

- 82, 1018–1040 (1992).
13. Sendai District Meteorological Observatory, Japan Meteorological Agency *The 1994 Far Off Sanriku Earthquake* (December 28, M7.5). 75–83 (Rep. 54, Coordinating Committee for Earthq. Pred., Tsukuba-city, Japan, 1995).
 14. Seno, T., Sakurai, T. & Stein, S. Can the Okhotsk plate be discriminated from the North American plate? *J. Geophys. Res.* **101**, 11305–11315 (1996).
 15. DeMets, C., Gordon, R. G., Argus, D. F. & Stein, S. Current plate motions. *Geophys. J. Int.* **101**, 425–478 (1990).
 16. Sheng-Tu, B. & Holts, W. E. Interseismic horizontal deformation in northern Honshu and its relationship with the subduction of the Pacific plate in the Japan trench. *Geophys. Res. Lett.* **22**, 3103–3106 (1996).
 17. Barrientos, S. E. Dual seismogenic behavior: the 1985 Central Chile earthquake. *Geophys. Res. Lett.* **22**, 3541–3544 (1995).
 18. Barrientos, S. E., Plafker, G. & Lorca, E. Postseismic coastal uplift in southern Chile. *Geophys. Res. Lett.* **19**, 701–704 (1992).
 19. Linde, A. T., Gladwin, M. T., Johnston, M. J. S., Gwyther, R. L. & Bilham, R. G. A slow earthquake sequence on the San Andreas fault. *Nature* **383**, 65–68 (1996).
 20. Tanioka, Y. & Satake, K. Fault parameters of the 1896 Sanriku tsunami earthquake estimated from tsunami numerical modeling. *Geophys. Res. Lett.* **23**, 1549–1552 (1996).

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Compression of visual space before saccades

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Saccadic eye movements, in which the eye moves rapidly between two resting positions, shift the position of our retinal images. If our perception of the world is to remain stable, the visual directions associated with retinal sites, and others they report to, must be updated to compensate for changes in the point of gaze. It has long been suspected that this compensation is achieved by a uniform shift of coordinates driven by an extra-retinal position signal^{1–3}, although some consider this to be unnecessary^{4–6}. Considerable effort has been devoted to a search for such a signal and to measuring its time course and accuracy. Here, by using multiple as well as single targets under normal viewing conditions, we show that changes in apparent visual

direction anticipate saccades and are not of the same size, or even in the same direction, for all parts of the visual field. We also show that there is a compression of visual space sufficient to reduce the spacing and even the apparent number of pattern elements. The results are in part consistent with electrophysiological findings of anticipatory shifts in the receptive fields of neurons in parietal cortex⁷ and superior colliculi⁸.

For most experiments, observers made 20° left-to-right saccades in a dimly lit room from a fixation point F_0 (at -10°) on an otherwise featureless red screen, to a target F_1 presented at $+10^\circ$ after a ready signal. Green equiluminant vertical bars were briefly flashed at various positions, and observers reported their location with reference to a ruler that appeared on the screen shortly after the end of each saccade. The results in Fig. 1 show that bars displayed at physical positions of either 0 or -20° (squares and triangles, respectively) were systematically mislocalized in the direction of the saccade. The shift effects begin 50 ms before the saccade, rising to a maximum (about 10°) in a critical period just before the saccade onset ($-25 < t < 0$ ms). After the saccade had finished, localization of the bar was again veridical, although it now fell on a different retinal location from before. The results were quite different for bars displayed to the right of the target F_1 at $+20^\circ$ (circles in Fig. 1). Here the apparent position was displaced against the direction of saccades before the eye movement. The apparent length of the long bars (50°) did not change significantly under any condition (data not shown). The continuous curves in Fig. 1 and in all other figures come from the simple model described in Methods, which assumes a change in the origin of perceptual space from F_0 to F_1 and a perceptual compression.

