

**Keeping vision stable: rapid updating of spatiotopic
receptive fields may cause relativistic-like effects**

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People shift their gaze more frequently than they realize, sometimes smoothly to track objects in motion, more often abruptly with a saccade to bring a new part of the visual field under closer visual examination. Saccades are typically made three times a second throughout most of our waking life, but they are rarely noticed. Yet they are accompanied by substantial changes in visual function, most notably suppression of visual sensitivity, mislocalization of spatial position and misjudgements of temporal duration and order of stimuli presented around the time. Here we review briefly these effects, and expound a novel theory of their cause. In order to preserve visual stability, receptive fields undergo a fast but not instantaneous remapping at the time of saccades. If the speed of remapping approaches the physical limit of neural information transfer, it may lead to the relativistic-like effects that are observed psychophysically, namely a compression of spatial relationships and a dilation of time.

Saccades are ballistic movements of the eyes made to reposition our gaze. They can be deliberate, but normally are automatic and go unnoticed. Not only do the actual eye movements escape notice, but so does the image motion they cause, and the fact that gaze itself has been repositioned. This problem has gained the attention of most visual scientists, including Alhazen (1083; Howard, 1996), Helmholtz (1866) and Sperry (1950). A general conclusion to emerge from a variety of studies was that saccades were accompanied by a “corollary discharge” (Sperry, 1950) or an “efference copy” (Von Holst & Mittelstädt, 1954) of the motor signal that corrected for the eye movement (for general review see Ross, Morrone, Goldberg & Burr, 2001).

There is now good evidence that many visual neurones are modified by a corollary discharge. Receptive fields of many neurones in the lateral intraparietal area (LIP) of monkeys change position before each saccadic eye movement (Duhamel, Colby & Goldberg, 1992), effectively anticipating its consequences. Similar effects have been found in other eye movement-related areas, such as superior colliculus (Walker, Fitzgibbon & Goldberg, 1995), frontal eye fields (Umeno & Goldberg, 1997) and even in earlier stages in the cortical visual system (Nakamura & Colby, 2002), V4, V3a and V2. The remapping of receptive fields in all these areas is consistent with psychophysical studies in the sixties that showed that briefly displayed visual stimuli are perceived erroneously when presented around the time of saccades,

displaced in the direction of the saccade (Matin & Pearce, 1965; Bischof & Kramer, 1968; Matin, Matin & Pearce, 1969; Matin, 1972).

Spatial and temporal mislocalization during saccades

If the errors in localization serve only to compensate for eye movements, they should always be in the same direction as the saccade. However, this is not always the case. Fig. 1A (from Ross, Morrone & Burr, 1997) shows that the direction of mislocalization of stimuli presented near the time of saccades depends strongly on the spatial position of the stimuli. Bars displayed at the centre of the screen or to the left of fixation (for a rightward saccade) were displaced rightward, in the direction of the saccade. However, bars flashed beyond the saccadic target were displaced leftwards, against the direction of the saccade. This results in a *compression* of visual space at the time of saccades. The compression is robust, capable of removing vernier offsets for lines flashed near saccadic onset, and causing multiple stimuli to merge into one. Compression does not occur during simulated saccades, where scenes are displaced by mirror movement with similar dynamics to saccades (Morrone, Ross & Burr, 1997).

More surprisingly, a recent experiment in our laboratory has shown that saccades cause not only a compression of space but also of time. Fig. 1B (from Morrone, Ross & Burr, 2005) shows how the apparent separation of two briefly-flashed bars varies with time of presentation. The actual separation of the bars was 100 ms, but when flashed near saccadic onset, the apparent duration was reduced to near 50 ms. As with spatial compression, the effect was maximal near saccadic onset, and follows very tight temporal dynamics. The timecourse may appear broader than that for spatial compression, but this is only because the actual stimulus was necessarily broad (100 ms); if this is taken into account, the dynamics are very similar.

