

Visual perception

Where are the things we see?

Joel M. Miller and Christopher Bockisch

Our visual perception of the direction of objects seems to be based on several inaccurate visuomotor processes, which are the subject of two studies by Ross *et al.*¹ and Cai *et al.*² on pages 598 and 601 of this issue. Even a simple sideways glance to grasp a coffee mug involves visuomotor complexities that we have only begun to unravel. Suppose you flick your eyes to the mug: that is, you prepare (during a 200-millisecond latency period) and execute (another 50 milliseconds) a 'saccadic' eye movement. You note the location of the mug and the orientation of its handle, and look back, as you begin reaching for the mug — the whole process takes, perhaps, half a second. If you don't find yourself grabbing at air or mopping up spilt coffee then, supposing you moved your arm without continuous visual guidance, you have accurately assigned the information from your visual 'snapshot' of the mug to its proper relative location in space.

Locating visual targets would be simpler if our eyes did not move. An image falling on the specialized central fovea of the retina would then indicate an object lying straight ahead. An image falling to the left of fovea would correspond to an object to the right, and so on. But because only the fovea supports high-acuity trichromatic vision, foveate animals constantly scan visual scenes with saccades (brief, rapid movements), which quickly bring successive images to the fovea. However, a given retinal locus must then signify different spatial directions, depending on the position of the eye. The suddenness of saccades (which reach 400° per second in about 20 milliseconds) and their frequency (several each second) probably imposes an extreme computational burden, which can be used to study localization mechanisms.

We easily understand the spatial arrangements represented in cinematic images. Although we have no direct information about camera movement, patterns of visual flow can provide indirect information about continuous or overlapping camera movements, so that we can understand the visual worlds they represent³. Even 'jump cuts' between non-overlapping camera positions, which provide the viewer with no information about movement, do not seem unnatural.

It is possible that our visual world is assembled, at least in part, like a jigsaw puzzle, on the basis of visual cues within fragmentary images. But where visual snapshots do not overlap, there is no intrinsic basis for assembling them — that is, jigsaw-puzzle mechanisms do not work for large saccades (Fig. 1). Even for small saccades, visual-pro-

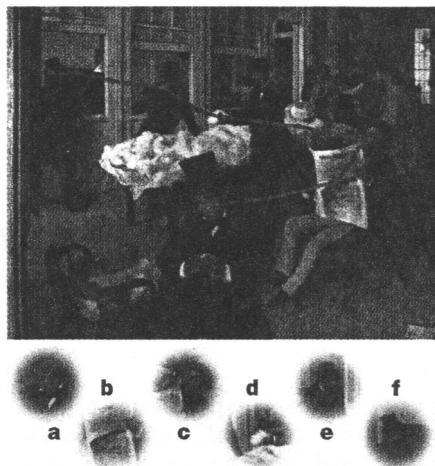


Figure 1 Detail of 'Portraits in an Office (New Orleans)' by Edgar Degas, with a hypothetical scanpath (red) showing six fixations joined by saccades. a–f indicate the predicted retinal content of these fixations. Based on information within the images, it seems possible that the visual system could properly relate the newspaper in b with its reader in c, and perhaps the cotton sample in d with the man to whom it is being presented in e. But information about eye position is probably required to ascertain that the man in f is watching the presentation, and that the man in a is self-absorbed.

cessing times imply that post-saccadic snapshots are not available for more than 50 milliseconds. In contrast, information about self-produced movement could be available for perception of direction even before a planned movement is completed. And it would be surprising if saccadic eye movements were not accompanied by information about 'camera' movement because, here, we are the cameramen.

Since at least the mid-nineteenth century, scientists have thought that the brain uses extraretinal (non-retinal) information about eye position (Fig. 2): knowing how the eyes have moved, the brain adds the angle of eye-rotation to the position on the retina of an object's image, to compute the spatial direction of the object^{4,5}. Several studies, placing retinal and extraretinal cues in conflict, have shown that rich visual information determines perceived changes in location, despite the contradictory extraretinal information⁶. But other experiments have shown the reverse⁷. Now, Cai *et al.*² describe a clear case in which extraretinal information is dominant, and Ross *et al.*¹ have mapped the time course of saccadic relocalization, and show that there are combined effects of retinal and extraretinal information. In both studies, the measured saccadic relocalization

was found to have systematic inaccuracies.