Figure 2 describes the pattern of results found within the critical period, -25 to 0 ms (relative to saccade onset), for bars displayed over a wide range of spatial positions. Bars displayed to the left of F_1 were displaced in the direction of the saccade, whereas those to the right were displaced in the opposite direction, with a tendency for the data to cluster around F_0 and F_1 (dotted lines). Bars falling over a wide range (-5 to 30°) were mostly perceived near F_1 , the saccade target. A similar pattern of results was observed for right-left, vertical and smaller (10°) saccades. These findings imply a compression of space within the critical interval. To confirm that the compression was real, we measured the vernier displacement of two half bars, first when spatially separated but displayed simultaneously and briefly. In this situation, the individual upper and lower bars behaved exactly like the full bars, resulting in the impression of

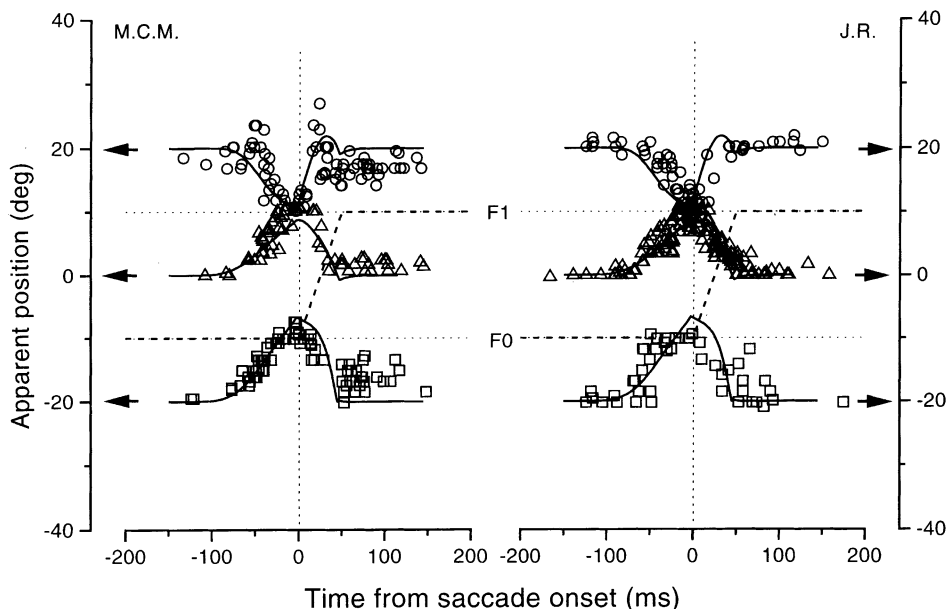


Figure 1 Apparent position of a vertical bar briefly flashed at positions -20° (squares), 0° (triangles) or $+20^\circ$ (circles), as a function of time relative to saccade onset. Each point represents a single observation. Saccades from F_0 to F_1 are indicated by the dashed line. The solid curves are simulations from the model described in Methods. Similar results have been obtained with 6 other observers, all initially naive of the aims of the experiment.

a collinear bar when the two halves were presented within the critical period, one at 0 and the other at +20°.

We also measured the apparent displacement of two half bars displayed collinearly but at different times, one 75 ms before the other. Subjects either reported the apparent separation of the bars (open circles in Fig. 3), or annulled it with a physical offset (filled squares: see Methods). The most interesting period is between -100 and -75 ms, when both bars were displayed in the same position to stationary eyes, but only the later bar fell just before saccade onset (when the mislocalization is strongest). When the spatial position of the bars was near 0°, the later bar was mislocalized with respect to the earlier in the direction of the saccade (positive offset for the observer). However, for bars displayed at 20° the effect inverted, showing a shift against the direction of the saccade. The model shown by continuous lines fits the results reasonably well, although the data measured at 20° eccentricity are more noisy.