Furthermore, the precision with which the judgment was made *improved* during saccades, brought out more clearly in the upper panels of Fig. 2 that show examples of psychophysical functions for test stimuli presented either well before saccadic onset (open squares) or peri-saccadically (filled circles). Subjects were required to compare the duration of the tests (pre- or perisaccadic) with a probe pair

presented 2 seconds later (see Morrone et al., 2005 for full experimental details). All data are well fit by cumulative Gaussian curves. The mean of these curves estimates the *point of subjective equality* (PSE) and the standard deviations estimate the precision of the match. Note that when the stimuli are presented peri-saccadically, the point of subjective equality shifts towards 50 ms, showing how time is compressed at that moment. But notice that the curves also become much steeper, showing that precision actually improves at the time of saccades. If one assumes that the precision of the judgment is determined by the neural noise associated with both test and probe stimuli, and that noise varies inversely with the number of ticks of an internal clock (Gibbon, 1977), then the compression of time and the improved precision in temporal judgments are consistent with slowing of the clock during saccades.

The lower panels of Fig 2 show another experiment where subjects were required to judge the duration of pairs of clicks (compared with a later probe). Here the results are quite different. Under all conditions, the judgments are more precise (in agreement with Westheimer, 1999 and others) but of more relevance to this discussion, the peri-saccadic and pre-saccadic results are indistinguishable. The effects of saccades on time are clearly modality specific, occurring only for visual stimuli.

Even more surprisingly, for certain intervals of stimulus presentation, duration was not only misjudged but temporal order was inverted. In a further experiment, subjects were asked to estimate the temporal order of the bars (which were always presented in random order). Figure 3A shows the results for stimuli presented 100 ms or more after saccadic onset: a typical psychometric function where the probability of correct response varies smoothly with the temporal separation of the bars. However when stimuli are presented just before saccadic onset (within the narrow range -70 to -30 ms) the psychometric function (Fig. 3B) is far from conventional, but becomes triphasic. For bar separations within the range -50 to +50 ms the function runs smoothly in the opposite direction to reality – as if time had reversed. Only for very large separations (greater than 100 ms or so) is temporal order perceived correctly.

Saccades and Special Relativity

The pairing of temporal with spatial effects that occur before saccades suggests a possible explanation: saccades induce a *relativistic* alteration of spatial and temporal metrics. In physics relativistic effects occur when objects move at a speed approaching c , the maximal speed that an electro-magnetic wave can carry information. Propagation of information through the nervous system occurs along axons and across synapses at a speed limited by biophysical constraints. As mentioned earlier, the receptive fields of many cortical neurons are modulated by eye position (Andersen, Essick & Siegel, 1985; Duhamel et al., 1992; Fogassi, Gallese, di Pellegrino, Fadiga, Gentilucci, Luppino, Matelli, Pedotti & Rizzolatti, 1992; Galletti, Battaglini & Fattori, 1995; Duhamel, Bremmer, BenHamed & Graf, 1997; Nakamura & Colby, 2002; Kusunoki & Goldberg, 2003), presumably to anticipate and offset the change in retinal positions. The modulation is fast but not instantaneous, often following similar dynamics to perceptual effects during saccades (Morrone et al., 1997; Ross et al., 1997; Diamond, Ross & Morrone, 2000). As the dynamic coordinate transformation must be rapid (to offset the effects of saccades), it seems reasonable that it will occur at a rate approaching the limit of neural information transfer; and this has immediate relativistic consequences in both space and time. If these neurons mediate the perception of space and also of time (Leon & Shadlen, 2003; Janssen & Shadlen, 2005), transient stimuli presented during the dynamic coordinate transformation will be measured against spatial and temporal scales that are dilated relativistically, following the Lorentz transform (Einstein, 1920): they will therefore appear compressed in one spatial dimension and in time. For neural propagations at about 87% maximum speed, objects will be compressed in both space and time by a γ factor of 2, agreeing well both with the results of spatial compression (Morrone et al., 1997; Ross et al., 1997; Lappe, Awater & Krekelberg, 2000; Kaiser & Lappe, 2004), and with the factor-of-two time compression reported more recently (Morrone et al., 2005). This suggestion also predicts increased temporal precision in temporal judgments during saccades, as the clock with which they are measured slows down, decreasing the number of “clock ticks” between the two events. It is also consistent with the independence on saccadic size (except for very small saccades), as it is the speed of the receptive field that matters, not the duration of the shift (although the duration may affect the range over which the compression occurs). Finally, it

