

Special Issue: Space, Time and Number

Saccades compress space, time and number

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It has been suggested that space, time and number are represented on a common subjective scale. Saccadic eye movements provide a fascinating test. Saccades compress the perceived magnitude of spatial separations and temporal intervals to approximately half of their true value. The question arises as to whether saccades also compress number. They do, and compression follows a very similar time course for all three attributes: it is maximal at saccadic onset and decreases to veridicality within a window of approximately 50 ms. These results reinforce the suggestion of a common perceptual metric, which is probably mediated by the intraparietal cortex; they further suggest that before each saccade the common metric for all three is reset, possibly to pave the way for a fresh analysis of the post-saccadic situation.

Space, time and number as visual primitives

Space, time and number are three central descriptors of visual events. By knowing where, when and how many, we have an approximate representation of a scene. We still do not know who or what, so we lack detail, but we have a crude and preliminary sketch sufficient to orient ourselves and to navigate through the environment. Over the past decade, many studies have suggested that these primitive descriptors share common processing paths in the primate visual system. In this review we interpret available behavioral, neuropsychological and neurophysiological data as evidence of the existence of a common metric for space, time and number. This hypothesis predicts that changes in the metric of the three perceptual attributes should covary. We show that during a saccadic eye movement – a critical moment for the visual system – space, time and number are all affected in a comparable way: the metric of all three is compressed.

A common metric for magnitude

S.S. Stevens [1], distrusting the assumption that just noticeable differences (JNDs) were subjectively equal [2], introduced the psychophysical method of magnitude estimation, which requires subjects to match the ratio of two sensory magnitudes (such as loudness) to the ratio of

two numbers. The ease with which subjects can make the match, and Stevens' success in amassing a mountain of evidence for a power law linking sensory to physical magnitudes, suggested the existence of a common metric [2]. The exponents of the power law can be greater than unity (expansive, such as pain), less than unity (compressive, such as loudness) or equal to one (linear). Interestingly, both space and time have exponents close to unity, suggesting that both are perceived in the same way as number, up to a scaling factor. More recently, Walsh [3] explicitly proposed that a single magnitude system, resident in the parietal cortex, is responsible for the approximate computation of quantity, be it number, space or time, or perhaps anything else.

A visual sense of number

Adult humans in literate and numerate societies have almost all learnt to count, which enables them to estimate number accurately, if slowly and laboriously. But when deprived of the ability or opportunity to count, we – along with many non-human species – can still give a rapid estimate of the number of items in a set, albeit with much reduced accuracy. As first observed by the economist Jevons [4], error increases with set size in accordance with

Glossary

Receptive field: structured region of a sensory surface (such as retina or skin) where an appropriate (or adequate) stimulus (such as a flash of light) causes a sensory cell to respond. Visual receptive fields can also be defined in external space.

Power law: law proposed by S.S. Stevens, according to which perceived magnitudes increase proportionally to physical magnitudes raised to a power. The exponent can be greater than unity (expansive), less than unity (compressive) or equal to one (linear). Much data collected using the Stevens method of magnitude estimation supports his law.

Saccades: rapid ballistic eye movements made on average three times per second to direct gaze towards objects of interest.

Spatial numerical association of response codes (SNARC): range of experimental findings showing that responses to smaller numerosities are faster and/or more accurate in the left space, whereas larger numerosities are advantaged in the right space.

Weber's law: Weber found that the difference between two stimuli that is just noticeable (jnd or differential threshold) increases linearly with the magnitude of the stimuli. Fechner used this finding to conclude that subjective magnitude is proportional to the logarithm of physical magnitude, calling this a law and naming it in honor of Weber. It is sometimes termed the Weber–Fechner law.