For a stronger test of compression of visual space, we displayed up to four bars within a 20° region centred on F₁ and asked observers to report how many they saw. Well before or after the saccade, observers seldom erred, but near the saccade onset they usually reported seeing only one bar, no matter how many were displayed (Fig. 4). However, if the bars differed in colour or orientation, the

observers could perceive them as separate items, grouped closely together. We also displayed briefly several natural scenes such as that shown in Fig. 4 (lower left). The image on the right shows the deformation predicted by the model of equation (1). Most observers, both trained and naive, agreed that the deformed image resembled closely what they saw when the bridge scene was presented just before saccade onset. No compression of either bar position or natural scene was observed during 'stimulated saccades' (created by viewing the display through a rotatable mirror displacing the image 20° at saccadic speeds).

Our results imply a bidirectional compression of space that cannot be explained by a simple translation of coordinates^{1-3,9}; this could cause a uniform change in apparent spatial position, but not position-dependent mislocalization of single targets, nor gross misjudgements of relative position and of number of display items, and deformation of natural scenes. The presaccadic mislocalization against the saccade is particularly surprising, and directly contradicts some previous studies¹⁰ that report displacement in the saccadic direction at all positions. There could be many reasons for the difference, including the fact that many experiments were done in the dark¹⁰. The use of equiluminant stimuli could also be important in bringing forward in time the effects of mislocalization

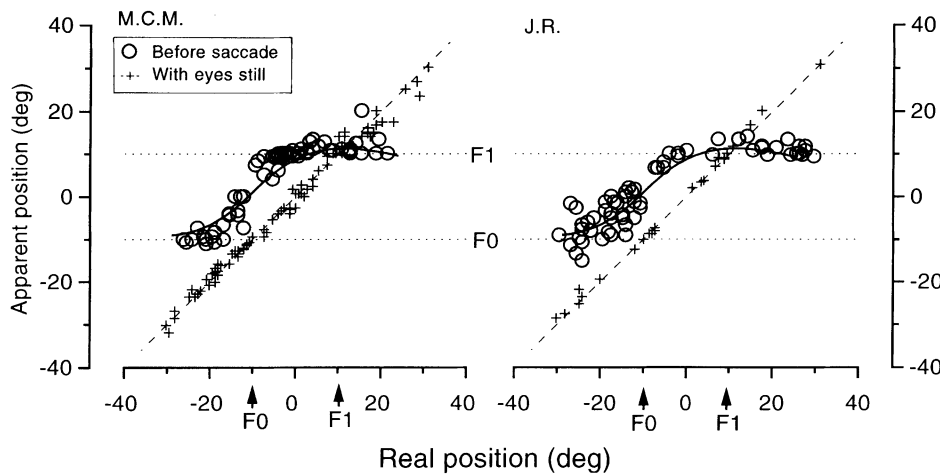


Figure 2 Apparent position of a green equiluminant bar present just before the saccade onset (-25 to 0 ms) as a function of real position (circles) as subjects M.C.M. and J.R. saccaded left to right. To avoid response stereotyping, the bars were presented randomly with various latencies, but only data with appropriate delays are plotted here. The crosses refer to measurements made for the same briefly exposed bars with constant fixation at F₀, demonstrating that judgements are veridical with normal viewing ($r > 0.995$ for both observers). The dashed line represents veridical judgement, and the solid line the simulation from the model described in Methods. This pattern of results has been verified with right to left and vertical saccades, and on 8 naive observers.

