

Saccadic eye movements cause compression of time as well as space

M Concetta Morrone¹, John Ross² & David Burr^{3,4}

There is now considerable evidence that space is compressed when stimuli are flashed shortly before or after the onset of a saccadic eye movement. Here we report that short intervals of time between two successive perisaccadic visual (but not auditory) stimuli are also underestimated, indicating a compression of perceived time. We were even more surprised that in a critical interval before saccades, perceived temporal order is consistently reversed. The very similar time courses of spatial and temporal compression suggest that both are mediated by a common neural mechanism, probably related to the predictive shifts that occur in receptive fields of many visual areas at the time of saccades.

We continually make ballistic eye movements, called saccades, in order to redirect the fovea to objects of interest. Although this strategy is highly efficient in allowing the visual system to analyze a wide field of view at high resolution, it poses serious problems for perception by changing the mapping of external space onto the retina. In normal viewing, stationary objects do not appear to shift their positions in space with eye movements, implying that continual corrective changes are made to neural frames of reference. But the corrections are not entirely successful. Experiments show that stimuli flashed briefly just before or early in a saccade are seen in false positions (for review, see ref. 1). Two components of error have been identified: a shift in the direction of the saccade^{2,3} and shrinkage of distances between stimuli, compressing them toward the saccade's target⁴⁻⁶. The compression is primarily one-dimensional, parallel to the saccadic path^{5,7}. The shift has been attributed to a mismatch between actual eye position during saccades and a prediction of position from an internal corollary discharge signal. But such a mismatch fails to explain compression: that remains a mystery. However, it has been suggested¹ that compression may be linked to the anticipatory shift of the receptive fields of neurons in many cortical areas, particularly the lateral intraparietal area (LIP), that become transiently craniotopic from well before until well after saccades, up to the next intention to move the eye⁸⁻¹⁰.

LIP neurons have recently been implicated in encoding temporal duration as well as spatial distance^{11,12}. If their perisaccadic activity is responsible for the perceived compression of space, we may well expect that the perception of intervals of time will also be altered when saccades are imminent or in progress. Here we show that time, like space, is indeed strongly compressed during saccades, following similar dynamics as spatial compression. Furthermore, during a critical duration just before saccade initiation, temporal order of briefly presented stimuli is consistently reversed.

RESULTS

Temporal compression

We asked observers to compare the time interval between two pairs of extended horizontal bars while they made large horizontal saccades (Fig. 1). The first pair was a test stimulus, with the interval between bars fixed at 100 ms, presented at unpredictably varying times relative to the saccade. The second pair was a probe stimulus of variable interval, presented 2 s after the test (see sample results for two subjects in Fig. 2a). The data for intervals well before saccadic onset are well fit by a cumulative Gaussian curve with a mean of 100 ms (corresponding to the point of subjective equality (PSE)) and s.d. of around 40 ms (corresponding to the precision of the match). The data for stimuli presented to stationary eyes just before saccadic onset are also well fit by a cumulative Gaussian, but its mean (and hence PSE) is not 100 ms, but 50 ms. This suggests that subjective time has been compressed by a factor of two. Results for stimuli presented perisaccadically to a region near the saccadic target, where attention is known to be directed well before saccades begin^{13,14}, were very similar to those with large peripheral targets remote from the saccadic target (Fig. 2a).

We observed compression over a wide range of saccade sizes (3.5 to 45°), with only modest variation of magnitude for the very short saccades, even though saccade duration varied from 30 to 120 ms over that range (Fig. 2b). The compression of time was specific to visual stimuli and to saccades. We did not observe compression for auditory clicks presented just before saccades, nor for visual stimuli presented just before a blink (known to cause saccade-like visual suppression^{15,16}). Comparing PSEs and judgment precision as a function of test presentation time shows that the compression of time was greatest when the test bars were presented near the start of saccades and extended over a period of some 300 ms around saccadic onset (Fig. 3a). Compression of time is associated with an improvement in

¹Facoltà di Psicologia, Università Vita-Salute San Raffaele, Via Olgettina 58, Milano 20132, Italy. ²School of Psychology, The University of Western Australia, Perth, Western Australia, Australia. ³Istituto di Neuroscienze del CNR, Via Moruzzi 1, Pisa 56100, Italy. ⁴Dipartimento di Psicologia, Università di Firenze, Via S. Nicolò 89, Firenze, Italy. Correspondence should be addressed to D.B. (dave@in.cnr.it).