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Weber's law [5,6], as it does for brightness, length, speed, shape and time [7], suggesting that, like them, subjective number (numerosity) is a perceptual attribute. Burr and Ross [8] pointed out that if number is a primary stimulus attribute, it should be susceptible to adaptation, and showed that it is: prior adaptation to a more numerous visual stimulus causes a subsequent test stimulus to appear startlingly less numerous (see the [supplementary material online](#)). Stimulus elements in the test stimulus seem to have disappeared after high adaptation and to have appeared out of nowhere after low adaptation.

Many have assumed that estimation of the numerosity of a dot cloud has little to do with other numeric tasks, and might even derive from other visual attributes, such as texture density [9]. However, a series of experiments clearly showed that numerosity is estimated directly and is not derived from texture density or anything else [10]. And importantly, the precision with which children can estimate the numerosity of a dot cloud predicts future mathematical ability [11].

Interactions between space, time and number

Space and number are intrinsically linked [12–14]. Hadamard, who interviewed many mathematicians of his day, reported that many 'see' their solutions first and verify them later [15]. Even more impressively, mental abacus users – who do mental arithmetic by moving the beads on an imagined abacus – are able to use their visual system to perform exact computations, reinforcing the role of spatial representation and showing that language is not necessary for the representation of exact number [16].

Sir Frances Galton hypothesized that numerosities are perceived spatially along a mental line, and that the perceptual machinery dealing with spatial extent is exploited to manipulate numerical quantities [17]. Sometimes people can describe their own internal number line; surprisingly, this varies widely across individuals and in most cases it is not straight or even regular. The notion of a number line has received support from a series of studies on the spatial numerical association of response codes (SNARC) effect, in which smaller numbers elicit faster responses in the left space and larger numbers in the right space, as if the mental number line were mapped onto a spatial representation going from left to right [18]. This link of number to space could help to explain why non-human species with highly developed visual systems can recognize numbers and perform some elementary arithmetic operations such as ordering, addition, subtraction and halving [19]. Interestingly, amblyopia, a visual condition closely associated with poor spatial resolution and spatial distortions, also affects numerosity judgments outside the subitizing range [20].

Experimental evidence has linked number to time as well as to space. Trained animals (rats or pigeons) discriminate duration and numerosity equally well, and administration of methamphetamine produces equal distortions in both tasks [21]. In double-task experiments, counting interferes with duration judgments and vice versa [22]. And a link between time and space has been repeatedly suggested in recent years. Spatial neglect is associated with overestimation of duration [23] and event time seems to be spatially local [24,25].

The intraparietal sulcus and the prefrontal cortex of the primate are both involved in encoding of space, time and number. Neurons tuned to number have been identified in non-human primates in parietal areas including the ventral (VIP) intraparietal and lateral intraparietal (LIP) areas, as well as in a lateral prefrontal region [26–28]. All these cortical structures have spatially selective receptive fields and are implicated in many important spatial tasks, such as attention and planning of saccades and reaching movements [29]. These areas are also involved in encoding time and number. Many cells respond to the number of items in their receptive fields in a graded manner [27], some preferring small numbers of items and others large numbers. This graded coding of numerosity could be the first step towards creating the selectivity to specific numbers observed within the fundus of the intraparietal sulcus and in prefrontal cortex [26]. Many LIP neurons are also modulated by judgments of sub-second intervals [30], indicating that these areas, implicated in numerosity and space processing, also encode temporal intervals. Many human fMRI studies indicate that posterior parietal areas are crucial both for the perception of time [31,32] and number [33], although the prefrontal cortex, subcortical nuclei (basal ganglia) and cerebellum are also involved in time perception [34,35]. Lesions to areas located in proximity to the intraparietal sulcus are

Box 1. Predictive remapping of visual neurons during saccades

Visual neurons encode space in retinotopic coordinates, meaning that the region where they respond to stimuli (receptive field) is fixed on the retina and hence moves with the eyes. A stimulus displayed at a given position in external space drives different populations of cells before and after an eye movement. How do we maintain a stable representation of the visual world across saccades?