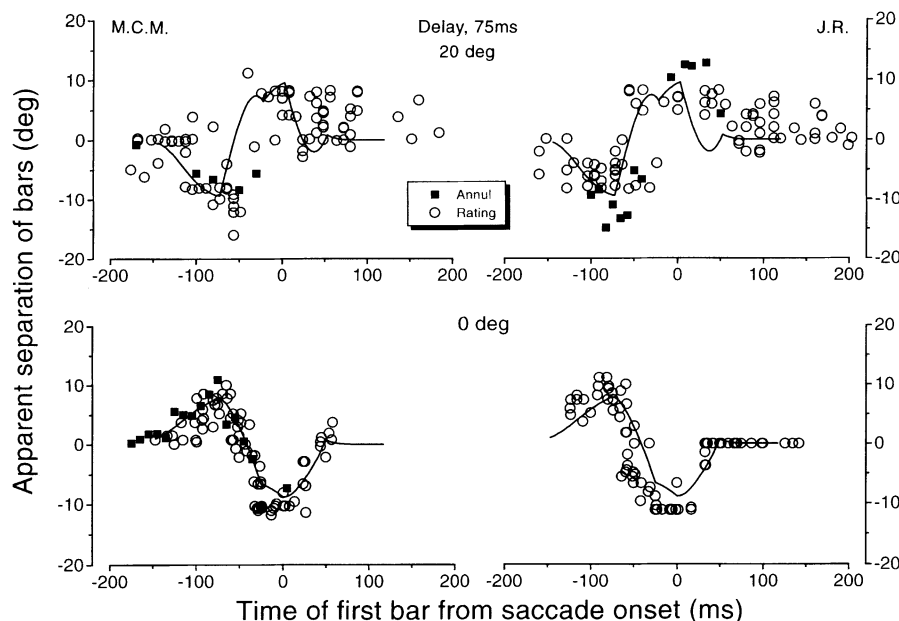


Figure 3 Vernier judgement or annulment of two collinear half bars. The top half bar was briefly displayed 75 ms before or after the bottom half, both at position of 0 or 20°. Open circles show observers' reports of the apparent size and direction of the displacement, and filled symbols the estimate obtained by the annulling technique described in Methods. For delays between -100 and -75 ms (when both bars were displayed to the same position to stationary eyes), there was a positive displacement (meaning that the later bar was displaced rightwards) when the bars were displayed near 0°, and a negative displacement when the bars were displayed at 20°. The trend later reversed in both cases to a maximum in the opposite direction at $t = 0$ ms. Smooth curves through the data are predictions of the model.

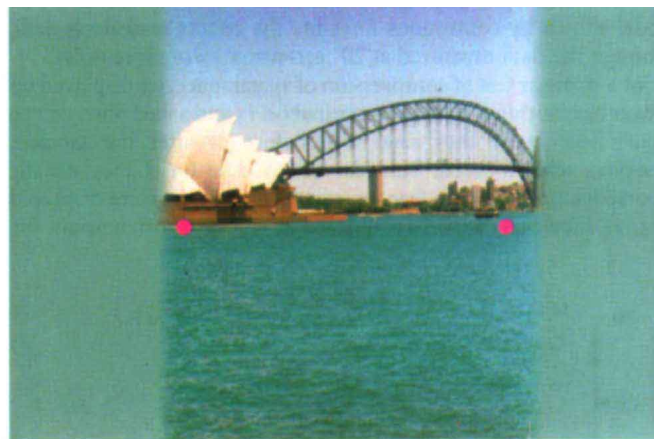
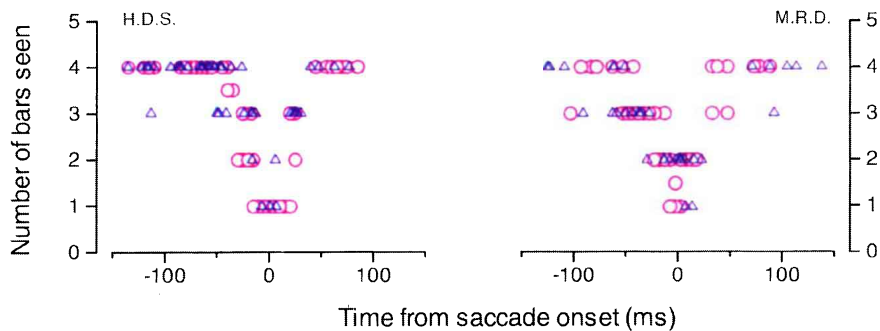