predicts that blinks will have no effect on perceived time (although they cause many suppression-like effects that mimic saccades, with similar time-course (Stevenson, Volkman, Kelly & Riggs, 1986; Ridder & Tomlinson, 1993), as they are not associated with shifts in receptive fields, and that non-visual stimuli (such as clicks) will not be compressed. In the following section we develop formally these ideas.

Maps in the Brain

Images on the retina form a map (see Morgan, 2003 for interesting discussion). Let us suppose that the brain registers this map but also develops a map of activity that codes the location of objects in external space, that we refer to as the craniotopic map and that this latter map is used for spatial and temporal order judgments. The craniotopic map (x', y', t') also receives a retinotopic input that will be shifted with each saccade by an amount to counteract the retinal shift, in order to establish the craniotopic specificity. However, if a new signal arrives and excites this map while it is being displaced, and if the displacement takes place at high speeds, many relativistic effects of temporal and spatial localization can be predicted.

The Lorentz Transformation

Let x, y and t be the retinal spatial and temporal Cartesian coordinates of the stimuli (x and y can be considered as signed eccentricities). Let x', y' and t' be the spatial and temporal coordinates of the craniotopic map used by our brain. The role of the craniotopic map is to assign a location of the external space and time: a stimulus that elicits a neuronal activity centered around x', y' will be localized at that external position independently of its retinal location, and the temporal separation between two peaks of activity (measured with the same neuronal clock that is used for the activity) will define the perceived delay of one stimulus over the other.

Assume that the saccade is executed horizontally from position 0 to f . Before the saccade the two maps are in register: $x'=x, y'=y$ and $t'=t$. After the saccade has been executed the two maps, retinal and craniotopic, will differ only by a constant spatial shift: $x'=x-f, y'=y$ and $t'=t$ where f is a constant that describes the position of the eye in external coordinates corresponding physiologically to the corollary discharge signal, in agreement with many models (Xing & Andersen, 2000; Pouget,

Deneve & Duhamel, 2002). Let us suppose that before the saccade, activity in the craniotopic map (x') begins reafference to change its input to the retinal afference that will be appropriate to maintain craniotopic invariance after the saccade. This rapid reafference can be described mathematically as a movement in the map to reach a displacement equal and opposite to f by the end of the saccade. Let us further suppose that the motion occurs at a speed close to the maximum physiologically possible speed for the cortical area that codes the map. Mmaximum speed will be limited by the number of synapses involved in the transfer of information, the total length of dendrites and axons to be traveled at the diffusion speed of horizontal connection – about 0.2 m/s (Tucker & Katz, 2003) – or of cortical to cortical connection of 3.5 m/s (Girard, Hupe & Bullier, 2001).

Any signal delivered at position x , y and time t will be represented by the dynamic map at positions x' , y' and t' given by the Lorentz transform:

$$\begin{aligned}x' &= \gamma(x - ut) \\t' &= \gamma(t - ux/c^2) \\y' &= y\end{aligned}\tag{1}$$

where

$$\gamma = \frac{1}{\sqrt{1 - u^2/c^2}}\tag{2}$$

and u is the velocity of the moving frame along the x axis (in the direction opposite to the saccade), c is the maximum speed of neural information transmission.

Spatial Compression

For simplicity let us consider only events that take place before that the eye actually moves (eye movement will alter only the actual retinal position (x) of the delivered stimuli, not the conceptual basis of the model). Consider two brief stimuli delivered during the motion of the localization map at a spatial separation of L , depicted in figure with the two green vertical lines. The distance estimate by the craniotopic map during its fast reafference will be:

$$L' = L/\gamma$$

This expression is easy to derive if the spatial separation is evaluated at the same temporal instant t' of the craniotopic activity. (To derive this expression just calculate eq 1 for difference of two impulses and assign at $\Delta x=L$ and $\Delta t'=0$).