In a landmark paper, Duhamel *et al.* reported that receptive fields of many neurons in the LIP area change drastically at the time of saccades, shifting in the direction of the saccade, before the eyes have moved [39]. They respond to a given position in external space both before and (for a brief period of time) after the eye movement, potentially bridging retinotopic maps across saccades [61]. fMRI experiments support the existence of the phenomenon in the human brain as well [62,63]. This predictive remapping has been observed in several areas of monkey cortex, including the frontal eye fields [64] and extra-striate visual areas [59,60], but the parietal cortex – particularly LIP – is the area where the predictive behavior is most pervasive, observed in 40–50% of cells [39]. There is evidence that the remapping is mediated by a non-visual corollary discharge, probably originating in the superior colliculus and acting on the prefrontal cortex [61]. The corollary discharge signal might reach parietal and extra-striate areas by top-down modulation from the prefrontal cortex.

Most researchers believe that the behavior of these cells is responsible both for perceptual stability and for the transient distortions of visual perception observed at the time of saccades. Predictive remapping produces a transient alteration of spatial codes and has been linked to the perisaccadic shift or compression of perceived position [40,48,52,65]. It has been shown that LIP neurons encode information about stimulus timing [30] and number [27], so they could also be implicated in the perisaccadic compression of time [48,49] and numerosity [51]. Recent evidence suggests that neurons in superior colliculus and frontal eye fields encode time with an amplitude magnitude code [66]. It is not yet known whether this encoding strategy is affected by the perisaccadic update, but this would seem to be very likely.

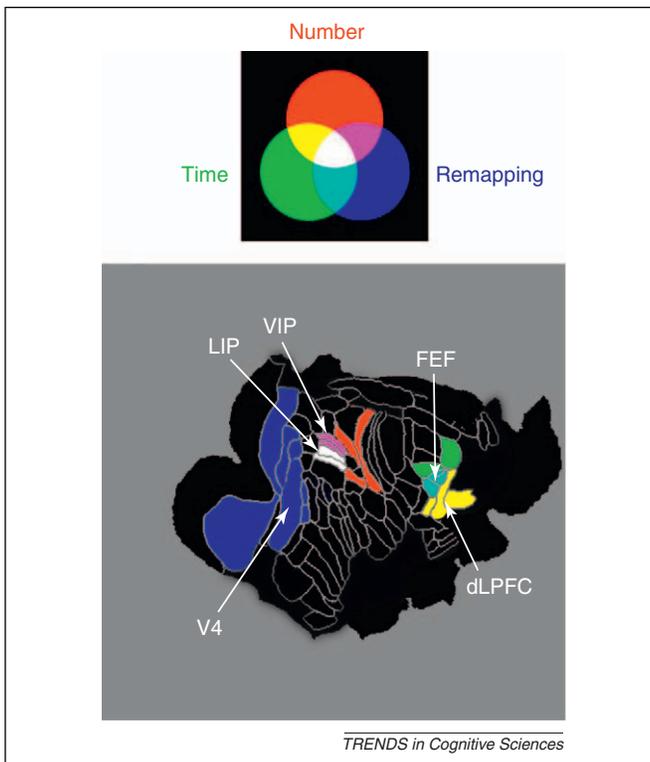


Figure 1. Time, number and perisaccadic remapping in the brain. Flattened cortical surface of a monkey right hemisphere; borders define cortical areas identified in the partitioning scheme by Lewis and Van Essen [57] (the anatomical image with the area borders was downloaded from the Sums database, <http://sumsdb.wustl.edu/sums/index.jsp>, and visualized with Caret, <http://brainvis.wustl.edu/wiki/index.php/Caret>). Areas where the studies in Table 1 identified neurons modulated by numerosity are colored red, those modulated by temporal duration are green, and areas where perisaccadic remapping has been reported are blue. The co-occurrence of two or more of these characteristics is indicated by the summation of the corresponding colors (see legend). Please note that this figure is intended only as a schematic representation and the reader is referred to the original papers for exact localization of the recording sites. It is clearly not an exhaustive account, but shows only the areas that have been studied for these attributes to date. VIP, ventral intraparietal; dLPFC, dorsolateral prefrontal cortex (which includes Brodmann areas 45 and 46).

associated with numerical deficits in patients [18,36], and repetitive transcranial magnetic stimulation affects both the SNARC effect [37] and temporal judgments [38].

