Exp Brain Res (2010) 206:121–128
DOI 10.1007/s00221-010-2334-z

REVIEW

Spatial maps for time and motion

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Received: 24 December 2009 / Accepted: 11 June 2010 / Published online: 23 June 2010

Abstract In this article, we review recent research studying the mechanisms for transforming coordinate systems to encode space, time and motion. A range of studies using functional imaging and psychophysical techniques reveals mechanisms in the human brain for encoding information in external rather than retinal coordinates. This reinforces the idea of a tight relationship between space and time, in the parietal cortex of primates.

Keywords Spatial coding · Time · Motion · Spatiotopicity · MT

Maps and visual stability

The problem of how a stable representation of the world is created from the output of sensors mounted on very unstable platforms (the eyes) is an old one that has fascinated many scientists, including Descartes, Helmholtz, Mach and Sherrington, and indeed goes back to the eleventh century Persian scholar Abí `Al 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 1083). Although the problem of visual stability is far from solved, tantalizing progress has been made over the last few years, some of which are related to the discovery of a stable *spatiotopic* representation of the world centred in real-world external coordinates that the brain construct from successive fixations.

Because of the spatial selectivity of individual neurones, the response of primary and secondary visual cortex forms a *map* (see Morgan 2003), similar in principle to that imaged on the retinae (except for distortions due to magnification of central vision). This *retinotopic* representation, which changes completely each time the eyes move, forms the input for all further representations in the brain. So a major question is how this retinotopic representation becomes transformed into the *spatiotopic* representation that we perceive, anchored in stable real-world coordinates. In this article, we review some imaging and psychophysical studies from our laboratory examining cortical mechanisms of spatial maps, in particular those involved in the perception of motion and of event time. We also report new original data showing that mechanisms involved in timing the duration of events are not only *craniotopic* (anchored in head-centred coordinates) but truly *spatiotopic* (anchored in external, real-world coordinates).

Electrophysiologic studies have shown that neurons in specific areas of associative visual cortex, including V6 (Galletti et al. 1993) and VIP (Duhamel et al. 1997), do show the selectivity that is at least craniotopic (head-centred), as their tuning is invariant of eye position. Indeed,

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even primary cortex V1 is modulated to some extent by gaze (Trotter and Celebrini 1999), particularly peripheral V1, with a tendency to privilege directions that are "straight ahead" (Durand et al. 2010). However, we are still far from understanding the mechanisms mediating the transformation from retinal to craniotopic coordinates. One influential suggestion is that the fusion of the retinal signal with eye position signals is sufficient in principle to generate craniotopic maps, probably acting via eye-position dependent modulation of the neural response, also referred to as "gain fields" (Zipser and Andersen 1988; Snyder et al. 1998; Pouget et al. 2002).

It is important to understand that constructing a spatiotopic representation or map does not mean that each detail, each pixel needs to be shifted 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 in a world-centred coordinate space. It should be pointed out that spatiotopicity is not the only solution to the stability problem. Other mechanisms, such as transient remapping (see for example Wurtz 2008), almost certainly contribute, but we will concentrate on spatiotopicity in this chapter.