If we consider that $c = 1$ and $u = 0.87c$, γ will be equal to 2, so

$$L' = L/2$$

This implies that apparent distance would appear compressed by about a factor of two (agreeing well with the psychophysics: Morrone et al., 1997; Ross et al., 1997; Lappe et al., 2000; Kaiser & Lappe, 2004). If only one stimulus is delivered, its position may be judged by the distance between the stimulus and one of the activities present in the dynamic map, usually the saccadic target, obtaining the same compression for stimulus location as for separation. If the speed of the dynamic remapping is low compared to maximum speed and equal to $\Delta f/\Delta t$, where Δt is the typical saccadic mislocalization temporal dynamics and Δf the cortical distance covered by the saccade, the distance of the two targets will be unaffected and their positions will be shifted in the direction of the saccade; as is sometimes observed in the dark for memory guided saccades (Cai, Pouget, Schlag-Rey & Schlag, 1997; Lappe et al., 2000).

The major spatial compression takes place within a 50 ms interval around saccadic onset (for a saccade of 20 deg). This implies a speed of information transfer of 400 deg/s and an estimate of the maximum speed of about 440 deg/s.

Compression of Time

A similar argument can be developed for the temporal judgments. The stimuli presented in this experiment encompass all spatial positions along x , although the two bars will excite different pools of neurons given their vertical offset. Each bar will be interpreted by the dynamic moving map as a stimulus that is encoded at different spatial positions (x') and time (t'). If we assume (conservatively) that the temporal judgments are performed by neurons that assume the same x' position of the moving map, the resulting estimate will be:

$$T' = T/\gamma = 100 \text{ ms}/2 = 50 \text{ ms}$$

where T and T' are the measured temporal separations of the stimulus pair in the two different inertial frames of reference. (Again to obtain this expression it is sufficient to repeat the procedure used for the spatial compression and assign $\Delta x'=0$ and $\Delta t=T$).

Given that each tick of the clock of the moving map lasts two ticks of the stationary (retinally anchored) clock, we should also have a decreased error if error is associated with number of ticks to be counted (Weber's law). This estimate holds when both stimuli are delivered during the dynamic phase of the map. In our condition this corresponds to when one bar is delivered 50 ms before the eye movement and the other 50 ms after the eye movement. To simulate the interval before or well after saccadic onset, we could consider that only some of the clock ticks are subject to time dilation induced by the dynamic remapping and this would necessarily decrease the time compression effect.

At some crucial intervals just before saccadic onset, the temporal order of the bars was consistently seen to be inverted. The reversal of apparent order does not follow immediately from special relativity alone, but could easily be accounted for within this framework by considering temporal "*postdiction*" (Libet, Wright, Feinstein & Pearl, 1979; Eagleman & Sejnowski, 2000). If each of the two successive bars is labelled independently, and referred backwards in time by N clock-ticks to compensate for delays in neural processing, the second bar will sometimes be pushed backwards beyond the first, if the clock was ticking more slowly at the time of second bar presentation.

Concluding remarks

The idea of a shift of reference to preserve visual stability is an old one: what is novel here is the suggestion that a shift can and does have relativistic consequences. This suggestion can explain why spatial compression is predominantly one-dimensional and why it is accompanied by temporal compression and reversal of temporal order. Shifts of reference are not rare: they occur whenever saccades are made, three times a second on average throughout waking life. The effects of saccades, common though they are, escape notice because they are nullified by an accompanying shift of frame

of reference: only transient stimuli, rare in nature, will be distorted and then only if they happen to appear while the rapid shifts of reference are in progress.