The intraparietal region, and area LIP in particular, is perhaps best known for its role in remapping spatial information during saccadic eye movements [39]. Just before each saccade, the receptive fields of many neurons shift in the direction of the saccade. Although the exact role of this anticipatory shift is still not clear (Box 1), most researchers assume that it is related to maintaining stability across saccades. As Figure 1 illustrates schematically, areas where

Table 1. Sources from which the schematic diagram of Figure 1 was constructed

Parameter	Study	Areas
Time	Leon and Shadlen [30]	LIP
	Genovesio <i>et al.</i> [58]	46, 8, 9, 6
Numbers	Sawamura <i>et al.</i> [28]	5, 2
	Nieder and Miller [26]	dLPFC, PPC
	Roitman <i>et al.</i> [27]	LIP
Remapping	Duhamel <i>et al.</i> [39]	LIP
	Tolias <i>et al.</i> [59]	V4
	Nakamura and Colby [60]	V2, V3, V3A
	Umeno and Goldberg [64]	FEF

perisaccadic remapping has been observed and areas where numerosity and temporal information are encoded overlap considerably: the three attributes are represented within frontoparietal networks, which intersect at the level of key areas such as LIP (Table 1). Imaging work suggests a similar picture in humans, although the complexity of the terminology used to identify human cortical areas makes the task of localizing functional circuits and their overlap particularly difficult. Note that Figure 1 is not intended as an exhaustive meta-analysis, but a schematic indication of the areas that have been studied to date; as more areas are studied in greater detail, the extent of overlap might well greatly increase.

Effects of saccades on space time and number

Although several investigators have postulated links between space, time and number, evidence of such links is often circumstantial and somewhat weak. Much relies on the coincidence of neural areas (e.g. intraparietal cortex) and on small advantages in reaction times that can often be put down to congruency effects. The fact that reaction times are faster to small numbers on the left and larger numbers on the right does not necessarily imply a hard-wired connection. For example, many of us who have spent far too much time producing graphs such as Figure 3b associate hot colors with large responses and cold colors with small ones. If we showed faster reaction times for large-red and small-blue, we would not necessarily believe that color and number were linked. To search for stronger links between the three attributes, we investigated the effect of saccadic eye movements on space, time and number. If spatial, temporal and numeral representations share a neural substrate in the posterior parietal cortex and if visual responses on these areas are strongly affected by saccadic eye movements (Box 1), then saccades should interfere in similar ways with the perception of all three perceptual attributes of space, time and number.

Saccades have dramatic but selective effects on visual processing [40]. Some stimuli (modulated in luminance at low frequencies) flashed before or during saccades are strongly suppressed, whereas others (chromatic, or high-frequency luminance stimuli) are not [41]. The effects begin before the eyes begin to move (and are therefore not caused by smearing) and do not occur when the saccades are simulated by fast motion of the scene [42]. The apparent position of visual stimuli flashed briefly around the time of a saccade is also misplaced [43–45], usually in the direction of the impending saccade. But the effects are in fact more complicated: saccades cause not only a simple shift in perceived position, but also a compression of visual space [46,47]. As Figure 2a shows, bars flashed briefly long before or after a saccade are seen veridically in their correct physical positions. Close to the time of the saccade, however, there are huge mislocalization errors and the direction of these errors is always towards the saccadic target: stimuli flashed to the left of the saccadic target (for a rightward saccade) are seen displaced rightwards, whereas stimuli flashed beyond it are displaced leftwards, in all cases towards the saccadic target. Stimuli flashed between -10° and $+20^\circ$ – some 30° of visual space – are all seen near the saccadic target at saccadic onset. This compression,

