
Constructing stable spatial maps of the world[†]

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Abstract. To interact rapidly and effectively with our environment, our brain needs access to a neural representation—or *map*—of the spatial layout of the external world. However, the construction of such a map poses major challenges to the visual system, given that the images on our retinae depend on where the eyes are looking, and shift each time we move our eyes, head, and body to explore the world. Much research has been devoted to how the stability is achieved, with the debate often polarized between the utility of spatiotopic maps (that remain solid in external coordinates), as opposed to transiently updated retinotopic maps. Our research suggests that the visual system uses both strategies to maintain stability. fMRI, motion-adaptation, and saccade-adaptation studies demonstrate and characterize spatiotopic neural maps within the dorsal visual stream that remain solid in external rather than retinal coordinates. However, the construction of these maps takes time (up to 500 ms) and attentional resources. To solve the immediate problems created by individual saccades, we postulate the existence of a separate system to bridge each saccade with neural units that are ‘transiently craniotopic’. These units prepare for the effects of saccades with a shift of their receptive fields before the saccade starts, then relaxing back into their standard position during the saccade, compensating for its action. Psychophysical studies investigating localization of stimuli flashed briefly around the time of saccades provide strong support for these neural mechanisms, and show quantitatively how they integrate information across saccades. This transient system cooperates with the spatiotopic mechanism to provide a useful map to guide interactions with our environment: one rapid and transitory, bringing into play the high-resolution visual areas; the other slow, long-lasting, and low-resolution, useful for interacting with the world.

Keywords: stable vision, saccades, remapping, spatiotopy, transsaccadic integration

1 Background

The theme of this paper is: how do we build the spatial representations of the world that correspond to our rich visual experience, and allow us to navigate through and interact with our environment? Vision starts in the eye, and so do the problems. The eye can be considered as a 500 kilopixel camera, in that it has about a million output axons, each pair of axons making up a pixel (one black, one white). But the pixels are not distributed uniformly over the retina: in the foveola (the most central part) the packing density is about one per 30 deg visual angle, but this reduces systematically with eccentricity. If the foveola resolution were applied to the entire retina, we would need not one million, but one billion, exiting axons, creating an optic nerve the size of an elephant’s trunk. The trick to avoid this is to create high-resolution machinery only in central vision, then scan the environment with this hotspot, positioning it to each interesting area of the scene, by a series of saccadic scanning movements.

Typically, we are not aware of our saccades, although we make them very frequently, up to three per second. Figure 1 shows a saccade scan path as an observer views a painting

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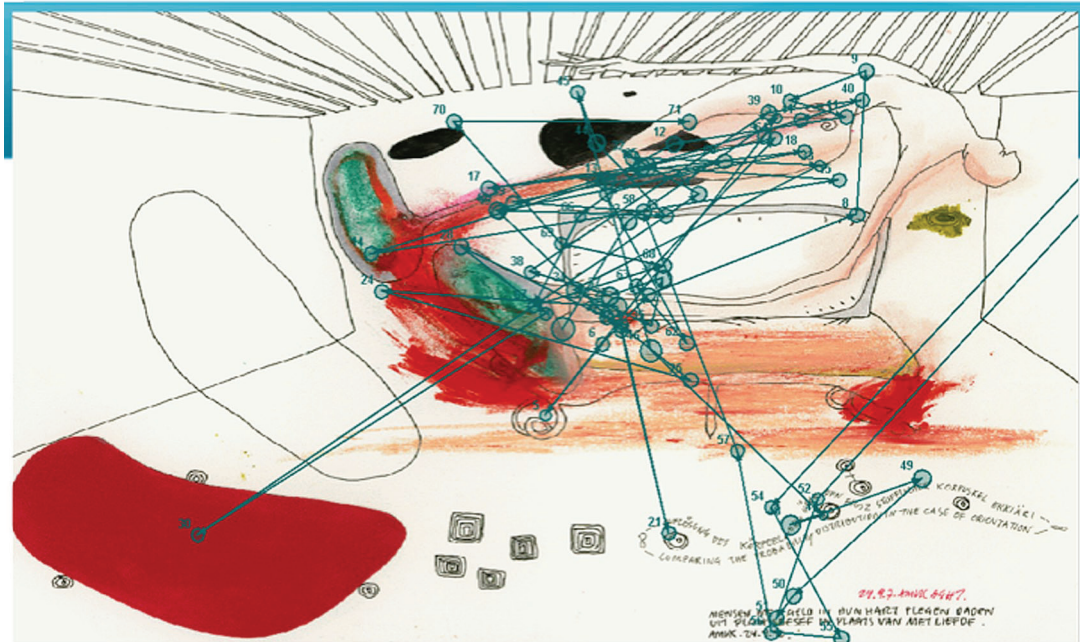


Figure 1. [In colour online, see <http://dx.doi.org/10.1068/p7392>] Scan path (straight green lines) as the artist Anee-Mie Kerckhoven views one of her paintings (“Kalligrafie No. 1”). What is interesting here is that the artist believed that she never moved gaze when observing her work, but “takes it all in in a single glance”. Reproduced with permission from Johan Wagemans.

(Wagemans 2011). This particular scan path was recorded from the artist herself, who claimed that she never moves her eyes when viewing her paintings, “but takes it all in on a single glance”. This demonstrates how automatic saccades tend to be, with targets selected largely subconsciously, although we can consciously override this semiautomatic function [see Krauzlis (2005) for a recent review of the mechanisms of saccade selection]. Interestingly, the less-automatic saccades have longer response latencies (Schutz et al 2012).

Saccades are clearly an integral part of active vision, but they also create problems. The continuous motion of the eye means that the images on the retinae are continuously changing: and as the retinae are connected topographically to visual cortex, the ‘neuronal’ images in early visual cortex also change on each saccade (see online appendix and supplementary movies 1–3 at <http://dx.doi.org/10.1068/p7392> for illustration of “what the brain sees”). So how does the brain construct a stable representation of the world from sensors mounted on such unstable platforms?

This is an old and venerable problem that has fascinated many scientists—including Descartes, Helmholtz, Mach, and Sherrington—and goes right back to the 11th-century Persian scholar Abū `Alī al-Hasan ibn al-Hasan ibn al-Haytham (latinized as Alhazen):

“For if the eye moves in front of visible objects while they are being contemplated, the form of every one of the objects facing the eye ... will move on the eyes as the latter moves. But sight has become accustomed to the motion of the objects’ forms on its surface when the objects are stationary, and therefore does not judge the objects to be in motion” (Alhazen 1989 [1083], page 194; Howard 1996).

Research into stability has been characterized by polarization of viewpoint. Helmholtz (1866) argued that image motion caused by eye movements is sensed but not perceived, and “the effort of will involved in trying to alter the adjustment of the eyes” (page 206) corrects for the image motion, while Sherrington (1918) argued that the position of the eye was determined

by proprioceptive sensors, rather than an intention-to-move signal [see Donaldson (2000) for an excellent discussion of ‘inflow’ and ‘outflow’ theories]. Later, MacKay (1973) introduced some fascinating and influential ideas, suggesting that neither signal was required—that the problem could be solved visually. The latest polarization is over retinotopic or spatiotopic representation, summarized recently by Wurtz (2008, page 2081):

“Research falls into two camps: one believes that we maintain only a map of what is currently on the retina, and that this retinotopic map is simply updated with each saccade; the other that a spatiotopic map [exists] within the brain and that each successive retinal image updates this higher-order map.”