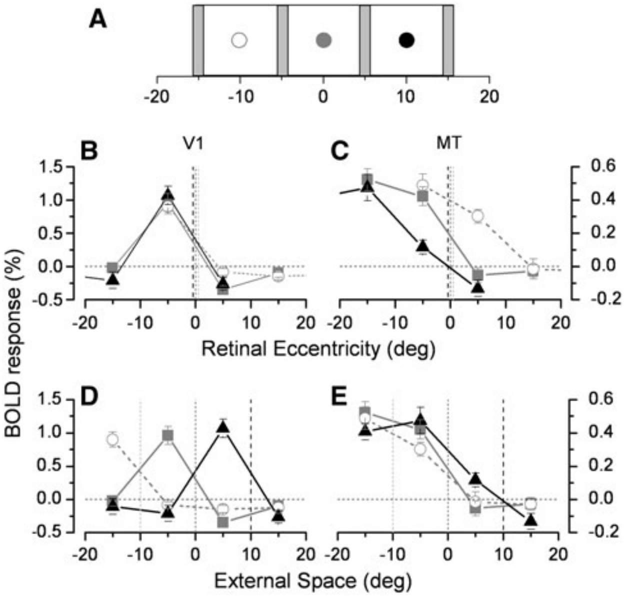

Fig. 1 Retinal and external tuning of V1 and MT BOLD response. **a** The icons illustrate the stimulus conditions: subjects fixated one of three positions (indicated by the *grayscaled dots* at 0 and ±10°, while vertically moving dot stimuli were displayed at one of four spatial positions (±7.5 or ±15°). **b** and **c** Response of V1 (**b**) and MT (**c**) of the three (*grayscaled*) fixations in retinal coordinates: Those of V1 line up well, those of MT clearly displaced. **d** and **e** The same responses plotted in external, screen coordinates: now the MT responses line up well, suggesting that MT code stimuli in external spatial coordinates. The responses of V1 clearly do not line up in external space

Spatiotopic coding in human cortex

Functional Magnetic Resonance Imaging has also indicated the existence of spatiotopic coding in human cortex, in LO (McKyton and Zohary 2007), an area involved in the analysis of objects, in a multisensory area with some similar properties to monkey VIP (Sereno and Huang 2006; Silver and Kastner 2009), and in human complex MT+ (Goossens et al. 2006), the presumed homologue of monkey area MT (middle temporal area). Our group (d'Avossa et al. 2007) has studied the human MT complex and shown that the BOLD response varies with gaze position in a way that is consistent with spatiotopic coding. We measured BOLD responses to random-dot motion stimuli presented at random to one of four screen positions while subjects maintained fixations at one of three different gaze directions, while stimuli were presented in one of four positions (chosen at random) for a duration of 15 s (see panel A in Fig. 1).

The other plots in Fig. 1 show BOLD responses for V1 and MT for the three gaze positions, plotted both as a function of retinal and of external (screen) space (panels B–C and D–E, respectively). In V1 (curves at left), gaze did not alter the retinotopicity of the response: for the three different fixations, the response curves are widely separated when plotted in screen coordinates, lining up with the fixation point (Fig. 1d). For MT, on the other hand, the curves almost line up in spatial coordinates, showing a clear selectivity for the contralateral region of visual space (Fig. 1e). Work in progress by Ong and Bisley (2010) has suggested a possible mechanism for the spatiotopicity. They show that that many cells in area MT show "post-saccadic remapping", a post-saccadic response to stimuli flashed in the "future receptive field" after the saccade has been completed.

Although these data showed clearly that the spatial tuning of MT is anchored in an external, spatiotopic coordinate system, this result is currently controversial: Gardner et al. (2008) report that under the conditions of their experiment, the response of MT is retinotopic rather than spatiotopic. One interesting possibility is that the difference in results relies on attention. In Gardner et al's study, attention was directed toward the fovea (the origin of the retinotopic coordinate system), while subjects in the d'Avossa et al. study were free to attend to the stimuli. We are currently testing this hypothesis by replicating our study under two conditions: passive fixation, as before, and while subjects performed an attention-demanding task at fixation. The results are surprising: with passive viewing many areas of the dorsal stream (MT, MST, LO and V6) are all clearly spatiotopic, but when attention is directed to fovea these same areas become retinotopic (Crespi et al. 2009). It is well known that attention can modulate the BOLD response in single neurons of MT. Indeed, attention can shift the peak of MT receptive fields but quite large amounts, toward the attended stimuli (Womelsdorf et al. 2006). While this in itself will not produce spatiotopicity, it does show that receptive fields are plastic and can be modulated by many factors.

Evidence shows that attention can be allocated either in retinal and spatiotopic coordinates (Sapir et al. 2004; Golomb et al. 2008) 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 spatiotopicity. As it is well know 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.

The fact that head-centred coding is more common in the dorsal area may suggest that it is necessary for action. The action system seems to update spatial maps much later than the perceptual system for a contingent movement (Cohen and Andersen 2002). Perhaps the updating of craniotopic maps takes time, but leads to more robust coding of information, explaining the resistance of the action system to saccadic mislocalization (Burr et al. 2001; Morrone et al. 2005a; Wurtz 2008). The perceptual system, on the other hand, may not always operate with a complete map anchored in external coordinates, and in some cases may be more efficient to operate on retinotopic coordinates.