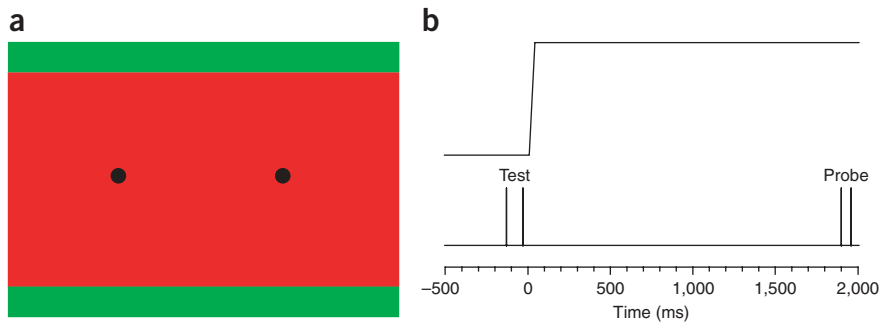


Figure 1 Schematic illustration of the experimental setup. **(a)** Impression of the screen, with fixation and target spots and upper and lower bar stimuli (which never actually appeared simultaneously). Both stimuli were brief (8 ms), $60 \times 6^\circ$ horizontal, near-equiluminant green bars, one 18° above and one 18° below screen center. Color and separation were chosen to minimize the sensation of motion (and subjects reported no motion perception). **(b)** Schematic saccade about 50 ms in duration, beginning at time zero (by definition). The lower trace illustrates the timing of the test and probe stimuli for the perceived duration experiment. The pairs of ticks illustrate the presentation time of upper and lower bars (order randomized). The test bars were always separated by 100 ms, the probe separation variable.

precision, both relative to early presentation and to presentation during fixation (Fig. 3a). Plotting precision against perceived duration for saccadic conditions for 100 ms tests and also for fixation with variable tests (Fig. 3b) shows this relationship more clearly. In both cases precision was directly proportional to perceived duration, yielding Weber fractions around 30%.

Temporal inversion

Observers were next asked to judge the temporal order in which a pair of horizontal bars had been presented. The order and temporal separation of the bars and the time of presentation relative to the saccade were all varied unpredictably. Figure 4a,b shows for two observers the proportion correct as a function of stimulus presentation time, for three ranges of bar separation. When bar separation was large (76–200 ms), temporal order was almost always judged correctly, with a small drop in accuracy for bins just before saccades. However, for shorter separations (20–44 ms and 44–75 ms), bars presented just before saccades were seen in reversed order, with very high probability. When presented at times remote from saccadic onset, order judgments within this range of bar separations were correct with high probability.

and perceived order was often inverted for stimulus separations less than 100 ms. Note that for some separations (around 70 ms), stimuli were sometimes reversed and sometimes not (leading to 50% performance in Fig. 4d), but the magnitude of the estimation never approached zero, which would imply perceived simultaneity.

DISCUSSION

Our results show that at the time of saccades, a strong compression of time accompanies the well-known shift and compression of space^{2–6}, suggesting a common cause for these phenomena. Both the temporal and spatial effects occur within approximately the same saccadic epoch, from shortly before to shortly after saccades, and both are maximal just at the start of saccades.

As eye movements and attention are known to be tightly related, it is worthwhile to consider the possible role of attention in temporal compression. Attention is known to influence perceived duration and also temporal order: salient, attention-grabbing stimuli have longer apparent duration^{17–19} and can be seen to precede less-attended stimuli that were presented earlier^{20–24}. The extended horizontal bars of this study presumably engage attention mechanisms, especially as subjects