2 Spatiotopic versus retinotopic

In this paper we suggest that dichotomies of this sort are artificial. The problem of creating a stable percept of the world is incredibly complex, involving neural representations to navigate through and rapidly interact with our environment, as well as furnishing the rich perceptual experience of a high-resolution, stable world. Given the evidence that space is encoded in multiple representations (Colby and Goldberg 1999), it seems highly likely that multiple mechanisms for spatial stability coexist. We propose here two classes of mechanisms for stability: (1) a rapid-acting, high-resolution system of transient spatiotopy, based largely on retinotopic representations that dynamically adapt on each saccade, bridging the disruption of the saccade to provide transsaccadic perceptual continuity; (2) a slowly developing, low-resolution system of spatiotopic maps, coarse representations of the world in real-world coordinates, tightly linked with perceptual memory and motor planning.

3 A rapid system of *transient craniotopy*

Some twenty years ago, Duhamel et al (1992) made an amazing discovery: just before monkeys make a saccade eye movement, the receptive fields of many cells in the lateral intraparietal cortex (LIP) shift, in the direction of the saccade, so they respond in anticipation to stimuli that will fall in the monkey’s receptive field at the conclusion of the saccade. Receptive fields had always been considered a fixed property of cells, emanating from hardwired neural connectivities to the retina; yet these cells seem to anticipate the action of the saccade, and have been termed ‘remapping cells’.

But what exactly does this remapping achieve? Why shift the receptive field in the direction of the saccade? As supplementary movie 4 shows, shifting in this direction not only does not help stability but exacerbates the problem: first the field shifts on the retina, then the retina shifts—in the same direction—with the eye movement so the receptive field is displaced from its original position by twice the saccade amplitude. The answer, we believe, lies in the fact that the remapping shifts are transient: after the shift they return to their resting retinotopic positions (Burr and Morrone 2011). Although this return has not been explicitly documented physiologically, it must occur at some time, as on the next trial the receptive field of the cell has returned to base. And this return to base is what we believe achieves stability. Figure 2 (and supplementary movie 5) sketches the idea: during the initial fixation, the ‘classic’ receptive field falls on the baptistery, to the left of fixation. The anticipatory remapping shifts the (‘future’) field to the cathedral facade, before the eyes start to move. Then, as the eyes move to the new fixation, the receptive field begins to relax back into its original (classic) position, remaining on the facade. For the entire duration covering the end of the current fixation to the beginning of the next, the receptive field remains on the facade, providing a basis for perceptual continuity. In other words, the return shift creates a period of what we can term ‘transient craniotopy’. Note that the return action from the remapping does not need to match exactly the dynamics of the saccade; as we will see later, the system tolerates a reasonable degree of mismatch.

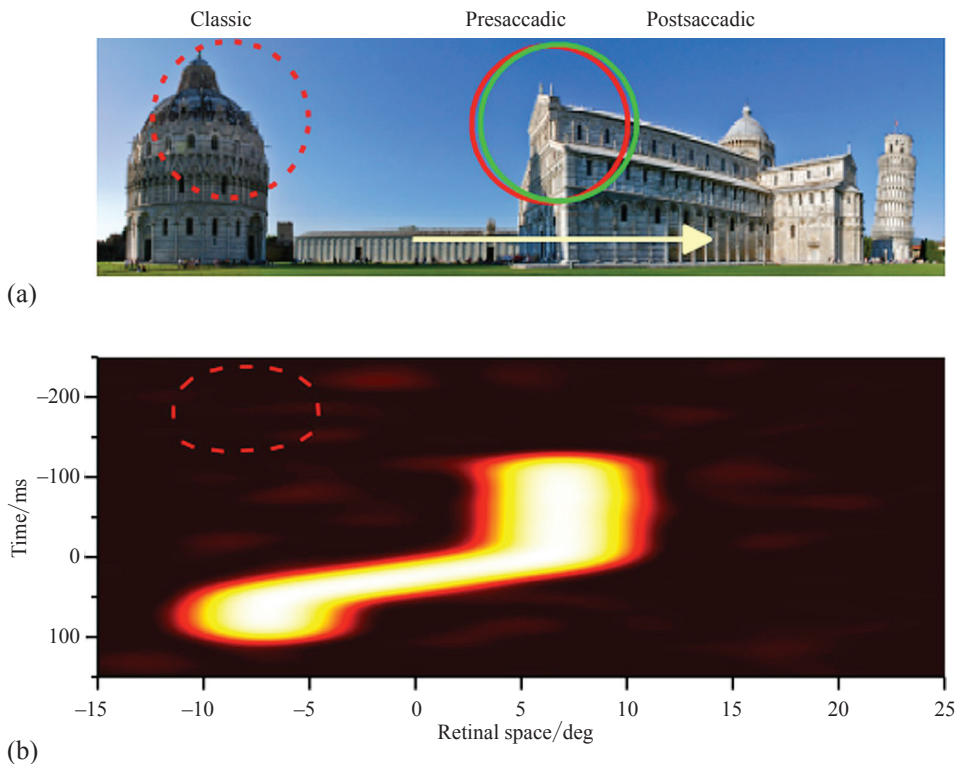


Figure 2. [In colour online.] (a) Illustration of ‘remapping’ of receptive fields (see also online supplementary movies 4 and 5). On the initial fixation the ‘classical’ receptive field of a particular cell will fall on the baptistery (dashed red circle). Then, just before the eye movement to the second fixation (white arrow shows gaze change), the receptive field *remaps* its position to fall on the cathedral facade (continuous red circle). Then, as the eyes move, the receptive field returns to its original ‘classical’ position (on the retina) so it remains on the facade in external space. (b) Schematic representation of the spatiotemporal response selectivity of the remapping neuron as it relaxes back to its resting position. In retinal coordinates this spatiotemporal ‘receptive field’ is oriented in space–time along the same direction as the retinal motion, and thereby annuls it. The dashed ellipse shows the tuning of the receptive field before the remapping shift.

It is useful to describe the spatiotemporal characteristics of the transient spatiotopy with a space–time response profile, which we can consider to be the *spatiotemporal* receptive field (figure 2b). In retinal space the spatiotemporal receptive field is slanted for an extensive period, reflecting the fact that the position of the receptive field changes with time as the receptive field returns to its resting position. The slant in space–time is roughly parallel to the trajectory of the saccade, and therefore annuls the displacement caused by it.

The idea that a receptive field oriented in space–time could annul the effects of saccadic eye movements is similar to that proposed to annul the effects of retinal motion. Motion detectors can also be described as having spatiotemporal receptive fields that are slanted in space–time, and it is the slant that facilitates blur-free perception of objects in motion (Burr and Ross 1986; Burr et al 1986; Burr and Thompson 2011). More recently, the concept of slanted spatiotemporal motion detectors has been applied to explain ‘nonretinotopic’ perception of moving objects (Boi et al 2009), which seems to be anchored in a motion-based rather than retinotopic coordinate system (Pooresmaeli et al 2012).