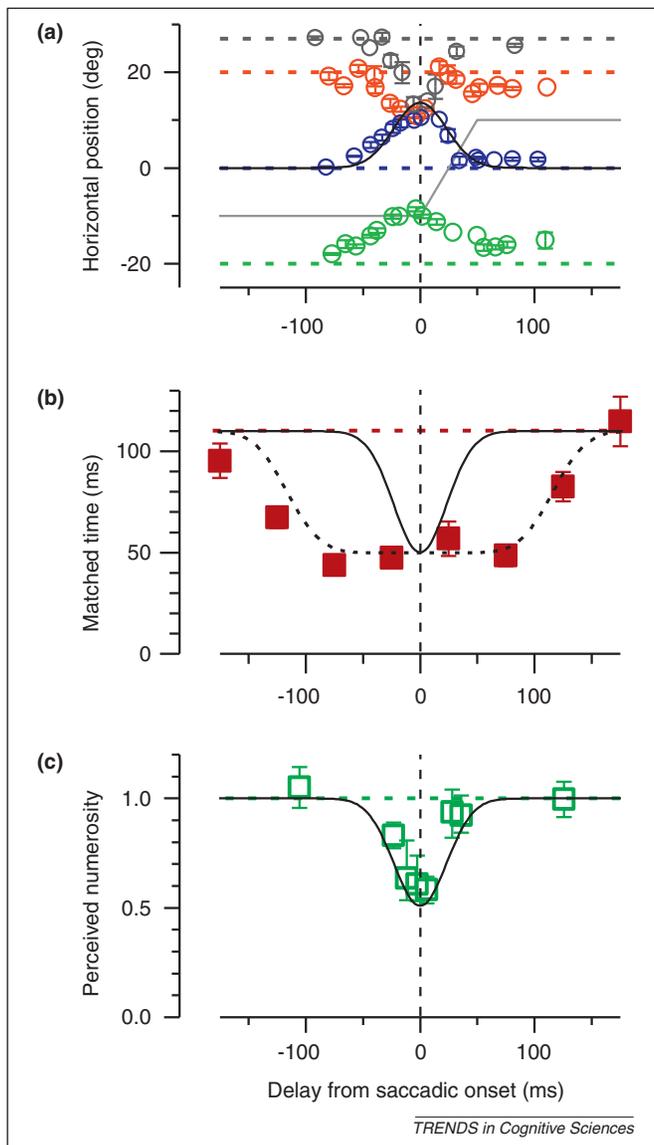


Figure 2. Perisaccadic distortion of space, time and number. Perceptual distortions for stimuli presented briefly at about the time of a large (20°) saccadic eye movement (continuous grey line in panel a). In all plots, saccadic onset is indicated by a vertical dotted line. (a) Perceived spatial location of a bar flashed at four different locations (hollow circles, separate colors) as a function of the time of its presentation relative to the saccade onset. For each presentation, subjects reported perceived bar location relative to a memorized ruler. Localization during fixation is shown by dotted lines. Modified with permission from [46]. (b) Perceived temporal separation of two bars flashed at an interval of 100 ms; the abscissa represents the average time for the bars relative to saccadic onset. Subjects reported (in forced choice) which of two pairs of bars (one perisaccadic, one postsaccadic) was separated by a longer temporal interval. The data were fitted using a cumulative Gaussian psychometric function, for which the mean is an estimate of the perceived duration of the perisaccadic interval (ordinate of the plot). From these data we calculated the predicted time course of the temporal compression signal (continuous curve) by deconvoluting the spline fit of the data (dashed line) with the temporal separation of the two markers in the experiment (100 ms). Note that the predicted time course is much more tightly tuned than the data, because the data were collected with a broad temporal stimulus (100 ms long) that necessarily blurs the effects over time. The dashed horizontal line depicts perceived duration under steady fixation conditions. Modified with permission from [49]. (c). Estimated relative numerosity for a set of 30 random dots flashed perisaccadically, normalized by the steady fixation estimate (dashed horizontal line) [51]. This experiment was similar to the time experiment, except that subjects judged which of two dot stimuli was more numerous: one with fixed numerosity, presented well before the saccade, the other with variable numerosity presented perisaccadically. For each time bin (relative to saccadic onset), and for fixation, we calculated a psychometric function, yielding a point of subjective equality. The plot shows the ratio of the number of dots in the probe when presented during fixation to the number presented during saccades. The black continuous curves in all plots are Gaussian functions with the same mean and standard deviation that best fit all the data.