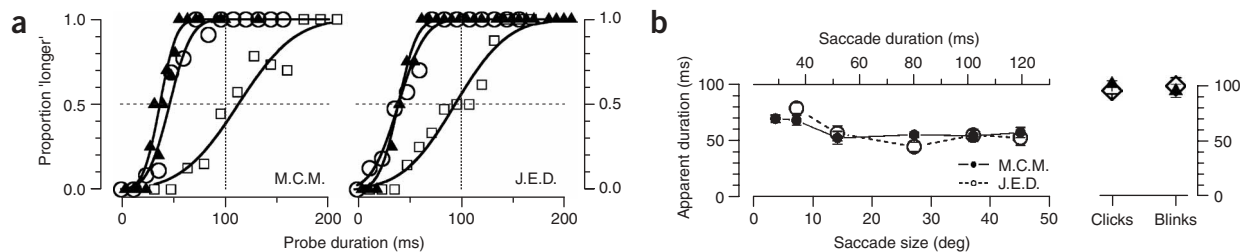


Figure 2 Compression of time during saccades. **(a)** Psychometric functions showing proportion of trials where two subjects (one author, M.C.M., and one naive, J.E.D.) judged the temporal separation of the probe to be longer than that of the test while they made large (30°) horizontal saccades. The interval between test bars was fixed at 100 ms, whereas that of the probe was varied as indicated by the abscissa. Open squares refer to presentations when the temporal center of the test pair fell between -400 and -200 ms before saccadic onset, and the open circles when it fell in the interval of -100 to -50 ms. Filled triangles show results when stimuli were short vertical bars ($6 \times 15^\circ$) near the saccadic target, -100 to -50 ms before saccadic onset. All data were fit with cumulative Gaussian functions to derive the PSE (given by the mean) and the precision (given by the s.d.). **(b)** Apparent duration of a 100-ms double-bar perisaccadic stimulus (-100 to -50 ms) as a function of saccadic amplitude (filled circles: M.C.M., open circles: J.E.D.). Upper abscissa: duration of saccades calculated from Carpenter's⁴⁰ formula $d = 2.2A + 20$ ms (d , duration; A , saccadic amplitude), which agreed well with our own measurements. Right panel shows results for two controls: the blink condition (when stimuli fell -100 to -50 ms before the onset of a voluntary blink) and the apparent temporal separation of clearly audible clicks (4-ms duration, 100-ms separation, -100 to -50 ms before saccadic onset). Vertical bars: s.e.m., bootstrap method.

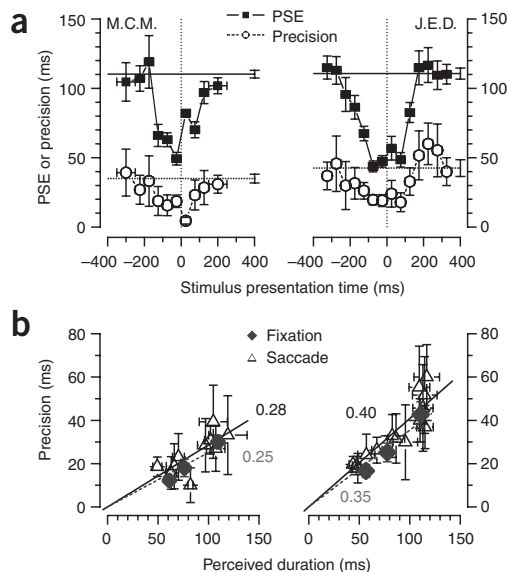


Figure 3 Compression and increased precision of time during saccades. **(a)** Point of subjective equality (PSE) and precision as a function of stimulus presentation time (mean time of the two bars relative to saccadic onset). The data were calculated from psychometric functions like those of **Figure 1**, with 50–80 trials per point. The upper solid horizontal line and the lower horizontal dotted line show estimates of PSE and precision during fixation. Vertical bars refer to s.e.m. (bootstrap method), and horizontal bars to the width of the averaging bin. **(b)** Precision of temporal judgment as a function of perceived duration, for test stimuli of 100 ms presented at various times relative to saccadic onset (open triangles, from **Fig. 2a**) and for tests of 50, 75 and 100 ms during fixation (gray diamonds). In all cases, precision is proportional to perceived duration, suggesting a Weber relationship. The dashed gray and black lines show the best linear regressions (constrained to pass through zero) for the saccadic and fixation data, respectively. The slopes of these fits give an estimate of the Weber fraction: 0.28 and 0.25, respectively, for saccadic and fixation for M.C.M., and 0.4 and 0.35 for J.E.D.

had to attend to them in order to judge their duration or temporal order. However, as all bars were of equal size, duration, brightness and eccentricity, it is unlikely that some were more attention-grabbing than others. As saccades cause shifts in spatial attention toward the saccadic target^{13,14}, it may be argued that the effects reported here are due to reduced spatial attention for stimuli not at saccadic target, but as compression also occurred for stimuli near saccadic target (**Fig. 2a**), this seems unlikely.

