temporal asymmetry in the pulvinar. *Neuroreport* 2002;13(5):693–7.
- [20] Pertzov Y, Zohary E, Avidan G. Rapid formation of spatiotopic representations as revealed by inhibition of return. *J Neurosci* 2010;30(26):8882–7.
- [21] Howe PD, Drew T, Pinto Y, Horowitz TS. Remapping attention in multiple object tracking. *Vision Res* 2011;51(March (5)):489–95.
- [22] Golomb JD, Nguyen-Phuc AY, Mazer JA, McCarthy G, Chun MM. Attentional facilitation throughout human visual cortex lingers in retinotopic coordinates after eye movements. *J Neurosci* 2010;30(31):10493–506.
- [23] Golomb JD, Marino AC, Chun MM, Mazer JA. Attention doesn't slide: spatiotopic updating after eye movements instantiates a new, discrete attentional locus. *Atten Percept Psychophys* 2011;73(1):7–14.
- [24] Hilchey MD1, Klein RM, Satel J, Wang Z. Oculomotor inhibition of return: how soon is it recoded into spatiotopic coordinates? *Atten Percept Psychophys* 2012;74(6):1145–53.
- [25] Zimmermann E, Weidner R, Fink RG. Spatiotopic representations in early visual areas; in press.
- [26] Grill-Spector K, Malach R. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol (Amst)* 2001;(1–3):293–321.
- [27] Kourtzi Z, Huberle E. Spatiotemporal characteristics of form analysis in the human visual cortex revealed by rapid event-related fMRI adaptation. *Neuroimage* 2005;28(2):440–52.
- [28] Pelisson D, Alahyane N, Panouilleres M, Tilikete C. Sensorimotor adaptation of saccadic eye movements? *Neurosci Biobehav Rev* 2010;34(8):1103–20.
- [29] Zimmermann E, Lappe M. Motor signals in visual localization. *J Vis* 2010;6:11.
- [30] Zimmermann E, Lappe M. Eye position effects in oculomotor plasticity and visual localization. *J Neurosci* 2011;31:7341–8.
- [31] Semmlow JL, Gauthier GM, Vercher JL. Mechanisms of short-term saccadic adaptation. *J Exp Psychol Hum Percept Perform* 1989;15:249–58.
- [32] Zimmermann E, Burr D, Morrone MC. Spatiotopic visual maps revealed by saccadic adaptation in humans. *Curr Biol* 2011;21:1380–4.
- [33] Havermann K1, Zimmermann E, Lappe M. Eye position effects in saccadic adaptation? *J Neurophysiol* 2011;106(5):2536–45.
- [34] Zimmermann E. The reference frames in saccade adaptation. *J Neurophysiol* 2013;109:1815–23.
- [35] Levy-Benchtou D, Pélisson D, Panouillères M, Urquizar C, Tilikete C, Pisella L. Adaptation of scanning saccades co-occurs in different coordinate systems. *J Neurophysiol* 2014;111(12):2505–15.
- [36] Ross J, Morrone MC, Burr DC. Compression of visual space before saccades. *Nature* 1997;384:598–601.
- [37] Morrone MC, Ross J, Burr DC. Apparent position of visual targets during real and simulated saccadic eye movements. *J Neurosci* 1997;17(20):7941–53.
- [38] Westheimer G. Eye movement responses to a horizontally moving visual stimulus? *AMA Arch Ophthalmol* 1954;52(6):932–41.
- [39] Hallett PE, Lightstone AD. Saccadic eye movements towards stimuli triggered by prior saccades? *Vision Res* 1976;16(1):99–106.
- [40] Bridgeman B, Hendry D, Stark L. Failure to detect displacement of the visual world during saccadic eye movements. *Vision Res* 1975;15:719–22.
- [41] Deubel H, Schneider WX, Bridgeman B. Postsaccadic target blanking prevents saccadic suppression of image displacement? *Vis Res* 1996;6(7):985–96.
- [42] Golomb JD, Chun MM, Mazer JA. The native coordinate system of spatial attention is retinotopic. *J Neurosci* 2008;28(42):10654–62.