which cannot result from the simple addition of a single efference-copy vector to the retinal eccentricity signal, is very real, causing multiple bars straddling the saccadic target to collapse down to a single bar [46,47] so great is the underestimation of the distance between them.

Saccades cause a shift and compression not only of space, but also in the perception of event time [48,49]. Figure 2b illustrates the compression. A pair of bars flashed 100 ms apart is seen veridically when displayed well before or after saccadic onset, but close to saccadic onset the apparent interval between them is strongly compressed to approximately half its true value. The compression follows a very similar time course to that for spatial compression. We have pointed out that the compression of space–time around the time of rapid shifts of information has strong analogies to special relativity [50].

Space and time are compressed just before and during saccades. What happens to the numerosity of visual elements? To address this question, we asked subjects to compare the number of elements in a random test array flashed at the time of a saccade to that in a reference stimulus presented well before the saccade [51]. Figure 2c illustrates how apparent numerosity varied with time relative to the saccade. Well before or after the saccade, numerosity estimation is veridical, but close to saccadic onset there is a large and systematic underestimation of number: perceived numerosity is nearly halved. The time course of the compression closely follows those of space and of time. As with saccadic compression, neither space, time or number is affected by simulating the saccade with a fast mirror motion [46,48,51].

Rarely in biology do independent and unrelated measurements follow so closely the same dynamics. Discarding the unlikely possibility of pure chance, the similar time courses point to the existence of common mechanisms – probably resident in parietal cortex (Figure 1) – that modulate the metrics of space, time and number. We presume that compression of all three attributes results in from neural processes that occur at the time of saccades to preserve visual stability. When the eyes move, the visual representation of the world must be remapped to new coordinates, and this remapping commences before the eyes actually move, with rapid and complex deformation of visual receptive fields, most commonly observed in the intraparietal cortex.

The shifting of receptive fields is best understood by considering both spatial and temporal events simultaneously [52,53]. Figure 3a is a cartoon drawn from a recording of an LIP neuron on stimulation to the future receptive field (the part of space that will become the postsaccade receptive field) before, during and after a saccade [54]. The responses are aligned to the saccade and are sorted by stimulus presentation time. The first spikes to all stimuli occur at approximately the same time, implying that pre- and postsaccadic stimulation to this part of space (corresponding to different retinal positions) causes very similar spike trains. A higher-order cell monitoring the response has no way of distinguishing whether a particular spike results from early presaccadic stimulation to the future receptive field or later postsaccadic stimulation of the classic receptive field. The region in space–time that elicits identical responses, all arriving