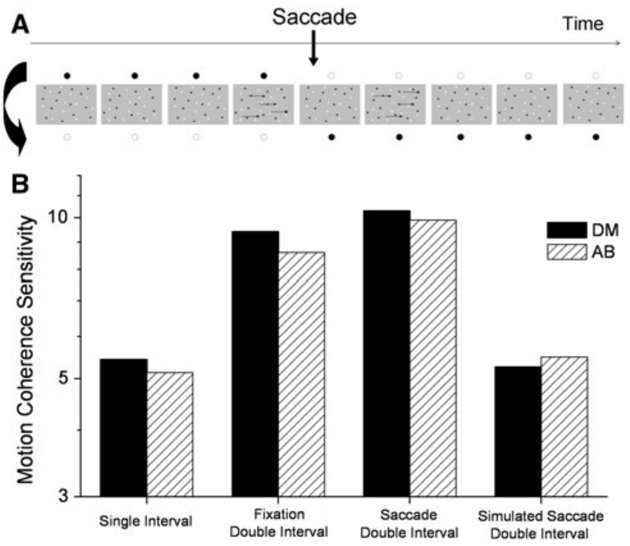

Fig. 2 Integration of motion signals across saccades. **a** Subjects fixated a point above a stimulus of random noise. A weak motion signal was presented for 9 frames, followed by a shift in the fixation point to the *bottom* of the display. Shortly after a saccade, another weak motion signal was presented at the same spatiotopic position. **b** Coherent Motion Sensitivity for a single motion interval and two motion intervals, during steady fixation, separated by a saccade (but in the same external coordinates) and in two different screen locations to mimic the effect of saccades. The retinotopic shift in stimulus location is equal in the saccade and simulated saccade condition; however, the two-fold improvement in sensitivity occurs only during real saccades

The fact that BOLD responses are selective in external coordinates does not in itself prove that those areas have a functional spatiotopicity. The origin of the BOLD signal is not well understood, and the possibility that it reflects feedback from higher areas 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. In a recent study, Melcher and Morrone (2003) showed that observers can integrate motion signals, individually below threshold (and hence not perceived when presented alone) across saccades, provided the two stimuli are spatially coincident. Two periods of coherent horizontal motion, each lasting 150 ms, were presented successively, separated by sufficient time to allow for a saccadic eye movement between them. On some blocks of trials, subjects saccaded across the stimulus between the two motion intervals, while on others they maintained fixation above or below the stimulus. As Fig. 2 shows, thresholds were similar in the two conditions, showing that the motion signals were temporally integrated across the saccade—but only when the two motion signals were in the same position in space, indicating that the brain must use a mechanism anchored to external rather than retinal coordinates. Importantly, the methodology excluded cognitive strategies or verbal recoding, since the motion signals presented before and after the saccade were each well below the conscious detection threshold—only by summating the two signals could motion be correctly discriminated. Recently, Ong et al. (2009) have shown that short-term memory for motion is encoded in spatiotopic coordinates, which they interpret as further evidence for spatiotopicity for in MT.

These results may appear to contrast with much evidence that stimuli are not integrated across saccades, but vision starts afresh on each fixation (Irwin et al. 1983; Jonides et al. 1983). We suggest that the reason for this is that information is integrated from one fixation to the next, but the integration occurs for features—such as motion and form—not light elements or pixels. The process is not like “sticking postage stamps on a tailor’s dummy”, integrating detailed “snapshots” within a trans-saccadic buffer with an external metric. Indeed, such a scheme could be problematic, as scenes change continuously as objects move and rotate: inappropriate *pixel-wise* integration could lead to very weird perceptual representations. This is of course consistent with the fact that V1 does not seem to be spatiotopic (at least as far as fMRI evidence is concerned), while MT and MTS are clearly spatiotopic. These areas would integrate motion signals across saccades, not the detailed description of the individual dots that generated the motion signals.

What about other higher level (or mid-level) properties, such as orientation and shape, and more specialized systems such as those involved in recognizing faces. Melcher's (2005) adaptation experiments suggest that all these attributes are encoded at least partially in external coordinates (see also Demeyer et al. 2009; see also Demeyer et al. 2010). Also color adaptation seems to be head-centred (Wittenberg et al. 2008). Contrast, on the other hand, seems to be purely retinotopic. This is consistent with the fact that contrast is processed primarily in V1, which shows less tendency toward spatiotopicity.