To date, most physiological experiments have concentrated on the preparatory shift in receptive fields, and have not measured in detail the dynamics of their return to resting state, so there is little direct evidence in support of what we conjecture. However, there does exist strong but indirect evidence in favour of transient spatiotopy, which we outline below.

4 Neural and perceptual latencies

There are two basic requirements for any motion mechanism: a displacement in space, and a commensurate delay in time. Therefore, a strong prediction from the spatiotemporally slanted receptive field is that neural (and perceptual) latencies should be longer for stimuli presented immediately prior to a saccade than for stimuli presented later. In other words, stimuli flashed anywhere along the slanted space–time map should arrive synchronously. And given the duration of a typical saccade, we would expect quite long delays, in the order 50–100 ms.

Figure 3a shows responses of a ‘remapping’ neuron in frontal eye fields (FEFs) to stimuli flashed just prior to the saccade, at various times, spanning a range of 70 ms (personal communication from Joiner and Wurtz). The response latency to stimuli presented earlier is longer than that for stimuli presented later, so all three responses arrive at the same time, as predicted by the slanting spatiotemporal receptive field. For any downstream neural structure these responses are indistinguishable. Wang et al (2008) have reported very similar results for neurons in the LIP.

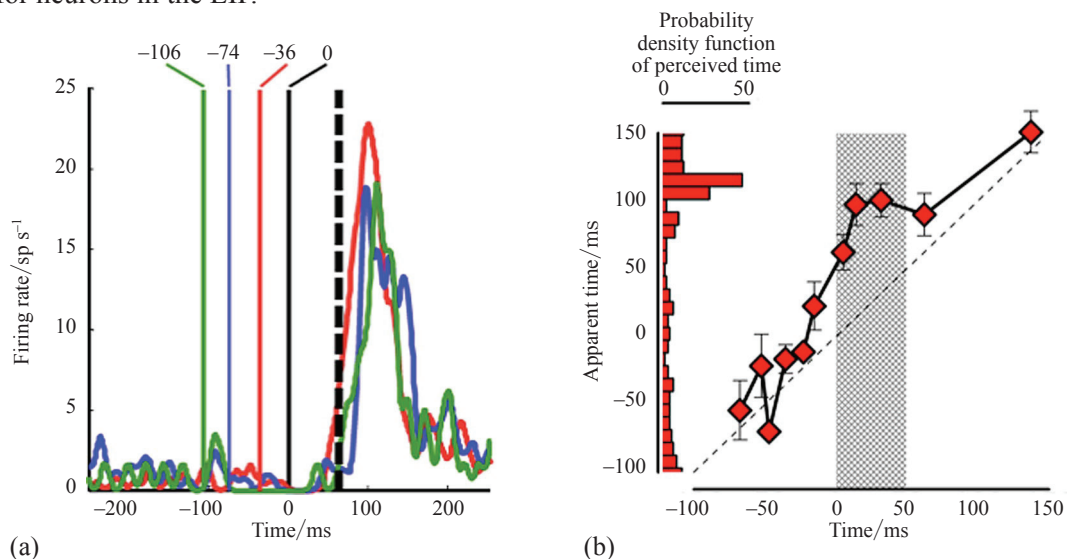


Figure 3. [In colour online.] (a) The response of a neuron in the frontal eye fields of a macaque monkey to stimulation at various times relative saccade onset: curves are aligned to the saccade (0 ms). For the three stimulation times (spanning a range of 70 ms) the responses all arrive at the same time, consistent with the tilt of the hypothetical spatiotemporal receptive fields of figure 2b. Reproduced with permission of Robert Wurtz. (b) Apparent time of presentation of visual flashes flashed (measured by comparison with an auditory standard) as a function of time from saccadic onset. Consistent with the electrophysiological recordings, stimuli presented over a wide range of physical times are perceived to arrive simultaneously, after completion of the saccade. The histogram to the left shows the probability of the stimulus being perceived at any particular time (normalized by physical frequency): there is a clear peak around 120 ms after saccadic onset. Reproduced with permission from Binda et al (2009).

Analogous effects are observable perceptually (Binda et al 2009). Figure 3b shows the results of a perceptual temporal order judgment, where subjects had to perceptually align a briefly flashed visual stimulus with a sound, yielding estimates of the perceived timing of the flash. For a long period spanning the saccade the perceived presentation time of the flash was strongly delayed, so all stimuli presented within the period indicated by the dashed line were perceived to arrive at the same time, around the time the saccade landed. This is also reflected in the probability density function at the left of the graph, showing that stimuli all tend to be perceived at the end of the saccade. It is not possible to compare absolute durations between the perceptual and physiological experiments (because of the different techniques in estimating time), but the general pattern is the same: stimulation over a wide temporal

range causes the physiological and perceptual responses to arrive at the same time. Work by Hunt and Cavanagh (2009) supports this conclusion: they showed that, when asked to report the time of a fast-moving clock as the eyes landed, the time was anticipated compared with controls, consistent with delays in processing at the time of saccades.

5 Classification images at the time of saccades

The use of *classification images* is an agnostic psychophysical approach to study the mechanisms subserving perceptual tasks (eg Eckstein and Ahumada 2002; Neri and Levi 2006). We have applied this technique to monitor changes in the spatiotemporal receptive fields around the time of saccades (Panichi et al 2012). The technique is essentially an inverse noise analysis. Subjects are required to detect a near-threshold target embedded in noise (see supplementary movie 6). After thousands of trials, all the noise images leading to identification of the target (both hits and false alarms) are added, and those leading to rejection (both misses and correct rejections) are subtracted, to form a global mean noise ‘classification image’, thought to reflect the shape of the response field of the underlying neural mechanisms.

Figure 4 shows examples of spatiotemporal classification images for a stimulus presented well before the saccade (upper image), and a perisaccadic stimulus (lower), 30 ms before saccadic onset (see supplementary movie 7 for an entire sweep). At 90 ms before saccadic onset the classification image superimposes the space–time position of the actual image