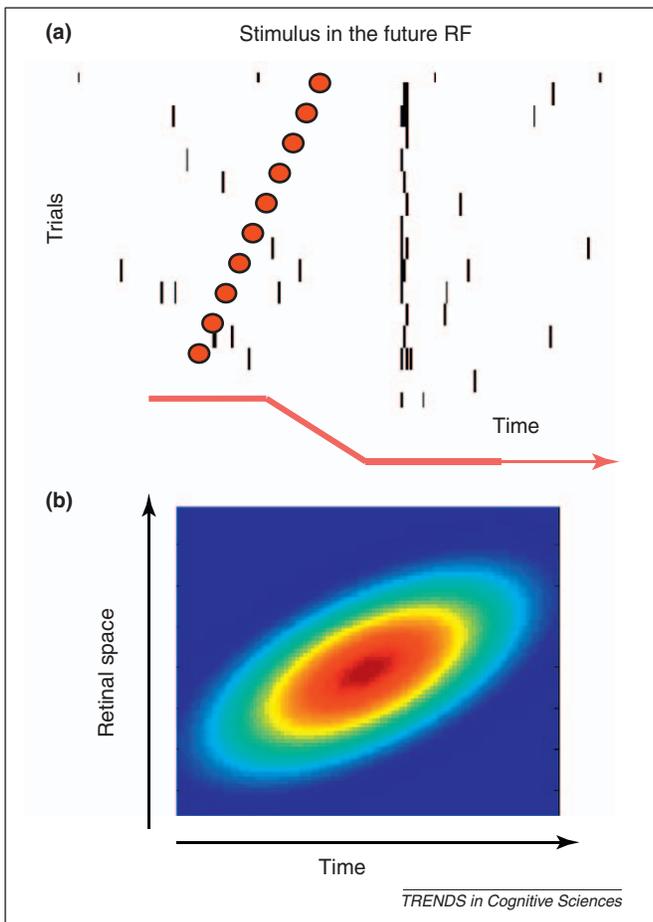


Figure 3. Transient spatiotemporal receptive field during remapping. (a) Cartoon drawn from data reported by Wang *et al.* [54] showing spike responses of a typical LIP cell (short bars) to stimulation in the future receptive field (that becomes the classical receptive field after eye movement). The responses are all aligned to the saccade and are sorted by stimulus presentation time. Systematic delays in the responses cause all spikes to occur at a similar time, and therefore they are indistinguishable. (b) Schematic spatiotemporal receptive field of the neuron, defining the region of confusion in space-time with the same spiking pattern (hot colors indicate stronger responses). The spatiotemporal receptive field is oriented in space-time along the same direction as the retinal motion, and thereby annuls it.

at the same time, defines the transient receptive field of the cell in space and in time, as illustrated schematically in Figure 3b. In retinal coordinates, it is oriented in space-time in the direction of the retinal motion caused by the saccade and therefore cancels its effect (a similar argument for motion was proposed in [55]). The spatiotemporal structure of the receptive field at the time of saccades shows how tightly space and time are linked. It is not immediately obvious how this will also lead to compression of number, other than that the same neural mechanisms that encode space and time also encode number and those with a graded response to number also have receptive fields clearly circumscribed in space.

Spatial location, duration and numerosity form an approximate representation of a stimulus set; thus, the three attributes might well be expected to undergo similar distortions, ensuring that they always co-vary. At this stage it is unclear whether it is the representation of these attributes that is changed or the mechanism that decodes them; either could cause compression. Concurrent deformation of space, time and number has the advantage of maintaining ratios, invariant with the area

of the stimuli on the retinal surface and its cortical representation (which changes considerably with each eye movement), which would facilitate transfer of information from one fixation to the next. Perhaps the brain cannot manage the usual large information bandwidth during the rapid perisaccadic updating process, so it reduces the informational load (keeping important ratios constant) by compression.

Conclusions

The results we consider here support the idea of close connections between space, time and number, perhaps because all three representations are mapped onto a common magnitude line, as assumed by Stevens [2] and proposed by Walsh [3]. The compression could be a direct result of the rapid shifts in receptive field accompanying (and preceding) saccades for the quasi-relativistic reasons suggested by Morrone *et al.* [50]. On each saccade, visual representations need to be updated to maintain stability as the retinal image is pitched about by movements of the eyes. Spatial updating cannot be a trivial process and presumably places heavy demands on the available visual resources. This might cause the system to compress the spatial, temporal and numeric information, reducing informational load and hence demand on processing resources. With all three compressed, the relationship between space, time and number would be preserved to allow trans-saccadic information to be rescaled to the postsaccadic retinal image, paving the way for a fresh analysis of the visual scene from the postsaccadic perspective [56].

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.tics.2010.09.005](https://doi.org/10.1016/j.tics.2010.09.005).

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