Coding of temporal duration

While spatial vision has been thoroughly studied over the last few decades, little effort has been dedicated to the complementary problem of the perception of time, such as how we judge the duration of visual events. It has long been thought that events are timed by counting ticks of a centralized clock, in the same way that a computer is controlled by a clock in its central processing unit (Treisman 1963). However, much recent work suggests that space and time are not independent, but tightly linked. And some evidence suggests that there exists not just one single clock, but many, positioned to cover the visual field.

Adaptation is one of the more effective of the psychophysicist's battery of tools. There are a myriad of examples of how adaptation changes the spatial appearance of the world, causing many well-known aftereffects (Thompson and Burr 2009). Recently, it has been shown that the duration of an event is also affected by adaptation, in a spatially specific manner. Johnston et al. (2006) have shown that adaptation can also affect apparent duration. After adapting to a fast moving grating, stimuli displayed to the adapted region of the retina appeared shorter than those displayed elsewhere. The reason for the altered duration is still unclear but, whatever the mechanism by which adaptation causes underestimation of duration, it is clear that the effects are spatially specific.

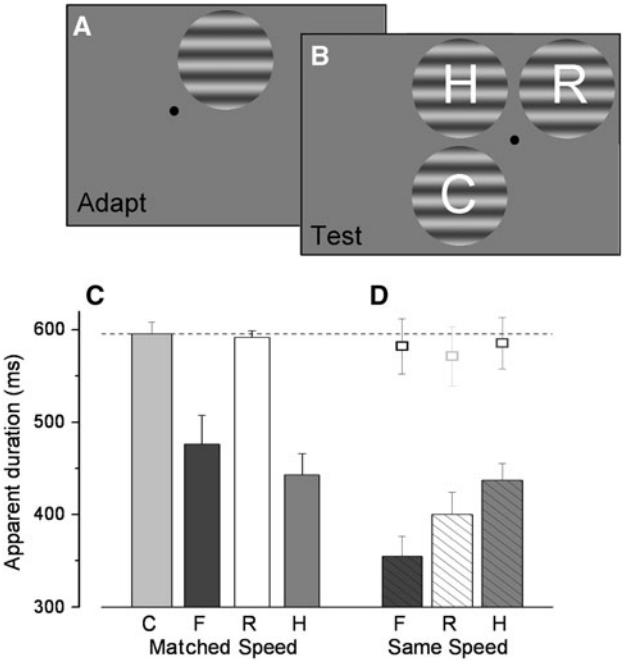

Fig. 3 Spatially selective adaptation to time. **a** Illustration of the stimulus used to study adaptation of apparent duration. Subjects fixated a point at left of centre, while the adapting stimulus—a grating drifting at 20 Hz periodically reversing direction—was presented in the upper central field (as shown). **b** The test could then appear in one of three different position: the same part of the screen as the adaptor (indicated *H* for head-centred); the same retinal position (*R*); or a control position (*C*) corresponding to neither retinal nor head-centred position. The test was presented for 500 ms, followed by a 500-ms pause, followed by the *probe* stimulus presented to the *lower right* position of the screen (where the test never appeared). For the results shown in **c**, the speed of the probe was adjusted to appear the same as the test, for the results in **d** the speeds were the same (10 Hz). Subjects judged in two alternative forced choice which presentation, the test or probe, appeared to be longer. Psychometric functions were calculated yielding the point of subjective equality (PSE) of the test and probe. **c** Apparent duration of the test (defined as the PSE of the psychometric functions comparing test and probe) for four conditions: full adaptation (F), where subjects' gaze remained at the initial fixation point and the test was displayed in the same position as the adaptor; and for the control, retinotopic and head-centred conditions described earlier. Both full and head-centred adaptation caused a large decrease in the apparent duration of the test. The *upper square symbols* in **d** show the mean durations measured in identical conditions without adaptation

We pursued further the adaptation of event duration and showed that the adaptation was spatially selective in external, or at least craniotopic coordinates (Burr et al. 2007). We used a technique introduced by Melcher (2005), where subjects stare at a fixation point to the left of a grating drifting rapidly (20 Hz) within a well-defined window (see Fig. 3). After extensive adaptation, the fixation point—and the subject's gaze—moves to the right. A drifting test grating (10 Hz) is then displayed for 600 ms in one of three possible positions: in the same position the adaptor had occupied on the screen (*craniotopic* condition), in the same position the adaptor occupied relative to fixation (*retinotopic* condition), or in a completely different position, below left of fixation (*control*). In separate sessions, the fixation dot did not move, and the test was presented in the same retinotopic and craniotopic position as the adaptor (*full* adaptation). One-second after the presentation of the test, a *probe* grating (of variable duration) was presented to the lower left of fixation, and subjects were required to report whether it seemed of shorter or longer duration than the test. Psychometric curves were calculated, from which the point of subjective equality (PSE) was estimated from the median. In order to ensure that the changes in apparent duration were not merely a result of the apparent slowing of the grating after adaptation, the physical speed of the probe was adjusted to match the apparent speed of the test (in practice this was necessary only for the retinotopic and full adaptation conditions).