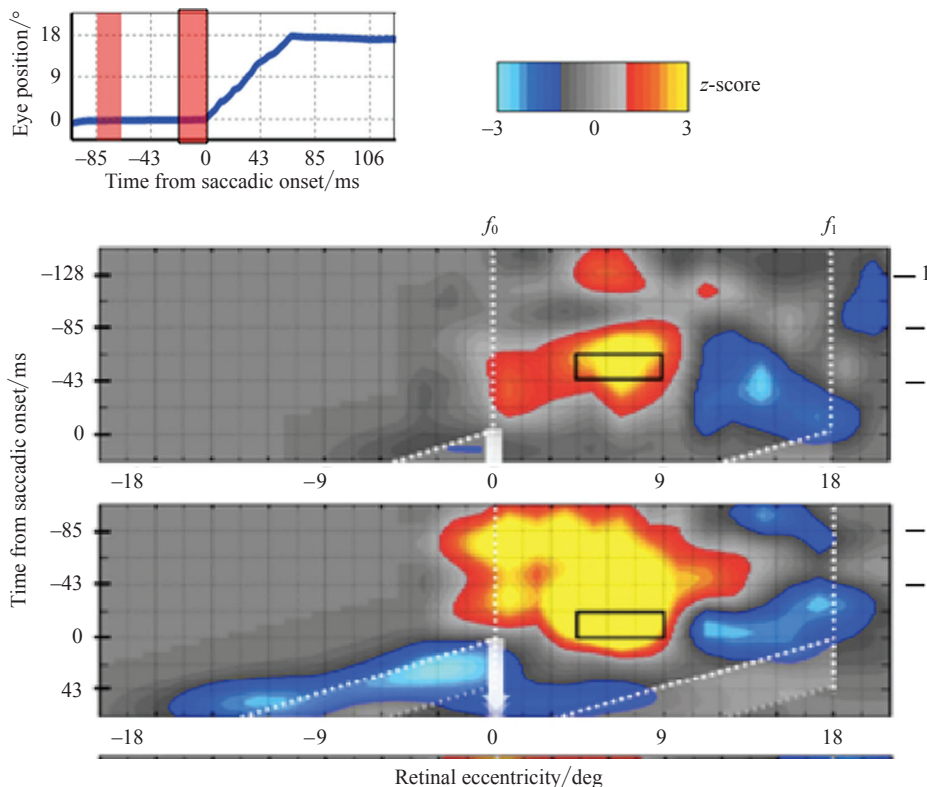


Figure 4. [In colour online.] Classification images for detecting a bar briefly flashed around the time of the saccade. The colour coding indicates the strength of the response, in z -scores. Supplementary movie 7 shows how the image develops over time. The upper plot is a classification image for a bar flashed 85 ms before saccadic onset (indicated by pink bar in time course at top left). The spatiotemporal selectivity of this image is very similar to that of the physical presentation (indicated by the black square). The lower figure shows the classification image for a bar flashed 30 ms before saccadic onset. Here the spatiotemporal selectivity of the image no longer follows the physical presentation, but is clearly oriented in space–time. Reproduced with permission from Panichi et al (2012).

(with some blur). However, when the stimulus is presented perisaccadically it creates a classification image that extends away from the stimulus in both space and time, consistent with the oriented spatiotemporal receptive field. If we accept—as most do—that the classification images reflect neural activity, this is very strong evidence for the existence of spatiotemporal receptive fields that become slanted in space–time at the time of saccades. And it is the spatiotemporal slant of these fields, we argue, that enables transient spatiotopy.

6 Perceptual localization of brief perisaccadic stimuli

It is well known that stimuli briefly presented around the time of saccades are mislocalized, usually towards the saccadic target (Honda 1989; Ross et al 1997). The functional role of the mislocalization has been somewhat of a mystery, although most agree it relates to processes mediating visual stability. Recently, we measured perisaccadic mislocalization of two successive bars, presented around the time of saccades (Cicchini et al 2012).

In one version of the experiment two bars were presented: a black *probe* bar followed 80 ms later by a white *reference* stimulus of similar size, shape, and vertical position. Subjects were required to report the apparent position of both probes. When the probe was presented well before or after saccadic onset, it was seen veridically, near 0°, where it was presented (figure 5). But when presented around the onset of the saccade, the bar was mislocalized towards the reference bar (that followed it by 80 ms) for the three possible positions of the reference. The reference, presented after the saccade had been completed, attracted the perisaccadic probe bar and stabilized it (although it remained perceptually distinct). The same occurred when the reference precedes the probe bar: the perisaccadic probe was mislocalized towards the stable reference. However, for this to occur the probe and reference must be of similar form and vertical position: orthogonal bars, or bars displaced

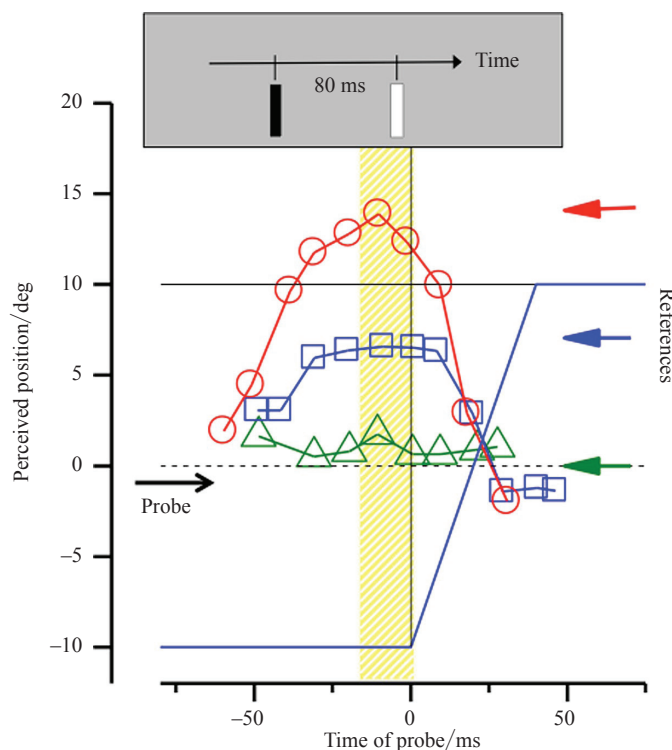


Figure 5. [In colour online.] Perceived position of a probe bar briefly flashed at screen centre (0°) as a function of time relative to saccadic offset. The probe was followed by a reference bar displayed 80 ms after the probe at horizontal positions of 0, 7, or 14 deg (colour-coded arrows at right). Just prior to saccadic onset, the probe tended to be mislocalized, towards the reference bar.

vertically, do not affect the position of the probe. The effect is, however, immune to colour, so black bars stabilize white, and vice versa (making the psychophysical judgments easier).

The effects occur over a wide spatiotemporal range, about 20 deg of space and 200 ms of time. Figure 6 shows the spatiotemporal range of interactions, the range where the more stable reference influences and displaces the labile probe. Figure 6a plots the interaction range in screen coordinates. The field is roughly parallel to the time axis, reflecting the fact that stimuli in similar positions on the screen are attracted to each other. However, when plotted in retinal coordinates (figure 6b) the plot is clearly slanted in space–time, in the direction of the saccade. The interaction range is not limited by retinal proximity, but by proximity in external space: it is the slant that ensures that stimuli in similar positions in external space (therefore highly likely to have been generated by the same object) are integrated over the saccade. These results are broadly consistent with observations from a very different paradigm—saccadic suppression of displacement (Bridgeman et al 1975; Deubel et al 1998).