Figure 4 Top, Multiple bars (between 0 and 4) were assigned at random to 4 positions straddling F_1 (0, 7, 14 and 20°), and briefly displayed simultaneously at random delays with respect to saccadic onset. Observers H.D.S. and M.R.D. never reported a bar when none had been displayed, and always reported accurately when only 1 had been displayed. The graphs show the results only for when 4 bars were actually displayed: errors occur when the bars are displayed near the onset of the saccade. Circles, equiluminant green bars; triangles, black bars. Bottom, Natural scenes such as that on the left were briefly displayed to 13

observers (most naive to the aims of the test) at various intervals relative to a saccade. When the scene was displayed just before the saccade ($-25 \text{ ms} < t < 0 \text{ ms}$), it appeared compressed, similar to the simulation shown on the right, produced by applying equation (1) with $t = -20 \text{ ms}$. Some subjects (two) saw the bridge as symmetrical, others (two) reported that the Opera House sometimes detached itself from the bridge, but all observers saw the scene compressed.

(as they have longer processing latencies¹¹). However, evidence for position-dependent mislocalization does exist^{5,12-15}, although none of the earlier studies highlighted the effects with the use of multiple rather than single stimuli, or tested compression in other ways. Here the evidence for compression is unmistakable, and not dismissible as artefact⁵. None of our results, such as seeing four widely separated bars as one, can be attributed to saccadic suppression, because we used equiluminant stimulus, no less visible in saccades than in normal viewing¹⁶, and compression does not occur during 'simulated saccades' when the scene is moved rapidly by mechanical means.

We have constructed a two-component model for our data: a presaccadic shift of the same direction and amplitude of the saccade, together with a compression. The shift fits well with the anticipatory behaviour of cells in the lateral intraparietal cortex (LIP) and superior colliculi^{7,8}. Many of the cells in these areas respond presaccadically to stimuli that will fall onto their receptive fields after the saccade has been completed, making them likely candidates to mediate the shift in visual coordinates that must accompany each saccade. The physiological substrate for the compression is not so clear, but the receptive fields of some LIP cells may change shape before saccades¹⁷ (often expanding in size), consistent with compression. It may also be relevant that the magnocellular pathway, which provides the major input to parietal cortical areas important for visual localization¹⁸, seems to be selectively suppressed during saccades¹⁶, and the suppression could lead to a distortion in the metric of the internal representation of space.

Whatever the neural substrate for the compression, its functional role may be to increase tolerance to mismatches between the intention-to-move signal and the actual displacement, possibly explaining why observers are so poor in detecting image displacement during saccades¹⁹. When stimuli are occluded for the critical period around the saccade onset, and so are not subjected to compression, detection of image displacements improves greatly²⁰. The compression of space may reflect a moment of maximal plasticity and uncertainty, when objects are compressed within a restricted region, to be relocated into their real positions only after the new coordinate system has been fully established, taking into account new visual information. This could allow for a remapping of the effects of eye movements with only two coarse signals, and without recourse to expensive memory maps of the external world. □

Methods

General. Observers, with normal or corrected acuity and normal oculomotility, fixated binocularly a point F_0 at -10° (left of screen centre) on an otherwise featureless red screen ($70 \times 50^\circ$ at 25 cm, mean luminance 17 cd m^{-2}), surrounded by 2-m-square white card, illuminated to similar luminance and colour. After a warning signal, they made a saccade to a target F_1 which appeared at $+10^\circ$ and remained on until the next trial. The stimulus (usually a green bar subtending $1.5 \times 50^\circ$) was presented for 1 frame (8 ms) to a random position after a random interval. For the experiments in Figs 1 and 2, observers reported verbally the apparent position of the centre of the bar with respect to a ruler presented one second later (other experiments are described

in the figure legends). The stimuli were generated on a Mitsubishi colour monitor at 120 Hz by a computer-controlled framestore (Cambridge Research Systems VSG). Horizontal eye movements were monitored by an infra-red eye tracker (HVS Image Ltd), and actual delay of target presentation (with respect to the saccade onset) were determined after each trial by computer. For the results shown in Figs 1–3, the bar was equiluminant with the background (as these stimuli are not suppressed during saccades¹⁶); the same pattern of results has been obtained with light or dark bars.