There is also evidence for a general damping of attention at the time of saccades^{25–27}, a time when information is least reliable²⁸. As perceived duration varies with attention, this inattention could reduce the apparent duration of stimuli presented at the time of saccades. However, although inattention can reduce perceived duration, the reported effects are small (about 12%) and are associated with an increase in variability in judgment¹⁸: our results (**Fig. 3**) show a decrease in perceived duration of about 50%, together with a decrease in variability (implying increased precision) in temporal judgments. The temporal inversion is even more difficult to account for by attention, as the prediction runs in the wrong direction. The inversion was maximal when the stimulus pair was centered 50 ms before saccadic onset, so the second bar occurred near saccadic onset. If the system were less attentive at saccadic onset, the second bar should have less attentional weight²² and therefore should be pushed even further

back in temporal priority, rather than ‘jumping the cue’ to invert perceived order. Although we cannot exclude completely the role of attention in this study, its precise role is far from obvious at this stage.

It is unlikely that the changes in perceived duration result from low-level processing of the stimulus. The use of widely separated equiluminant stimuli minimized the impression of apparent motion (and indeed, no subjects reported the sensation of motion). Saccades change neither the amplitude nor the dynamics of the temporal impulse-response function for equiluminant stimuli²⁹. For luminance-modulated stimuli, the impulse response becomes slightly faster (consistent with a decrease in contrast gain), but the difference in peak response is only about 8 ms, far shorter than needed to account for the results reported here.

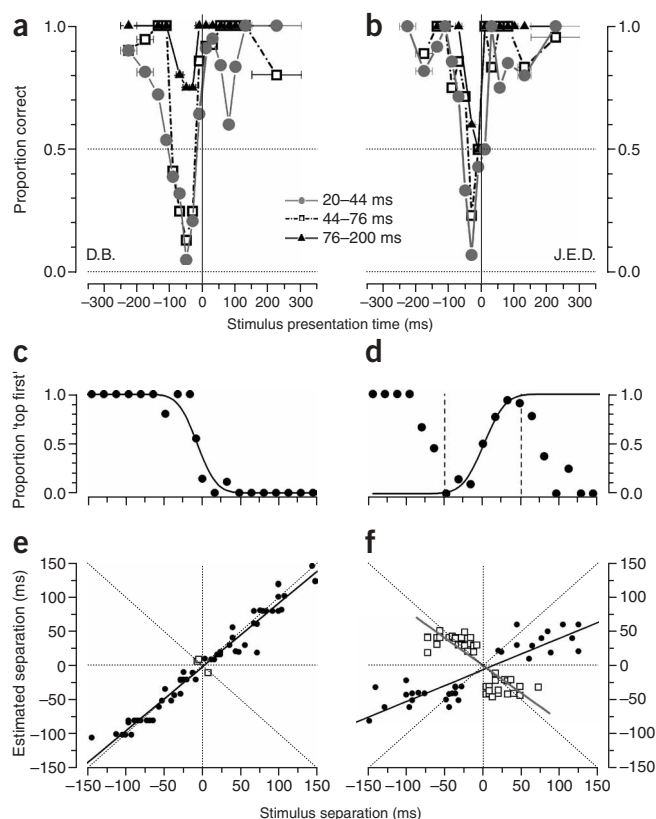


Figure 4 Temporal inversion. **(a,b)** Proportion of correct judgments of temporal order for two observers (averaging ‘top first’ with ‘bottom first’) as a function of stimulus presentation time (the average time of the pair from saccadic onset), for three levels of separation of stimulus pairs. **(c,d)** Two psychometric functions from the data of **Figure 3a** (subject J.E.D.) for presentation times more than 100 ms after saccadic onset **(c)** and for a critical perisaccadic interval -70 to -30 ms **(d)**. Each curve incorporates about 150 trials. **(e,f)** Magnitude estimations of perceived duration for a subset of the data in **c,d** (61 points for **e**, 81 for **f**). For presentation times 100 ms after saccadic onset **(e)**, the judgments were near veridical (slope of linear fit of all points 0.93, $r = 0.98$, solid black line). During the interval -70 to -30 ms **(f)**, magnitudes were underestimated and consistently reversed (non-inverted data indicated by solid black line: slope 0.47, $r = 0.90$; inverted data by solid gray line: slope -0.80 , $r = 0.82$). For clarity, the inverted data points of both graphs are shown as open squares.