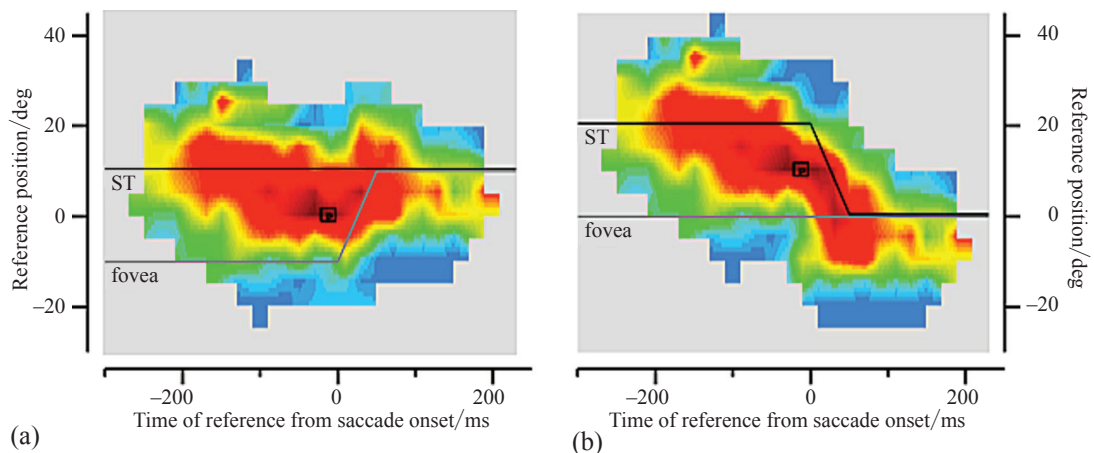


Figure 6. [In colour online.] Spatiotemporal map of interactions between a perisaccadic probe presented at screen position -1° (black square). The abscissa shows the time of the reference bar and the ordinates the horizontal position of the reference bar, in both (a) screen coordinates and (b) retinal coordinates. The grey and black lines show the position of the fovea and of the saccade target, respectively. The interaction indices at these coordinates were interpolated and smoothed to generate the map (hot colours indicate strong interaction). As predicted, the interaction map is oriented in space–time in retinal coordinates.

What is most striking about this result is the similarity to the classification image of figure 4b. The techniques were completely different: one was simply a detection task, identifying whether the stimulus was in the upper or lower half of the screen; the other required subjects to report on the apparent position of a briefly flashed bar. But both techniques led to the receptive field slanted in space–time, as predicted by considering the behaviour of remapping neurons, and as predicted by mechanisms that demonstrate transient spatiotopy.

Observation of the space–time response fields of figure 6 reveals the action of two mechanisms: one extraretinal and one based on visual information. The extraretinal signal—the change in selectivity of the receptive field as it returns to its resting position—creates the slant in the receptive field, so it integrates stimuli that are close in space rather than on the retina. But the response field is broad, so integration occurs for stimuli falling within a wide range around this preferred spatiotemporal configuration. The remapping of the receptive fields sets the *roadmap* for the search for likely candidate features to integrate, then visual mechanisms perform the integration, within these rough constraints. The problem is loosely analogous to that of stereofusion, combining the two images for stereovision. Vergence movements bring the images into rough alignment, and then visual mechanisms solve the *correspondence problem* (knowing what should fuse with what). Many solutions

have been proposed for solving the correspondence problem, the most successful involving cross-correlation mechanisms (Filippini and Banks 2009). Similar mechanisms could be involved in matching presaccadic and postsaccadic images.

We have outlined three separate lines of evidence in support of our notion of oriented spatiotemporal receptive fields, which create transient spatiotopy at the time of saccades. Neurons with these receptive fields will integrate presaccadic and postsaccadic stimuli, bridging the perceptual gap. This is very much a forward-looking mechanism, anticipating the problems that the saccade will cause and solving them preemptively. At the time the eye movement is planned (well before it actually occurs), receptive fields of many units shift in the direction of the saccade to the position they will occupy after the eyes move. Then as the eyes move, the receptive fields relax to their resting positions. During this entire period from the moment the remapping shift is completed until the next remapping, the receptive field is centred on the same region of space: in other words, it is *transiently spatiotopic*. As the intention-to-move signal is necessarily coarse and sluggish, this defines only the general range over which matching could occur. Visual mechanisms, akin to cross-correlations, may then merge the presaccadic and postsaccadic glimpses.

7 Spatiotopic maps

The mechanism described above works essentially with retinotopic neural representations, transiently updated across saccades. But does this mean that this is the only system at work: “That we maintain only a map of what is currently on the retina, and that this retinotopic map is simply updated with each saccade” (Wurtz 2008)? We think not. We believe that there exists another more long-term system, which preserves the updated spatial information in a spatiotopic coordinate system. We present here evidence for spatiotopy from imaging, adaptation, and eye-movement studies. It is important to understand that constructing a spatiotopic representation or map does not mean that each detail, each ‘pixel’, needs to be updated with each eye movement. The map is a representation of image features, such as information about form, spatial relationships, motion, and duration of events. Thus if spatiotopic maps exist, they must represent space, motion, and time—and perhaps number—in a world-centred coordinate space.

Electrophysiological studies have shown that neurons in specific areas of associative visual cortex, including V6 (Galletti et al 1993), and VIP (Duhamel et al 1997), show spatiotopic selectivity, as their tuning is invariant of eye position. Indeed, even primary cortex V1 is modulated to some extent by gaze (Celebrini et al 2009; Durand et al 2010).

The BOLD response of the human MT complex also varies with gaze position, in a way that is consistent with spatiotopic coding (d’Avossa et al 2007). We measured BOLD responses to random-dot motion stimuli presented separately at four horizontal screen positions, while subjects maintained fixations at one of three different gaze directions. Figure 7 shows BOLD responses for V1 and MT for the three gaze positions (indicated by the dotted vertical lines), plotted in screen coordinates. In V1 the responses are clearly retinotopic, so they move with external space to remain aligned with the fixation point. For MT, however, the curves are far more aligned in spatial coordinates, showing a clear selectivity for the contralateral region of visual, rather than retinal space.

We define an index of spatiotopy, essentially the degree to which the response curves at the different fixations are more similar when aligned in spatiotopic or retinotopic coordinates (Crespi et al 2011). Using this index, the BOLD response is spatiotopic in much of the dorsal visual cortex (figure 8a). While the response of V1, V2, and most of ventral cortex is clearly retinotopic (yellow/red colour code), much of dorsal cortex is spatiotopic (blue code).

We next asked to what degree the results may rely on attention, by repeating the measurements while subjects were required to perform an attentionally demanding task at

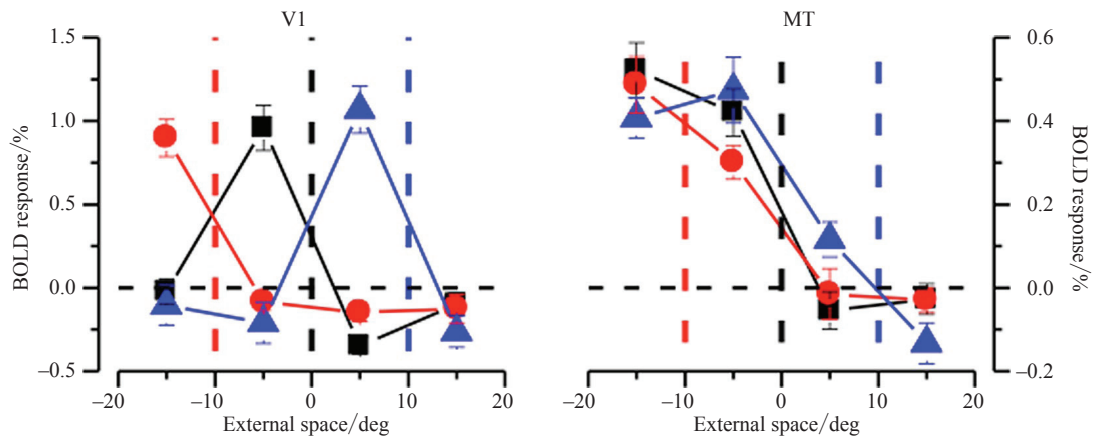


Figure 7. [In colour online.] Tuning of BOLD responses of areas V1 (left) and MT (right), plotted in external (screen) coordinates. Subjects fixated one of three positions (indicated by the colour-coded vertical dashed lines at 0 and ± 10 deg), while vertically moving dot stimuli were displayed at one of four spatial positions (± 7.5 deg or ± 15 deg). While the responses of V1 are clearly retinotopic, aligned with fixation rather than screen centre, those of MT line up in screen coordinates, suggesting that MT codes stimuli in external rather than retinal spatial coordinates. Adapted with permission from Crespi et al (2011).

the centre of the screen (the origin of the retinotopic coordinate system), rather than allowing subjects to attend to the stimuli. The results (shown in figure 8b) are surprising: 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 (2008), who also reported retinotopic BOLD responses for the entire visual cortex when attention was directed to the fovea.