- [43] Alahyane N, Pelisson D. Eye position specificity of saccadic adaptation? *Invest Ophthalmol Vis Sci* 2004;45(1):123–30.
- [44] Al hazen I. Book of optics. In: The optics of Ibn al-Haytham translated and edited by Sabra AI. London: Warburg Institute; 1989 [1083].
- [45] Burr DC, Morrone MC. Constructing stable spatial maps of the world. *Perception* 2012;41(11):1355–72.
- [46] Duhamel JR1, Bremner F, Ben Hamed S, Graf W. Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 1997;389(6653):845–8.
- [47] Fattori P, Galletti C, Battaglini PP. Parietal neurons encoding visual space in a head-frame of reference. *Boll Soc Ital Biol Sper* 1993;68(November (11)):663–70.
- [48] Hernandez TD, Levitan CA, Banks MS, Schor CM. How does saccade adaptation affect visual perception? *J Vis* 2008;8:3–16.
- [49] Von Holst E, Mittelstädt H. Das Refferenzprinzip *Naturwissenschaften* 1954;37:464–76.
- [50] Honda H. Perceptual localization of visual stimuli flashed during saccades. *Percept Psychophys* 1989;45:162–74.
- [51] Hopp JJ, Fuchs AF. The characteristics and neuronal substrate of saccadic eye movement plasticity. *Prog Neurobiol* 2004;72:27–53.
- [52] Mathot S, Theeuwes J. Gradual remapping results in early retinotopic and late spatiotopic inhibition of return. *Psychol Sci* 2010;21(12):1793–8.
- [53] Mathot S, Theeuwes J. A reinvestigation of the reference frame of the tilt-adaptation aftereffect. *Sci Rep* 2013;3:1152.
- [54] Melcher D. Spatiotopic transfer of visual-form adaptation across saccadic eye movements? *Curr Biol* 2005;15(19):1745–8.
- [55] D'Avossa G1, Tosetti M, Crespi S, Biagi L, Burr DC, Morrone MC. Spatiotopic selectivity of BOLD responses to visual motion in human area MT. *Nature Neuroscience* 2006;10:249–55.
- [56] Burr DC, Holt J, Johnstone JR, Ross J. Selective depression of motion sensitivity during saccades. *J Physiol* 1982;333:1–15.
- [57] Burr D, Tozzi A, Morrone MC. Neural mechanisms for timing visual events are spatially selective in real-world coordinates. *Nat Neurosci* 2007;10(4):423–5.
- [58] Crespi S, Biagi L, D'Avossa G, Burr DC, Tosetti M, Morrone MC. Spatiotopic coding of BOLD signal in human visual cortex depends on spatial attention. *Plos One* 2011;6(7):e21661.
- [59] McLaughlin SC. Parametric adjustment in saccadic eye movements. *Percept Psychophys* 1967;2:359–62.
- [60] Schlag J, Schlag-Rey M. Through the eye slowly: delays and localization errors in the visual system. *Nat Rev Neuroscience* 2002;3(3):191–215.
- [61] Dassonville P, Schlag J, Schlag-Rey M. Oculomotor localization relies on a damped representation of saccadic eye displacement in human and nonhuman primates. *Vis Neurosci* 1992;9(3–4):261–9.
- [62] Lappe M, Awater H, Kregelberg B. Postsaccadic visual references generate pre-saccadic compression of space. *Nature* 2000;403(6772):892–5.
- [63] Zimmermann E., Morrone M.C., Burr, D. Visual mislocalization during saccade sequences. (in press).
- [64] Milner AD, Goodale MA. Two visual systems re-viewed. *Neuropsychologia* 2008;46(3):774–85.
- [65] Bridgeman B. Complementary cognitive and motor image processing. In: Obrecht G, Stark L, editors. *Presbyopia Research: From Molecular Biology to Visual Adaptation*. New York: Plenum Press; 1991. p. 189–98.
- [66] Rossetti Y. Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Conscious Cogn* 1998;7(3):520–58.
- [67] Knapen T, Rolfs M, Cavanagh P. The reference frame of the motion aftereffect is retinotopic. *J Vis* 15, 9(5): 16 1-7 (2010).