Previous studies³⁰ have shown that saccades and other voluntary movements can cause time distortions, increasing the apparent duration of stimuli following saccades. This effect, termed ‘chronostasis’, is thought to compensate perceptually for the time lost during saccadic suppression. Chronostasis may be related in some way to the compression and inversion effects reported here, but the connection is not obvious: chronostasis shows a strong dependency on saccadic size and duration, is neither tightly linked to the saccadic time course nor restricted to saccades^{31,32}, and also occurs in the auditory domain³³. The temporal compression reported here does not occur with blinks or auditory clicks, follows a precise time course and is almost independent of saccadic size. Chronostasis is thought to compensate for the time lost during saccades, with a lengthening of post-saccadic time (a ‘cut and stitch’ model), but we find no lengthening of apparent duration as late as 500 ms after the saccade; the time lost by compression during saccades is not recovered. Perhaps chronostasis is more related to perceptual compensations for movement intentions³⁴ and attention.

The effects observed here were specific for visual stimuli and for saccades, implicating a timing mechanism for visual stimuli that is modulated by saccade-related neural circuitry. Neurons in parietal cortical area LIP have been implicated both in anticipatory remapping around the time of saccades⁸ and also in encoding brief temporal durations in behaviorally relevant locations^{11,12}. Although the effect of saccades on the temporal encoding of these neurons has not yet been measured, it is conceivable that it changes markedly around the time of saccades, as these neurons shift receptive fields. Our results suggest that the change is tantamount to a slowdown of the neural clock on which judgments of time depend. Not only were temporal intervals for stimuli presented near saccades seen as shorter, but the precision of the temporal judgment was higher, with the Weber fraction remaining constant as a function of perceived rather than actual duration (Fig. 3b). This is to be expected if the precision of the judgment is determined by neural noise that varies inversely with the number of ticks of an internal clock³⁵. If the clock slows momentarily around the time of saccades, fewer clock ticks will occur during stimulus presentation, so the temporal match should be less noisy. It is worth emphasizing that temporal judgments are one of the very few tasks that actually improve during saccades, and by a significant amount (see ref. 36).

The slowing of a neural clock at the time of saccades does not in itself explain temporal reversal. However, the reversal can be explained within this framework by incorporating the notion of ‘retrospective perception’³⁷ or ‘postdiction’^{38,39}, that has been applied successfully to describe temporal phenomena such as the ‘flash-lag’ effect. If each of the two successive bars is labeled independently and then referred backward in time by N clock ticks (to compensate for delays in neural processing), the second bar could be pushed backward beyond the first if the clock were ticking more slowly when the second bar was presented.

Saccades, common though they are, have effects that can escape notice in normal viewing because they are partially nullified by an anticipatory shift of spatial frame of reference. Our results make clear that temporal compression is found only with saccades, not with blinks, and, like spatial compression, occurs just when the predictive remapping of receptive fields that shifts frames of reference is in progress. Perhaps the spatial and temporal distortions that we find for transient stimuli are a consequence of these fast, but not instantaneous, shifts; they may be fast enough to cause both a dilation of clock time and a compression of spatial metric.

METHODS

Stimuli and procedure. Observers fixated a 1° black disk 15° left of center of an otherwise uniformly red screen (CEI $x = 0.55$, $y = 0.40$, mean luminance

17 cd/m²) of an NEC monitor running at 250 Hz and subtending 60 × 42° from the viewing distance of 30 cm (Fig. 1). On warning, the fixation spot disappeared and a black 1° saccadic target appeared 15° right of center, to which the subject saccaded (with the individually stereotypical latency of about 160 ms). After a randomly variable delay from saccadic target presentation, a pair of horizontal green bars (near-equiluminant; 6 × 80°; CEI $x = 0.26$, $y = 0.63$, mean luminance 17 cd/m²) were displayed at the top and bottom of the screen, each for 8 ms (two frames) with onset asynchrony of 100 ms. The eccentricity, wide separation and color were successfully chosen to minimize the sensation of motion. Two seconds later a comparison pair appeared, whose onset asynchrony varied randomly from 8 to 200 ms. Subjects reported verbally which stimulus pair appeared longer. The experimenter recorded the responses after verifying that the saccade had been correctly executed (eye movements were monitored with an HVS SP150 limbus eye tracker at 1,000 Hz); otherwise the trial was aborted. Data were analyzed by an offline program that binned and averaged responses according to their presentation time relative to saccadic onset.