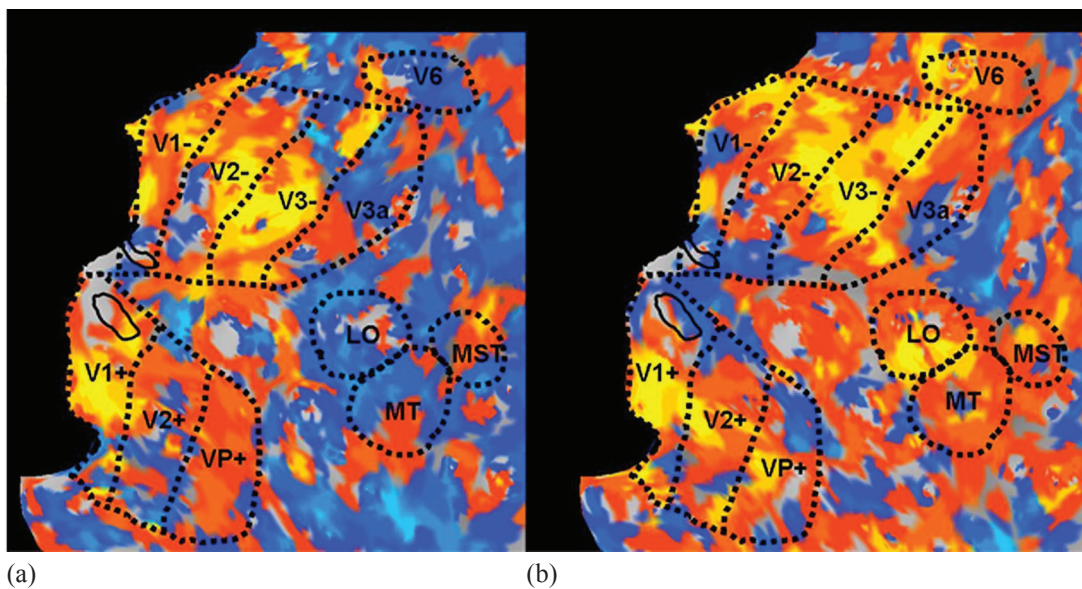


Figure 8. [In colour online.] Flatmaps of visual cortex showing spatiotopic selectivity for one observer, while she (a) viewed the moving stimuli passively or (b) simultaneously performed a demanding concurrent task in the fovea. The spatiotopic index (the degree to which the responses lined up well in spatiotopic or retinotopic coordinates) is colour-coded from -1 (blue) indicating spatiotopy to 1 (red-yellow) indicating full retinotopy. Large areas of dorsal cortex (including areas MT, MST, and LO) are spatiotopic during the single task condition, but become retinotopic during the dual task. Adapted with permission from Crespi et al (2011).

Much evidence suggests that attention is allocated in spatiotopic coordinates (Sapir et al 2002; Golomb et al 2008; Pertzov et al 2010; Howe et al 2011) and could be an important mechanism mediating spatiotopic coding (Cavanagh et al 2010). This raises the fascinating possibility that attention is essential for the creation of spatiotopy. 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 neurons in the area being scanned, cannot be ruled out. It is therefore imperative that the imaging studies should be backed up by solid psychophysics showing that observers can integrate information across saccades, and then this should be used to improve performance.

Psychophysical evidence for spatiotopy abounds. Melcher and Morrone (2003) showed that motion signals can be integrated across saccades, provided they are spatially coincident, and Ong et al (2009) have shown that short-term memory for motion is encoded in spatiotopic coordinates—further evidence for functional spatiotopicity in motion areas such as MT. Melcher (2005) has applied adaptation techniques to show that orientation is encoded at least partially in external coordinates (see also Demeyer et al 2010). Colour adaptation also seems to be head-centred (Wittenberg et al 2008), while contrast (thought to be processed primarily in V1) seems to be purely retinotopic (Melcher 2005).

But what about motion aftereffects? As imaging studies reveal dorsal cortex to be spatiotopic, the motion aftereffect, or ‘waterfall illusion’, would appear to be a prime candidate. However, Addams’s (1834) original report suggests that it is primarily retinotopic:

“Having steadfastly looked for a few seconds at a particular part of the cascade ... and then suddenly directed my eyes to the left to observe the sombre age-worn rocks contiguous to the water-fall, I saw the rocky surface as if in motion upwards” (page 373).

In other words, the spatial selectivity of the effect moved with the eyes, from the waterfall to the sombre age-worn rocks. This casual observation has been confirmed more formally in two laboratories (Wohlgemuth 1911; Wenderoth and Wiese 2008; Knapen et al 2009).

However, adaptation to motion affects perception in many ways, including the perception of space. Supplementary movie 8 shows an example of the *positional motion aftereffect* (PMAE): after adapting to opposing motion in the two windows for a brief period, the windows seem to be displaced in the direction opposite to the motion direction when the motion stops (Snowden 1998; Nishida and Johnston 1999). The motion clearly distorts a spatial map for a brief period of time: is this map spatiotopic or retinotopic? We adapted subjects to fast motion with the eyes viewing one fixation point, then tested them after they shifted gaze to a second fixation target (Turi and Burr 2012). The adaptation and test stimuli were aligned in either retinotopic or spatiotopic coordinates (or in neither, for the control condition).

The results were clear-cut. When the physical speed of the test was adjusted so that it appeared stationary after adaptation (cancelling the classical motion aftereffect), the positional motion aftereffect was entirely spatiotopic (figure 9a). This also occurred for brief test gratings, which did not appear to drift. However, the classic motion aftereffect (figure 9b), measured under identical conditions, is almost entirely retinotopic, as others have found (Wenderoth and Wiese 2008; Knapen et al 2009). This suggests that motion is analyzed at various levels: some (presumably early) are retinotopic, giving rise to the retinotopic MAE, while other higher-order areas show a spatiotopic reference map. These higher areas seem to be more related to processing space, rather than velocity per se.