Cai *et al.*² exposed their subjects to a sparsely furnished visual world: there was nothing visible within 200 milliseconds of the subjects' saccades to a target, except for a vernier probe composed of a vertical pair of dots (which were visible from the start of the trial), and a briefly flashed dot (which was vertically centred between the flanking dots). The flashed dot preceded the movement of the eye to the target, at various horizontal locations in the neighbourhood of the saccade target, and subjects judged whether the flashed dot was collinear with the flanking dots. An accurate collinearity judgement might have been made from retinal-image information alone, during the brief period when flashed and flanking dots were simultaneously shown. Strikingly, in the 100-millisecond period before a saccade, flashes at all horizontal locations were mislocalized in the direction of the saccade, by about one-quarter the magnitude of the saccade. So visual direction is influenced by an extraretinal signal, even when more accurate, purely retinal, information is available. But there is a hint in the study of Cai *et al.* that the retinal information is also involved, because other studies⁸ involving only extraretinal information find even larger mislocalizations.

Ross *et al.*¹ asked subjects to make saccades from a fixation point to a target spot in a dimly lit environment, and to judge the horizontal position of a single vernier-probe flash relative to a ruler that was shown to them afterwards. In a second experiment, one component of a vernier probe was flashed early in the saccadic latency period (so as to be unaffected by relocalization processes), and the other was flashed just before the saccade (when large localization errors are typically found). The authors found that visual objects presented in the 100-millisecond period around the beginning of a saccade are mislocalized by as much as half the magnitude of the saccade.

Ross *et al.*¹ and Cai *et al.*² have consolidated previous findings that probes around the fixation spot, and short of the saccade target, are mislocalized in the direction of the saccade. Ross *et al.* also show that probes which are presented beyond the target can be mislocalized in the opposite direction to the saccade. So, around the time of a saccade, the retinal direction-map not only translates — as it must to compensate for the movement of the eye — but also compresses in the vicinity of visual targets. That is, the retinal mechanisms, which are usually thought to be highly accurate, introduce a distortion here. In a third experiment, Ross *et al.* confirmed the compression effect by presenting horizontally spaced compound probes around the saccade target, and asking the subjects to judge them for separateness.

Although Cai *et al.* describe clear evidence for extraretinal influence on perceived direc-

tion (mislocalization of probes flashed beyond the saccade target, in the direction of the saccades), this is the opposite of the direction found by Ross *et al.* The studies straddle an interesting territory in which the visual system responds to both extraretinal and purely visual determinants of direction, and subtleties in the task determine the weight that is given to each. So, the study by Cai *et al.* shows (and that of Ross *et al.* is consistent with) imperfect compensation for eye movement, based on extraretinal information. The results from Ross *et al.* further indicate that visual objects, or the attention that is directed to them, can exert an attractive bias on the perceived locations of other objects. In both cases, the perceived directions of objects depend on complex interplay between many sources of flawed information.

Because vision is so important for effective behaviour, we would expect visuomotor mechanisms to exploit all possible sources of information about distal objects in a lighted environment. Distortion of biological signals, and the computational limitations of any single mechanism, may be overcome by using several mechanisms, to improve overall performance in a range of situations. The worst failings of such a 'patchwork' system can be minimized by still other mechanisms. For example, the visual instability that would be expected to result from transient mislocalizations around saccades is simply sup-

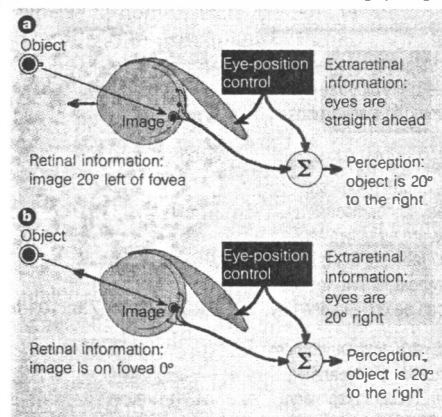


Figure 2 Simple scheme for combining retinal and extraretinal information on direction. The image of an object located 20° to the right is projected onto the retina, which signals the location of the image to a summing junction (retinal information). A copy of the command that determines eye position provides extraretinal information to the summing junction. The algebraic sum (Σ) appears at the output, and this is the perceived direction of the object. If retinal information accurately reflects the position of the image, and extraretinal information accurately reflects the position of the eye, then perceived direction is accurate, whether the eye is looking at the object (b) or elsewhere (a). But, as Ross *et al.*¹ and Cai *et al.*² now show, both sources of information are inaccurate around the time and destination of saccades.

pressed in normal vision^{9,10}. Future studies in specially contrived visual situations could determine how several information sources interact in normal vision. This should allow improved design of, and performance in, artificial, high-information-flow environments, such as aircraft, in which, for example, suppressive mechanisms are undesirable. □

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Metrology

Stars and ships and superfluids

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In two elegant experiments, Schwab, Bruckner and Packard (on page 585 of this issue¹) and Avenel and Varoquaux², have measured the rotation of the Earth to 0.5% and 2% respectively by exploiting the macroscopic quantum properties of superfluid helium. Given the many current applications of gyroscopes, we may ponder the technical future of such exotic rotation sensors — and their relevance to ancient, still unsettling questions about absolute rotation.