Figure 3c shows the perceived durations for the four conditions, averaged over 5 observers. In the control condition, the average duration was about 600 ms, close to the real physical duration of the stimulus. Interestingly, the average perceived duration for the retinotopic condition was also around 600 ms, not significantly different from the control, while for the craniotopic condition the average duration was 440 ms, similar to the full adaptation condition. This suggests that under these conditions, with probe speed matched to the apparent speed of the test, the adaptation is primarily craniotopic. In another control condition (Fig. 3d), probes of the same physical speed as the test were used, yielding retinotopic-specific adaptation, similar in strength to the craniotopic effect (hatched bars at right).

These results suggest that at least two mechanisms are involved in adaptation of duration, one retinotopic and the other craniotopic or spatiotopic. As mentioned earlier, apparent duration of visual stimuli is known to increase with increasing speed (Kanai et al. 2006; Kaneko and Murakami 2009), and adaptation to fast stimuli decreases apparent speed of subsequently viewed stimuli (Wohlgemuth 1911; Thompson 1981). Thus, the retinotopically selective decrease in apparent duration, which occurred only when the apparent speed of the test and probe were not matched (so the probe seemed to drift more quickly than the test), is probably an indirect consequence of the adaptor causing a reduction in the neural representation of speed, rather than direct action on neural timing mechanisms. Craniotopic adaptation, on the other hand, occurred for both the speed-matched probes (which in practice changed little) and the 10-Hz probes, suggesting that its effects do not depend on changes in apparent speed (that are probably mediated by lower-level mechanisms), but reflect direct action on the neural mechanisms of interval judgment, or their afferents. Further studies showed that *dichoptic* adaptation (adapt one eye, test the other) was craniotopically but not retinotopically selective also suggesting that craniotopic adaptation occurs at a higher level than retinotopic adaptation, as there is no anatomic convergence of eye input before V1, with strong functional interactions occurring only at later stages (Macknik and Martinez-Conde 2004).

Head-, object- or external-centred coordinates?

One of the questions that remains is whether the spatial tuning for mechanisms that time events are anchored in head-centred or word-centred coordinates. That is, if the head is turned as well as the eyes, will the tuning remain spatiotopic—anchored to the external screen—or will the tuning move with the head? To answer this, we repeated the experiment with new observers, under two separate conditions: one like the previous one, where observers kept their heads still, nose pointing toward the centre of the screen, and followed the fixation dot with a saccadic eye movement; in the other condition, the subjects head was oriented toward the fixation point, and when it moved the subject tracked it with both eye and head movement. The movement brought the adapter and test stimuli on two different sides of the head: if the adapted neurons were head-centred rather than world-centred, different populations would be activated.

The results are shown in Fig. 4. The open symbols show the results for the craniotopic (head still) condition, the closed symbols for the head-turning spatiotopic condition, both plotted against the retinotopic condition (with head still). As before, the retinotopic condition resulted in no reduction of duration (on average), while the spatiotopic conditions, both with head still and head turning, produced a 15% reduction in perceived duration. Thus, it would seem that the mechanisms that measure event time have a truly external reference frame that takes into account both eye and head movements. Note that also for this new data it was important that the apparent speed of the test and probe are matched. In this case to produce the match the speed of the test was increased in average by 65% (SE = 7%) for the retinotopic, while very little altered for the other two conditions (11% for the craniotopic and 10% for the spatiotopic).

The fact that the adaptation was spatiotopic is interesting. Area LIP does not seem to be truly spatiotopic, but its receptive fields are strongly affected by eye movements in a way to give it a transient spatiotopicity (Duhamel et al. 1992). This area has been shown to be involved with event timing of sub-second intervals (Leon and Shadlen 2003; Janssen and Shadlen 2005), making it a plausible candidate for the spatiotopic-specific adaptation of duration. TMS studies (Bueti et al. 2008) have also implicated this area in duration judgment in humans. All this fits well with our present results, implicating parietal areas like LIP in event duration timing.