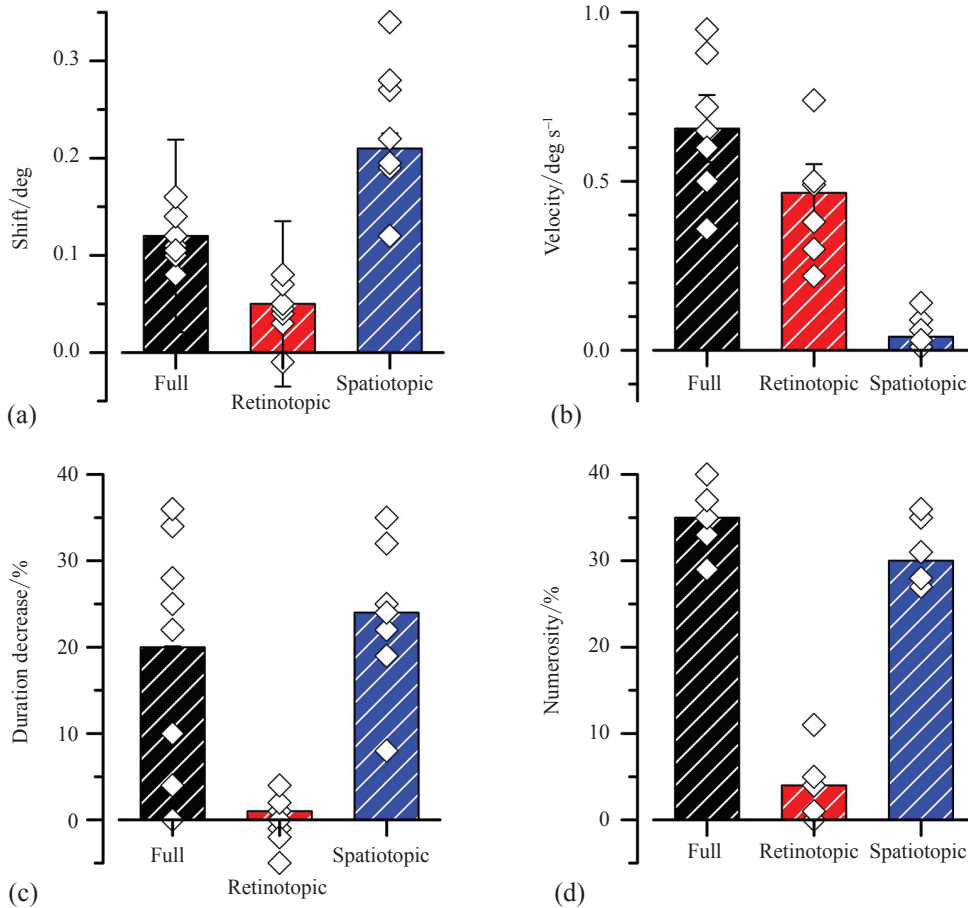


Figure 9. [In colour online.] Spatiotopic versus retinotopic adaptation for four different aftereffects. In all cases subjects were adapted to stimuli in one position, then moved their eyes before presentation of the test in either the same retinal (red) or screen (blue) position. As a baseline, adaptation was also measured with no intervening eye movement ('full' adaptation: black). (a) The positional motion aftereffect: the change in apparent position after adapting to fast motion. In this example the velocity of the test was adjusted so that it appeared to be stationary, producing entirely spatiotopic effects. (b) The classic motion aftereffect: the apparent motion of opposite direction after adapting to continuous motion. This aftereffect is almost entirely retinotopic. (c) Reduction in perceived duration of a grating presented for 600 ms after adapting to fast (20 Hz) motion. As with the positional motion aftereffect, the velocity of the test grating was adjusted so that it appeared stationary; and, again, the effects were entirely spatiotopic. (d) Adaptation to numerosity. In this variant subjects adapted to fast or slow streams of serially presented stimuli, then estimated the numerosity of subsequently displayed serial stimuli. For this form of numerosity adaptation (but not the more standard form) the effects were entirely spatiotopic. Adapted with permission from Turi and Burr (2012) and Burr et al (2007).

That the maps can be warped by relatively brief periods of motion adaptation suggests that they are not permanently hardwired, but highly plastic, readily modified by sensory input. Adaptation probably reflects recalibration processes (Barlow 1990): that it should adapt to motion signals suggests that the map is very much a dynamic one, coding both position and velocity of objects. This could be an important property for predictive saccading to moving targets.

Using a different paradigm (the tilt aftereffect), Zimmermann et al (2012) showed that spatiotopy takes time to develop. After a period of adaptation to a tilted grating, subjects saccaded to a target, either immediately or after variable duration. The results show that only when the saccade was delayed for at least 500 ms was there a strong spatiotopic effect, suggesting that spatiotopy requires both time and attentional resources to construct.

What else does the spatiotopic map encode? Elsewhere, we have argued that the neural representations of space and time are inherently linked (Burr and Morrone 2006). One line of evidence for this is that the perception of event duration can be adapted by motion signals, and the adaptation is spatially specific (Johnston et al 2006). Is the spatial selectivity retinotopic or spatiotopic? Figure 9c (from Burr et al 2007) shows that, when the speed of the probe stimulus is adjusted to match the apparent speed of the test, the effect is entirely spatiotopic, like the PMAE. This result has been replicated on a large subject set (Burr et al 2011).

Most recently, we asked whether the perception of number, or numerosity, was spatiotopic. Like other primary sensory attributes, numerosity shows strong adaptation, and the adaptation is spatially specific (Burr and Ross 2008). Again, we can ask what the spatial coordinate system of the adaptation is. With the standard adaptation paradigm introduced by Burr and Ross (2008) adaptation is primarily retinotopic (unpublished observations). However, in a variant presented at ECVF 2012 the adaptation was spatiotopic (Arrighi et al 2012). In this experiment subjects were adapted to a temporal sequence of events presented at a fast or slow rate: the fast stream caused a subsequently presented spatial pattern of dots to appear less numerous; a slow stream caused them to appear more numerous. Again, the effect was spatially specific; and, again, the specificity was entirely spatiotopic (figure 9d). Why the *cross-format* (serial versus parallel) form of adaptation should reveal spatiotopic processes, while the more standard adaptation is primarily retinotopic, is not clear. Perhaps adapting to spatial arrays can be confounded by texture adaptation, which may have primarily a retinotopic origin.

The picture that clearly emerges is that there exist spatiotopic neural maps in human visual cortex. But these maps are not static snapshots, but highly plastic *information maps* signalling the position, velocity, duration, and numerosity of objects. Elsewhere, we and others have argued that these attributes—space, time, and number, and also motion—are intrinsically interrelated, and share neural resources (Walsh 2003; Burr et al 2010). They also seem to share a spatiotopic neural representation.

8 Spatiotopy and saccades

How is spatiotopy related to the planning and execution of saccades? Eye movements clearly provide a potential source of information for spatiotopy. Therefore, we may expect that interfering with the saccades—for example, by systematic false feedback—should impact on the spatiotopic maps.

A standard technique of conditioning saccades by false feedback is ‘saccadic adaptation’. Subjects saccade towards a target, but at the onset of the saccade the target is displaced systematically by a set amount: after a few trials the system adapts to the displacement—presumably interpreting it as an error signal—and saccades go directly to the displaced position. There is much debate about where the adaptation occurs, in the visual system or the motor plant, but there is good evidence that for outward adaptation (displacement of the target away from fixation) the adaptation has a strong visual component (Ethier et al 2008). There is also evidence that the adaptation affects visual maps, even when no saccades are made (Awater et al 2005; Zimmermann and Lappe 2010, 2011). So it is natural to ask whether the visual component of saccadic adaptation is retinotopic or spatiotopic.