Macroscopic quantization is a peculiar phenomenon in superconductors and superfluids, related to Bose-Einstein condensation but best understood by comparing the superconducting case with the de Broglie picture of the hydrogen atom. In hydrogen, stable electron orbits occur when the wavefunction of the lone electron closes on itself around the orbit. Fritz London conjectured³ in 1950 that an analogous condition holds in a superconductor, not for single electrons but for the collective behaviour of the roughly 10¹⁶ electrons (strictly, electron pairs) that constitute a circulating supercurrent.

This phenomenon has several intriguing consequences. One is that the magnetic flux through a superconductor is quantized in units of $hc/2e$ (h being Planck's constant, c the velocity of light and e the charge on the electron). Another, recognized in 1962 by Brian Josephson⁴, is that if one introduces one or more thin insulating layers (or other 'weak links') into a superconducting loop, there occur interference effects, resembling optical interference, which can be exploited to measure very accurately the magnetic field through the loop.

In superfluid helium it is vorticity rather than magnetic flux that is quantized, the unit of quantization being not $hc/2e$ but h/m , where m is the mass of the helium atom. An old experiment by G. B. Hess and W. M. Fairbank^{5,6} illustrates it. They cooled a tiny rotating bucket of liquid helium through its superfluid transition (2.16 K). Above 2.16 K,

1. Ross, J., Morrone, M. C. & Burr, D. C. *Nature* 386, 598–601 (1997).
2. Cai, R. H., Pouget, A., Schlag-Rey, M. & Schlag, J. *Nature* 386, 601–604 (1997).
3. Gibson, J. J. *The Ecological Approach to Visual Perception* 1–332 (Houghton Mifflin, Boston, 1979).
4. von Holst, E. *Br. J. Anim. Behav.* 2, 89–94 (1954).
5. von Helmholtz, H. *Treatise on Physiological Optics* (Dover, 1925).
6. Matin, L., Picoult, E., Stevens, J., Edwards, M. & MacArthur, R. *Science* 216, 198–201 (1982).
7. Rine, R. M. & Skavenski, A. A. *Vision Res.* 37, 775–787 (1997).
8. Honda, H. *Vision Res.* 33, 709–716 (1993).
9. Bridgeman, B., Hendry, D. & Stark, L. *Vision Res.* 15, 719–722 (1975).
10. MacKay, D. M. in *Handbook of Sensory Physiology* 7, Part 3 (ed. Jung, R.) 307–331 (Springer, Berlin, 1973).

the helium behaves normally and is dragged viscously like water. For the superfluid, at slow rotations — where the total initial angular momentum is less than half h/m — the liquid stops rotating altogether, and the bucket correspondingly speeds up. Superfluid circulating through a thin hollow ring behaves similarly, but one can place a diaphragm with a minute hole in it (in practice, of diameter $\sim 1 \mu\text{m}$) across the section of the ring to form a 'weak link' in the superflow, producing a hydrodynamical Josephson effect. That is the key to the new rotation sensors. By modifying the topology of the ring to make the orifice part of a resonant chamber driven by a vibrating membrane, one can, as Schwab, Bruckner and Packard remark¹, determine "the state of absolute rotation of the containment vessel".

But what does that innocent phrase *absolute rotation* mean? We are drawn back to Newton's famous rotating bucket experiment. Centrifugal force makes a rotating liquid surface parabolic; so what is that rotation relative to? Not the bucket, for the surface can clearly be flat or parabolic with identical relative rotations. Newton concluded that it must be rotation with respect to 'absolute space'. Enter two centuries later Ernst Mach. He argued that inertia originates not from space but from the matter in space. According to Mach's principle, if we abolish from the Universe all matter except the bucket and water, the water will stay flat — centrifugal forces vanish.

Einstein made Mach's principle a founding assumption of General Relativity. He was, therefore, vastly annoyed when Kurt Gödel, having recovered from destroying mathematics, derived from General Relativity a most un-Machian model universe⁷. Gödel's universe is not ours, but that misses the point, which is that without special extra assumptions General Relativity does not explain inertia. One escape is *frame-dragging*. According to General Relativity, rotating massive bodies like the Earth partially