Vernier annulment. For the vernier annulment task, the top half of the bar was briefly displayed 75 ms before or after the bottom half, and physically misaligned. Observers reported whether the top half appeared displaced to the left or right. Adaptive routines adjusted the physical offsets at each display time, based on the previous responses. Final thresholds were estimated by fitting a cumulative gaussian to the probability-of-seeing curves, comprising 80–250 data points. The standard deviation of the gaussian which gives an estimate of error, was on average 0.7°, and did not vary systematically with display time.

Model. To simulate the data of Figs 1–4, we assume that apparent visual direction P of any point x in external space is given by:

$$P(x, t) = E(x, t) \times C(x, t) + O(t) \quad (1)$$

$E(x, t)$ is retinal eccentricity (the difference between physical external space and eye position); $C(x, t)$ is a compression function weighting the eccentricities; $O(t)$ is an 'extra-retinal' signal, that can be considered to set the origin of the internal representation of space, usually given by eye position (ignoring head movements for now). On each saccade, $O(t)$ changes gradually, following the sum of the fade-out and fade-in functions that weight the present and future eye position:

$$O(t) = F_0 \left(1 - \int_0^t e^{-\frac{(t-\tau_0)^2}{2\sigma_0^2}} d\tau \right) + F_1 \int_0^t e^{-\frac{(t-\tau_1)^2}{2\sigma_1^2}} d\tau$$

The function $C(x, t)$ is given by

$$C(x, t) = e^{-k \left| \frac{E(x, t)(O(t) - Y(t))}{(F_0 - F_1)} \right|^{\beta}}$$

where k is a constant and $Y(t)$ is eye position. $C(x, t)$ bears a similarity to the inverse of the cortical magnification function²² (and may reflect a visual process designed to compensate for it). The free parameters in the equations were adjusted to achieve best fits to all the data for both subjects: $\sigma_0 = 30$ ms, $\sigma_1 = 38$ ms, $\tau_0 = 20$ ms, $\tau_1 = -40$ ms, $k = 1.48$, $\beta = 1.35$.

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1. von Helmholtz, H. *Handbuch der Physiologische Optik* (1866); translated by Southall, J. P. C. *Treatise on Physiological Optics* (Dover, New York, 1963).
2. Sperry, R. W. Neural basis of the spontaneous optokinetic response produced by visual inversion. *J. Comp. Physiol. Psychol.* **43**, 482–489 (1950).
3. Von Holst, E. & Mittelstaedt, H. Das Reafferenzprinzip. *Naturwissenschaften* **37**, 464–476 (1954).
4. Mackay, D. M. Elevation of visual threshold by displacement of visual images. *Nature* **225**, 90–92 (1970).
5. O'Regan, J. K. Retinal versus extraretinal influences in flash localization during saccadic eye movements in the presence of a visible background. *Percept. Psychophys.* **36**, 1–14 (1984).
6. Sperling, G. in *Eye movements and their role in visual and cognitive processes* (ed. Knowler, E.) 307–351 (Elsevier, Amsterdam, 1990).
7. Duhamel, J.-R., Golby, 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).
8. Walker, M. F., Fitzgibbon, J. & Goldberg, M. E. Neurons of the monkey superior colliculus predict the visual result of impending saccadic eye movements. *J. Neurophysiol.* **73**, 1988–2003 (1995).
9. Matin, L. in *Handbook of Sensory Physiology VII/4: Visual Psychophysics* (eds Jameson, D. & Hurvich, L. M.) 331–380 (Springer, Berlin, 1972).
10. Dassonville, P., Schlag, J. & Schlag-Rey, M. Oculomotor localization relies on a damped representation of saccadic eye movement displacement in human and nonhuman primates. *Visual Neurosci.* **9**, 261–269 (1992).
11. Bowen, R. W. Latencies for chromatic and achromatic visual mechanisms. *Vision Res.* **21**, 1457–1466 (1981).
12. Matin, L. & Pearce, D. G. Visual perception of direction for stimuli flashed during voluntary saccadic eye movements. *Science* **148**, 1485–1487 (1965).
13. Bischof, N. & Kramer, E. Untersuchungen und Überlegungen zur Richtungswahrnehmung bei willkürlichen sakkadischen Augenbewegungen. *Psychol. Forsch.* **32**, 185–218 (1968).
14. Honda, H. Saccade-contingent displacement of the apparent position of visual stimuli flashed on a dimly illuminated structured background. *Vision Res.* **33**, 709–716 (1993).
15. Honda, H. Visual mislocalization produced by a rapid image displacement on the retina: examination by means of dichoptic presentation of a target and its background. *Vision Res.* **35**, 3021–3028 (1995).
16. Burr, D. C., Morrone, M. C. & Ross, J. Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature* **371**, 511–513 (1994).
17. Ben Hamed, S. & Duhamel, J.-R., Bremner, F. & Graf, W. Dynamic changes in visual receptive field organization in the macaque lateral intraparietal area (LIP) during saccade preparation. *Soc. Neurosci. Abstr.* Part 2, 1619 (1996).
18. Mishkin, M., Ungerleider, L. G. & Macko, K. A. Object vision and spatial vision: two cortical pathways. *Trends Neurosci.* **6**, 414–417 (1983).