Zimmermann et al (2011) investigated the spatial coordinate system of saccadic adaptation with a memory-guided, double-saccade, outward-adaptation task, designed to maximize visual adaptation and to dissociate the visual and motor corrections (see figure 10 and supplementary movie 9). When the memorized saccadic target was in the same external position as that used in the adaptation training, saccade targeting was strongly influenced by adaptation; but when in the same retinal, but different external spatial position, targeting was unaffected by adaptation, demonstrating spatiotopic selectivity (figure 10). Analogous effects have been observed in macaque monkeys (Wulff et al 2012).

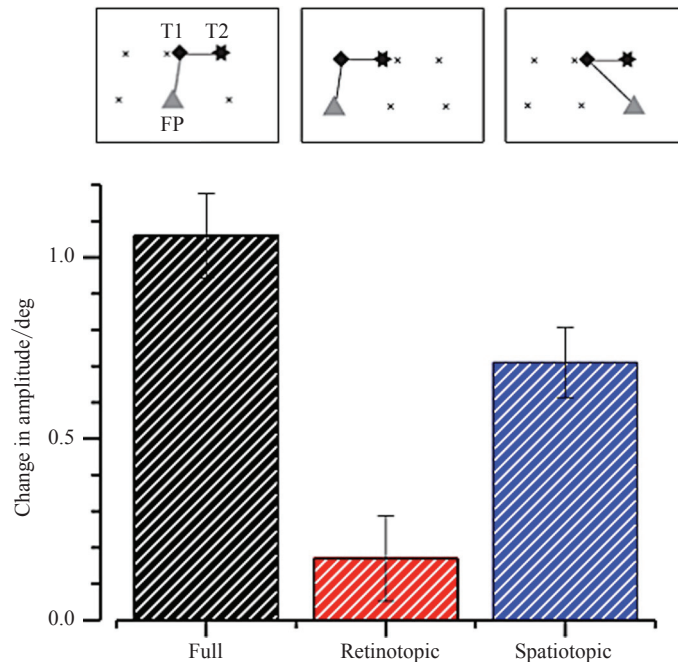


Figure 10. [In colour online.] Spatial framework of saccadic adaptation. The upper-left icon shows the sequence of saccadic adaptation, from the fixation position (FP) to T1 then T2. At the onset of the second saccade (to T2); T2 was displaced outwards by 10%. After a few trials the system adapts to the displacement and goes straight to the displaced position of the target. During testing in the ‘full’ condition, the same layout was used, but the saccades were to remembered positions rather than actual targets. For the retinotopic condition (middle icon) all three targets were shifted leftwards, preserving the retinal specificity while changing that on the screen. In the spatiotopic condition only FP was shifted rightwards, so T1 and T2 occupied different retinal but identical screen positions. The bar graphs show the results, expressed in degrees of saccade overshoot. The spatiotopic condition was significant, and nearly as strong as the full condition, while the retinotopic condition showed no significant effect (** $p < 0.001$).

With the head stable, the spatiotopic selectivity is consistent with both spatiotopic and craniotopic selectivity. To disentangle the two, we interspersed a head-turn between the adaptation and test phase. Under these conditions adaptation selectivity remained anchored in external, rather than head-centred, coordinates. These results point to the existence of a spatiotopic neural representation for eye-movement control, which adapts in response to saccade error signals. The error signals seem not to be a single vector, to be applied across the whole field (as may be expected if, for example, a particular muscle had weakened), but a calibration matrix, or map, anchored in spatiotopic coordinates.

Spatiotopic maps may be connected with saccades in two ways: they may serve as the basis for saccade planning (Mays and Sparks 1980; Pertzov et al 2011), as they remain solid with successive eye movements. But the connection could also go the other way: saccades serve to *build* spatiotopy, providing the information necessary to update the map in external coordinates.

If eye movements do provide the spatial information for the spatiotopic maps, what is the source of the information? Is it, as Helmholtz (1866) suggested, an efferent signal accompanying each saccade, the so-called ‘efference copy’ (Von Holst and Mittelstädt 1954) or corollary discharge (Sperry 1950); or, as Sherrington (1918) affirmed, an afference signal from proprioceptive output. Poletti et al (2012) reported, at ECVF, data suggesting that both signals are used, combined together in a statistically optimum fashion. These results sit well with the physiological evidence for both efferent (Sommer and Wurtz 2002, 2006) and afferent (Wang et al 2007) extraocular signals.

9 Concluding thoughts

In this paper we have examined some of the mechanisms responsible for encoding and representing space as the eyes move. We believe the evidence points to (at least) two mechanisms, one fast and transient, the other slower and long-lasting. The fast system of transient spatiotopy comes into action as the saccade is planned, long before the eyes actually move. It anticipates the physical saccade by what we can consider as ‘virtual saccade’, a shift of the receptive field in the direction of the saccade; then, when the physical saccade begins, the receptive field relaxes to its original position, counteracting the saccadic displacement and maintaining continuity. Preparing for the consequences of the saccade well before its onset ensures that there is no gap in visual continuity: the neuron has anticipated the saccade motion, and has simply to revert to its resting state to remain spatiotopic during the saccade. This process is somewhat approximate, not cancelling precisely the effects of saccades, so visual mechanisms also come into play to help align presaccadic with postsaccadic images. This system of transient spatiotopy does not require the construction of additional higher-order spatial maps, but can use the retinotopic representations of primary visual cortex: and these are the only high-resolution maps of the cortex.

However, the evidence for a more permanent spatiotopic map is also very compelling. These maps are not static snapshots, but are rich with information about position, motion, time, and number. They are strongly connected with eye movements, as saccadic adaptation readily modifies the maps. These spatiotopic maps are extremely malleable, changing properties after relatively short periods adaptation (especially to fast motion) and to systematically false saccade-error signals. The maps are not updated immediately, but only after 500 ms or so, and require attentional resources for this process. The high malleability of the maps suggests that they are not hardwired, but dynamically constructed online from a range of signals, both retinal and extraretinal (efferent and afferent), and these require continual calibration. Adaptation interacts with the calibration. The existence of these maps is consistent with the physiological evidence for multiple representations of space in parietal cortex, in different reference frames, crucially dependent on attention (Colby and Goldberg 1999).

The exact purpose of the long-term spatiotopic maps is still not entirely clear. Their most probable function is connected more with action than perception, guiding our physical interaction with the world: navigation, object grasping, and guidance of saccades, all of which require a relatively stable reference frame. We suspect that they could also be connected with the ‘saliency maps’ that, among other functions, help choose saccade fixations. And their longevity suggests that they could also be connected with visual memory, a record of the immediate history of world. However, it is interesting that while their function may well be more for action than perception per se, adaptation of these maps also changes appearance, suggesting much cross-talk between action and conscious perception. Future research would be to examine not only how they depend on eye movements but also how they interact in general with action systems, including vestibular and other representation of body position (Land 2012).

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