Other evidence that LIP is involved in event duration is the fact that estimates of event duration are severely compressed during saccades: stimuli flashed around the time of saccades are perceived as being far shorter than they actually are, about half the physical duration (Morrone et al. 2005b). Furthermore, at some critical times relative to saccadic onset, the perceived temporal order of stimuli can be inverted (Morrone et al. 2005b; Binda et al. 2009).

Interestingly, not only do gaze direction and saccades (Morrone et al. 2005b) affect perceived duration, so does

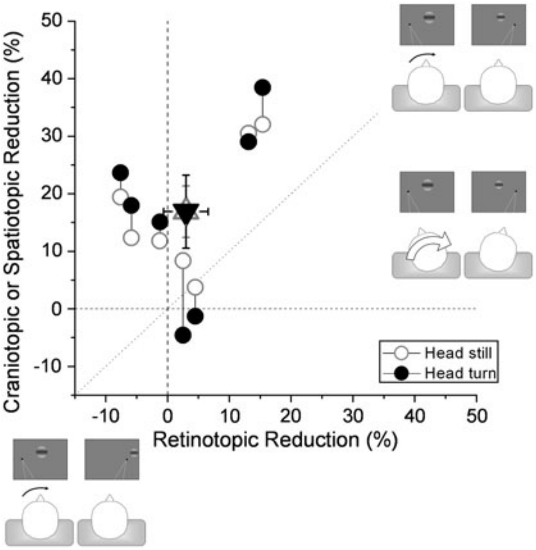

Fig. 4 Effect of adaptation in head-centered and world-centered coordinate systems. Reduction of perceived duration caused by an adapter in the same spatial position as the test, but different retinal position (eyes moved with head still) or different craniotopic position (head moved with eyes fixed relative to head), both plotted against the reduction induced by an adapter in the same retinotopic position. In the head-still condition (*top icons* on the *right*), the adapter and the test stimulus were always in sagittal midline of the subject but the adapter and test stimuli were displayed in different retinotopic positions (*hollow symbols*). In the head-turn condition (*icons* in second row on the *right*), the adapter and the stimuli have different retinotopic and craniotopic positions (*black symbols*). In the retinotopic condition (*icons* on the *bottom*), the test stimulus shifted screen position maintaining the retinotopic position of the adapter after the gaze shift. The test stimulus was a drifting grating whose apparent speed was matched to that of the probe stimulus across all conditions. Individual data points are represented with *circles*, group average with *triangles*. *Vertical bars* connect data from the same subject. Spatial frequency was 1 cpd, distance 58 cm, luminance 35 cd/m^2, contrast 85%. The temporal frequency of the adapter was 20 Hz, of the probe 10 Hz, the temporal frequency of the test varied between 14 and 19 Hz for the retinotopic condition, and 9.7 and 12.5 Hz for the head-still and head-turn condition. *Error bars* are S.E.M

allocation of spatial attention. Much evidence shows that attention can affect apparent duration (Rose and Summers 1995; Enns et al. 1999; Tse et al. 2004). As LIP is also strongly affected by attention (Gottlieb et al. 1998; Ben Hamed et al. 2002), it may be expected that covert shifts in spatial attention, which often precede eye-movements (Deubel and Schneider 1996), could also affect apparent duration, in a similar way to overt eye movements.

These results reinforce those of Johnston et al. (2006) in suggesting that event timing is spatially localized, and the localization is in external, spatiotopic coordinates. Of course this leaves open the question of whether spatially localized timers can be monitored simultaneously by some more central timing mechanisms: some recent evidence (e.g Giora et al. 2006) suggests that they cannot. However, mechanisms with spatiotopic selectivity could serve to time perceptual events that occur in specific spatial positions: when watching a field of fireflies, we have a very clear idea of both the duration and the spatial position of any given flash, and this does not change if we make saccades. As humans saccade on average 3 times per second, it is certainly advantageous that the spatial selectivity of interval-timing mechanisms is grounded in external rather than retinal coordinates.