19. Bridgeman, B. & Stark, L. Ocular proprioception and efference copy in registering visual direction. *Vision Res.* **31**, 1903–1913 (1991).
20. Deubel, H., Schneider, W. X. & Bridgeman, B. Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Res.* **36**, 985–996 (1996).
21. Bridgeman, B., Van der Heijden, A. H. C. & Velichkovsky, B. M. A theory of visual stability across saccadic eye movements. *Behav. Brain Sci.* **17**, 247–292 (1994).
22. Daniel, P. M. & Whitteridge, D. The presentation of the visual field on the cerebral cortex in monkeys. *J. Physiol. (Lond.)* **159**, 203–221.

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Perceived geometrical relationships affected by eye-movement signals

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To determine the location of visual objects relative to the observer, the visual system must take account not only of the location of the stimulus on the retina, but also of the direction of gaze¹. In contrast, the perceived spatial relationship between visual stimuli is normally assumed to depend on retinal information alone, and not to require information about eye position. We now show, however, that the perceived alignment of three dots—tested by a vernier alignment task^{2,3}—is systematically altered in the period immediately preceding a saccade. Thus, information about eye position can modify not only the perceived relationship of the entire retinal image to the observer, but also the relations between elements within the image. The processing of relative position and of egocentric (observer-centred) position may therefore be less distinct than previously believed^{4–6}.

Our perception of a stable visual world is achieved, in part, by computing the egocentric position of stimuli through summing their retinotopic location with an internal representation of the direction of the eye⁶. However, this process is not always perfect and can sometimes lead to mislocalization. Hence, if a flash is presented shortly before a saccade, owing to the large delay in the afferent visual pathway (up to 100 ms), the internal representation of the eye position may have already started to change in the saccade direction by the time the visual signal reaches the cortex. The spatial location of the visual stimulus would then be miscalculated⁷. Indeed, it is known that a single point of light flashed within a critical period (about 100 ms) before a saccade is perceived as displaced in the direction of the saccade (a phenomenon called presaccadic mislocalization)^{7–10}. It has also been shown that a continuously lit spot of light, starting before the critical period and extinguished before saccade onset, is not mislocalized, presumably because its stable location has already been established¹⁰.

We investigated whether the perception of the relative position of nearby dots can be affected by the imminence of a saccade. We used a 3-dot vernier test in which the lower and upper dots were continuously lit until the presentation of the middle dot (for 4 ms), and then all three dots were extinguished together (Fig. 1, and see Methods). We carried out this test during the latency period of a visually evoked saccade (saccade trial) and compared the results with those obtained in the absence of an impending saccade (the