Magnitude estimation. In the second experiment, the subject was required to report which of the two bars appeared first. Presentation order, bar separation duration and display latency after saccade target were all varied randomly from trial to trial. For the latter half of the trials, subjects were required to report both the apparent order of the bars and the apparent separation. After their response, a stimulus pair with the reported separation and order was presented (during post-saccadic fixation); subjects either confirmed their estimate or revised it. They were given extensive training on fixation before the experiment and, in practice, rarely needed to revise their estimates.

Control experiments. Three control experiments were performed for compression. In one, the stimuli were short vertical, equiluminant bars (6 × 15°) straddling the saccadic target, one above and one below but overlapping by 6°. In another control condition subjects were required to blink on cue. As before, the stimuli were presented just before the blink (measured by the eye-tracker). Finally, we measured apparent temporal separation of auditory clicks. The procedure was otherwise the same as that described above, except the bars were replaced with a pair of 4 ms clearly audible clicks.

Four subjects were used in this experiment, two naive and two authors (all of whom provided informed written consent). Complete data is reported only for naive observer J.E.D., and authors M.C.M. and D.B.

ACKNOWLEDGMENTS

We acknowledge relevant previous work in our laboratory by M.R. Diamond. This research was funded by grants from the Australian National Health and Medical Research Council and the Australian Research Committee and by the Italian Ministry of Education, Universities and Research (Progetti di Ricerca di Interesse Nazionale).

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

Received 22 February; accepted 23 May 2005

Published online at <http://www.nature.com/natureneuroscience/>

- Ross, J., Morrone, M.C., Goldberg, M.E. & Burr, D.C. Changes in visual perception at the time of saccades. *Trends Neurosci.* **24**, 113–121 (2001).
- Matin, L. in *Handbook of Sensory Physiology vol. VII/4: Visual Psychophysics* (eds. Jameson, D. & Hurvich, L.M.) 331–380 (Springer-Verlag, Berlin, 1972).
- Honda, H. Perceptual localization of visual stimuli flashed during saccades. *Percept. Psychophys.* **45**, 162–174 (1989).
- Ross, J., Morrone, M.C. & Burr, D.C. Compression of visual space before saccades. *Nature* **386**, 598–601 (1997).
- Morrone, M.C., Ross, J. & Burr, D.C. Apparent position of visual targets during real and simulated saccadic eye movements. *J. Neurosci.* **17**, 7941–7953 (1997).
- Lappe, M., Awater, H. & Krekelberg, B. Postsaccadic visual references generate presaccadic compression of space. *Nature* **403**, 892–895 (2000).
- Kaiser, M. & Lappe, M. Perisaccadic mislocalization orthogonal to saccade direction. *Neuron* **41**, 293–300 (2004).
- Duhamel, J.R., Colby, C.L. & Goldberg, M.E. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* **255**, 90–92 (1992).
- Nakamura, K. & Colby, C.L. Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proc. Natl. Acad. Sci. USA* **99**, 4026–4031 (2002).