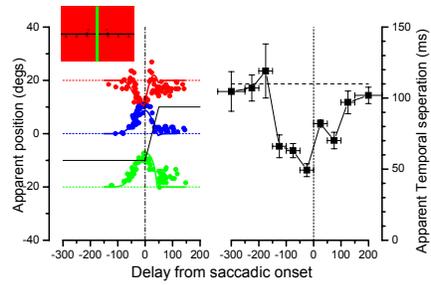


Figure 1

Effect of saccades on spatial position (A) and temporal separation (B). For the spatial task, bars were briefly displayed in one of three spatial positions (-20 , 0 and 20° , indicated by dashed lines). During a limited interval near the onset of the saccade, the bars were systematically misperceived towards saccadic target, indicating compression of space at the moment of the saccade. For the temporal task, the apparent temporal separation of two briefly flashed bars was measured with a matching technique (see Fig. 2): at presentation times near the onset of the saccade, the apparent duration of the interval was halved, indicating temporal compression.

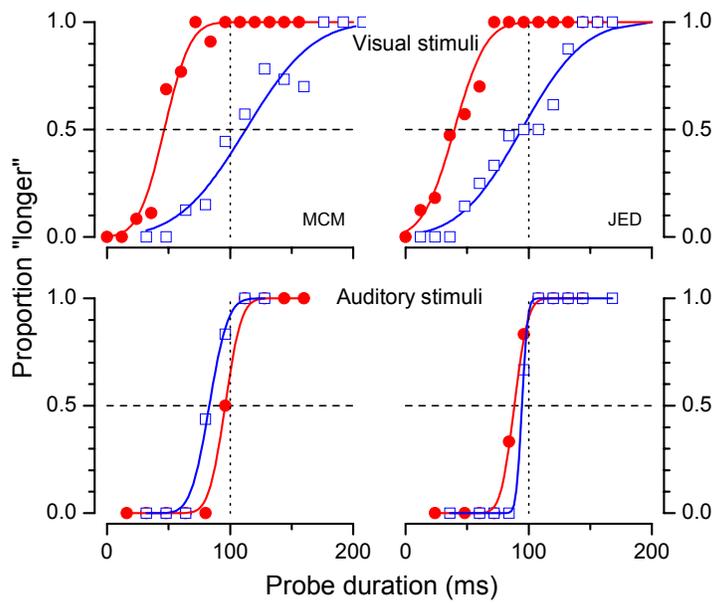


Figure 2

Psychometric functions for the temporal judgments of Fig. 1. For the upper curves, a pair of horizontal bars separated in time by 100 ms was presented either well before (open squares) or just prior to saccadic onset (filled circles). Subjects were required to report whether this stimulus pair appeared shorter or longer than a probe pair (of variable duration) that appeared 2 seconds later. With perisaccadic presentations the curves were shift to the left, implying strong compression of time, and were steeper, implying greater precision of temporal judgements. For auditory stimuli (brief clicks) there was no temporal compression accompanying the saccade.