Attention and perceived duration

We have recently investigated this possibility measuring the apparent separation between two visual stimuli manipulating the subjects' attention with a dual task design (Reeves and Sperling 1986). While maintaining fixation on a central point, subjects allocated their spatial attention to judge which of two laterally positioned circles had undergone a slight expansion (primary task) (Cicchini and Morrone 2009). Two distinct horizontal bars were displayed with 430 or 630 ms separation at two crucial SOAs from the onset of primary task stimuli. As a secondary task, subjects were required to compare the apparent interval separating these bars to a later probe interval. The covert shift in spatial attention causes a strong compression in perceived duration (Fig. 5, black symbols) when the bars are in two different locations. When the bars are in the same location (red symbols), attention has no effect on apparent duration and the interval can be resolved veridically, although it is very long compared to typical visual processing time.

Overall, the results show that the integration of temporal information across space is an attentional demanding process and can be easily distorted. The robustness to alteration of time, measured for one location may indicate the existence of specialized time mechanisms that are tuned for spatial location.

It is interesting to compare the distortion of time caused by attention with that contingent on a saccade. The attentional effect is less extreme (about 30% instead of 50% of its original value), and follows broader dynamics (Cicchini and Morrone 2009). In addition, the attentional effect is multiplicative, about 30% for all intervals up to about 1 s, while saccades cause an overall loss of about 50 ms, which changes very little with the time or the amplitude of the saccade. The saccadic effects are so profound that they not only cause a compression but a delay of about 100 ms of the saccadic stimuli and in particular cases even an inversion of the temporal order, never observed under the attentional condition. Probably the two effects have different origins, but in both cases may be related to a shift in space either of the attention allocation or of the reference frame contingent to the gaze.

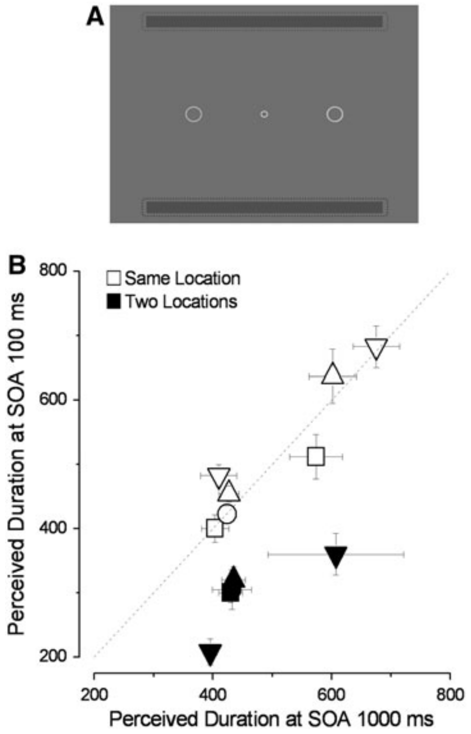

Fig. 5 Effect of attentional shift on perceived duration. *Upper Panel*: Two peripheral red bars separated by an interval of 430 or 630 ms were flashed at two asynchronies (SOA 100 and 1,000 ms) from the stimulus onset of the primary task (size change of one of two circles on the *horizontal midline*). *Lower Panel*: Effect of attention on perceived duration. Perceived duration at an SOA of 100 ms is plotted against the perceived duration at a SOA of 1,000 ms. Data points below the diagonal indicate an underestimation of perceived duration under attentional load. *Black Symbols* refer to intervals marked by *bars* in two different locations, *hollow symbols* to *bars* in the same spatial location. *Different symbol* types indicate different subjects. *Error bars* are S.E.M

Concluding words

The results of these three lines of experiments join with many others (for example Walsh 2003; Bueti and Walsh 2009) in showing that space, time and motion are intrinsically interconnected in the brain. Timing of visual events is achieved by mechanisms that are spatially selective, and selective in a real-world, not retinal, frame of reference. fMRI studies show that many structures of visual cortex are tuned in a spatiotopic manner and that spatial attention plays an important role in building the spatiotopicity. Attention also affects the perception of duration, in a spatially specific manner. These results not only help in understanding that unrelenting mystery of visual stability in the face of continual eye-movements but could also have interesting consequences in understanding pathologies such as spatial neglect, which involve drastic impairment of attentional systems, along with spatial distortions of the world.

Acknowledgments Supported by EEC framework 6 (MEMORY) and 7 (ERC: STANIB) and Italian Ministry of Universities and Research.

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