10. Kusunoki, M. & Goldberg, M.E. The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. *J. Neurophysiol.* **89**, 1519–1527 (2003).
11. Leon, M.I. & Shadlen, M.N. Representation of time by neurons in the posterior parietal cortex of the macaque. *Neuron* **38**, 317–327 (2003).
12. Janssen, P. & Shadlen, M.N. A representation of the hazard rate of elapsed time in macaque area LIP. *Nat. Neurosci.* **8**, 234–241 (2005).
13. Deubel, H. & Schneider, W.X. Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Res.* **36**, 1827–1837 (1996).
14. Gersch, T.M., Kowler, E. & Doshier, B. Dynamic allocation of visual attention during the execution of sequences of saccades. *Vision Res.* **44**, 1469–1483 (2004).
15. Stevenson, S.B., Volkman, F.C., Kelly, J.P. & Riggs, L.A. Dependence of visual suppression on the amplitudes of saccades and blinks. *Vision Res.* **26**, 1815–1824 (1986).
16. Ridder, W.H., III & Tomlinson, A. Suppression of contrast sensitivity during eyelid blinks. *Vision Res.* **33**, 1795–1802 (1993).
17. Rose, D. & Summers, J. Duration illusions in a train of visual stimuli. *Perception* **24**, 1177–1187 (1995).
18. Enns, J.T., Brehaut, J.C. & Shore, D.I. The duration of a brief event in the mind's eye. *J. Gen. Psychol.* **126**, 355–372 (1999).
19. Tse, P., Intriligator, J., Rivest, J. & Cavanagh, P. Attention and the subjective expansion of time. *Percept. Psychophys.* **66**, 1171–1189 (2004).
20. Titchener, E.B. *Lectures on the Elementary Psychology of Feeling and Attention* (MacMillan, New York, 1908).
21. Reeves, A. & Sperling, G. Attention gating in short-term visual memory. *Psychol. Rev.* **93**, 180–206 (1986).
22. Sperling, G. & Weichselgartner, E. Episodic theory of the dynamics of spatial attention. *Psychol. Rev.* **102**, 503–532 (1995).
23. Shore, D.I., Spence, C. & Klein, R.M. Visual prior entry. *Psychol. Sci.* **12**, 205–212 (2001).
24. Park, J., Schlag-Rey, M. & Schlag, J. Spatial localization precedes temporal determination in visual perception. *Vision Res.* **43**, 1667–1674 (2003).
25. Bridgeman, B., Hendry, D. & Stark, L. Failure to detect displacement of visual world during saccadic eye movements. *Vision Res.* **15**, 719–722 (1975).
26. McConkie, G.W. & Zola, D. Is visual information integrated across successive fixations in reading? *Percept. Psychophys.* **25**, 221–224 (1979).
27. Henderson, J.M. & Hollingworth, A. Global transsaccadic change blindness during scene perception. *Psychol. Sci.* **14**, 493–497 (2003).
28. Niemeier, M., Crawford, J.D. & Tweed, D.B. Optimal transsaccadic integration explains distorted spatial perception. *Nature* **422**, 76–80 (2003).
29. Burr, D.C. & Morrone, M.C. Temporal impulse response functions for luminance and colour during saccades. *Vision Res.* **36**, 2069–2078 (1996).
30. Yarrow, K., Haggard, P., Heal, R., Brown, P. & Rothwell, J.C. Illusory perceptions of space and time preserve cross-saccadic perceptual continuity. *Nature* **414**, 302–305 (2001).
31. Park, J., Schlag-Rey, M. & Schlag, J. Voluntary action expands perceived duration of its sensory consequence. *Exp. Brain Res.* **149**, 527–529 (2003).
32. Yarrow, K. & Rothwell, J.C. Manual chronostasis: tactile perception precedes physical contact. *Curr. Biol.* **13**, 1134–1139 (2003).
33. Hodinott-Hill, I., Thilo, K.V., Cowey, A. & Walsh, V. Auditory chronostasis: hanging on the telephone. *Curr. Biol.* **12**, 1779–1781 (2002).
34. Haggard, P., Clark, S. & Kalogeras, J. Voluntary action and conscious awareness. *Nat. Neurosci.* **5**, 382–385 (2002).
35. Gibbon, J. Scalar expectancy theory and Weber's Law in animal timing. *Psychol. Rev.* **84**, 279–325 (1977).
36. Santoro, L., Burr, D. & Morrone, M.C. Saccadic compression can improve detection of Glass patterns. *Vision Res.* **42**, 1361–1366 (2002).
37. Ross, J. in *Department of Psychology Research Report 4* (University of Western Australia, Perth, 1972).
38. Libet, B., Wright, E.W., Jr., Feinstein, B. & Pearl, D.K. Subjective referral of the timing for a conscious sensory experience: a functional role for the somatosensory specific projection system in man. *Brain* **102**, 193–224 (1979).
39. Eagleman, D.M. & Sejnowski, T.J. Motion integration and postdiction in visual awareness. *Science* **287**, 2036–2038 (2000).
40. Carpenter, R.H.S. *Movement of the Eyes* (Pion, London, 1988).