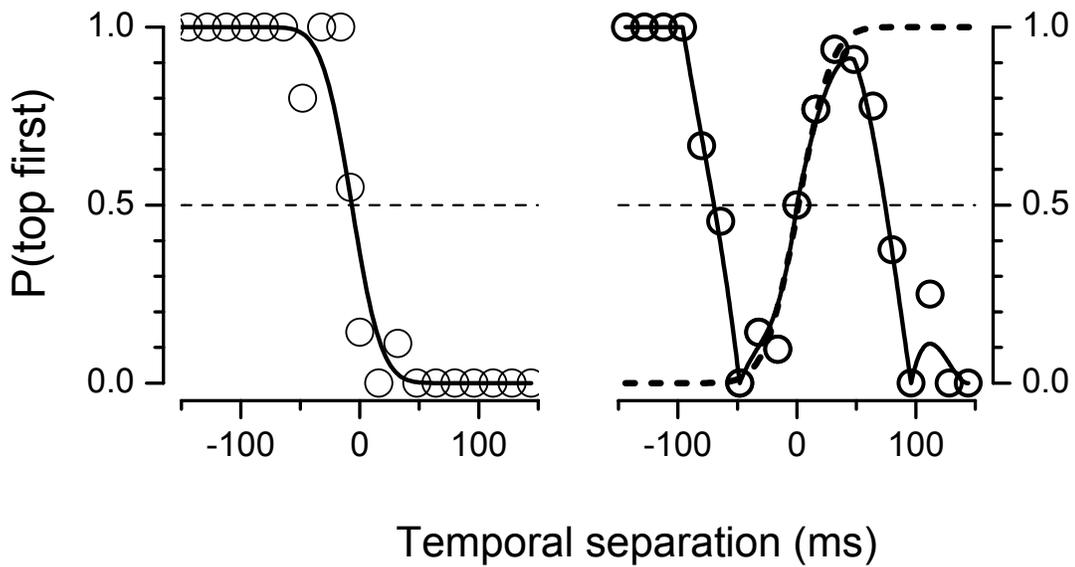


Figure 3

Psychometric functions for a temporal order judgement task in which the observer was required to judge whether the top or bottom bar was presented first, as a function of temporal separation (positive times mean bottom first). The curve at left is a standard psychometric function for bar presentations at least 100 ms after saccadic onset. The curve at left shows data for the critical peri-saccadic interval -70 to -30 ms. This psychometric function is actually inverted over the range of ± 50 ms, recovering to veridicality for very large separations (the curve was fit to the circular points within the dashed lines). This implies that for a limited range, temporal order is inverted.

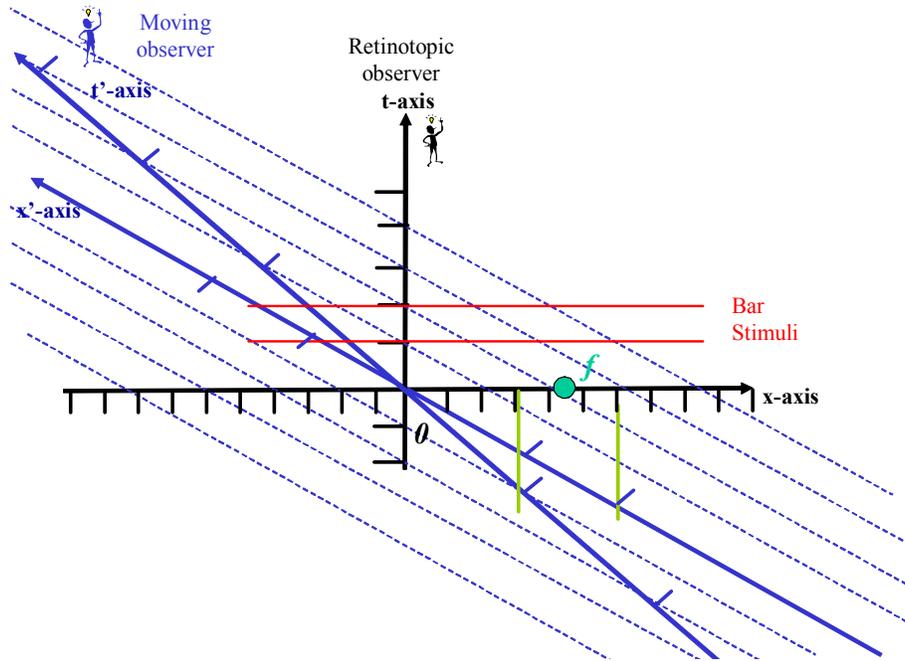


Figure 4

Schematic illustration of the effect of the Lorentz transform on the stimuli of this study. Observers fixate O , then saccade to the target f that appears abruptly when the fixation spot disappears. (The saccade is assumed to occur outside the temporal limits of this graph). At a variable time relative to saccade onset, a pair of extended horizontal bars are presented 1 clock-tick apart. For an observer moving at relativistic speeds, in this case $0.87c$, the spatial and temporal axes (x' and t') will be rotated in space-time, following the Lorentz transformation (equation 1). To visualize geometrically the resulting temporal dilation, consider that all lines parallel to the x' axis have constant t' (dotted lines in figure). Their intersection with the t' axis will produce a dilated timescale, with ticks more than double those of the t axis. A similar argument occurs in space, explaining spatial compression. The two short green lines represent two stimuli separated by L for the stationary map, but by L/γ for the retinotopic map.

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