Vision: **Visual space is not what it appears to be**
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The location of visual objects in the world around us is reconstructed in a complex way from the image falling on the retina. Recent studies have begun to reveal the different ways in which the brain dynamically re-maps retinal information across eye movements to compute object locations for perception and directing actions.

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Our perception of the visual locations of objects around us needs to be veridical — a true representation of where those objects are physically situated in space. That we can reach for an object and manipulate it with ease adds to our sense that knowing where something is located is effortless: we know where something is because we can see where it is. Vision researchers have appreciated for some time that representing space is not quite so simple. First, despite movements of our eyes, head or trunk — all of which can lead to displacements of the object image on the retina — the perceived locations of static objects around us remain constant. So, representations of visual space also need to take into account information about the movement of body parts that displace the retina. And second, images of objects in central vision — at the fovea — are far better represented than those of objects in peripheral vision, which are resolved very poorly. Despite this, we have the impression that space is isomorphic, with all parts of the visual world — both at and away from the fixation point — being represented in an equivalent way.

These two examples both suggest that, far from being a passive reflection of the retinal image, our representations of visual space are actively constructed. A recent study by Burr, Morrone and Ross, published in *Current Biology* [1], illustrates how dynamic these representations of visual space can be, and offers important clues regarding the mechanisms which underlie these representations.

When observers are asked to localise a briefly flashed visual 'probe' stimulus, they systematically misjudge it to have been presented closer to the point of fixation than it actually was. Furthermore, if the time between probe presentation and perceptual judgement is delayed, this mislocalisation drifts even closer towards the fixation point

[2]. Thus, with time, the representation of visual location appears to become compressed towards the point of fixation. Such a dynamic change occurs not only in visual memory, but also with every eye movement. Probe stimuli that appear very briefly at a wide range of stimulus locations immediately prior to the execution of a saccadic eye movement are not perceived to be in their veridical positions, but are instead reported to be at locations compressed toward the target of the saccadic eye movement — the intended new point of fixation or direction of gaze [3,4].

The new work of Burr *et al.* [1] has further illustrated the dynamic nature of the representations of visual space immediately prior to the execution of saccadic (fast) eye movements. In their study, subjects executed horizontal saccadic eye movements and were required to report the location of a probe stimulus (a large vertical bar) that was briefly flashed at a random location before, during or after the saccade. Only probe stimuli appearing before the saccadic eye movement are considered here. Subjects reported the location of the probe verbally (by calling out a number corresponding to a visual or memorised scale), or by pointing to its perceived location, with vision of the pointing limb occluded from view. Trials in which subjects made a verbal report showed the previously-found pattern of spatial compression toward the target of the saccadic eye movement (or intended new point of fixation). In contrast, trials where subjects indicated the position of the probe stimulus by pointing to it showed a remarkable dissociation between reaches in which post-saccadic visual information was present, and those where it was not.

Post-saccadic visual information was prevented either by having subjects shut their eyes immediately after executing the saccade, or by occluding vision using liquid crystal lenses 75 milliseconds after presentation of the target stimulus. In both cases where post-saccadic visual information was unavailable, subjects' localisation of the probe stimulus by pointing was extremely accurate — almost veridical. In contrast, when the subjects' vision was not occluded, their pointing responses were highly inaccurate, exhibiting the characteristic compression toward the target of the saccadic eye movement. Thus, without post-saccadic vision, subjects were able to point accurately; but with post-saccadic vision, their pointing responses (and verbal reports) were inaccurate.

Burr *et al.* [1] suggest that these effects are consistent with two separate visual systems — one for conscious perception and another for the control of action (see also Milner

and Goodale [5,6]). The former is considered to be plastic and subject to spatial distortion, while the latter is not. Our view is that the findings of Burr *et al.* [1] are consistent with recent demonstrations of separate neural systems for representing movements in eye-centred and body-centred coordinates [7–9]. For example, when some patients with hemispatial visual neglect following posterior cortical lesions reach toward visual targets, their trajectories may be spatially distorted, but this distortion does not occur when they reach to proprioceptively-defined targets [8]. More broadly, there is emerging evidence that movements may be planned and controlled within multiple coordinate systems, each one attached to a different body part [10–13]. It is likely that eye-centred representations may be responsible for dynamic remapping across saccades, whereas body-centred representations are not.

Where in the brain are the representations underlying these 'compression' effects? Several lines of evidence point to the posterior parietal cortex (PPC). In the monkey, electrophysiological studies have identified multiple representations of space within this area [10–13], each associated with different types or combinations of action, such as saccadic eye movements and reaching or grasping movements of the upper limb. Recordings made from the parietal area LIP (Figure 1) while monkeys make saccadic eye movements have suggested that neurons in this region may be involved in a dynamic re-mapping of space [14], with the representation of visual stimuli being re-mapped from a coordinate system with the initial fixation point as its origin, to one with the upcoming fixation point as its origin.

Exactly how such an eye-centred re-mapping is achieved is still not known, but it is possible that such re-mapping is the mechanism underlying the spatial 'compressive' effect. Some LIP neurons continue to encode both the original point of fixation as well as the new intended point of fixation at around the time of the saccade, effectively encoding space in a coarser representation. Furthermore, many neurons in LIP appear also to be involved in maintaining a memory trace for the location of saccadic targets across delays [13,15]. The re-mapping and memory-related activity within this region of the parietal cortex may therefore play an important role in the 'compressive' effects observed in healthy humans both at around the time of a saccade [1,3–4] and with increasing time delays without saccades [2].

What happens when parietal areas are damaged? In humans, a profound spatial deficit may be observed in patients with lesions involving the intraparietal sulcus. Such patients appear to be impaired in spatial re-mapping across saccades when tested on 'double-saccade' tasks [16,17]. In such tasks, individuals are required to fixate in
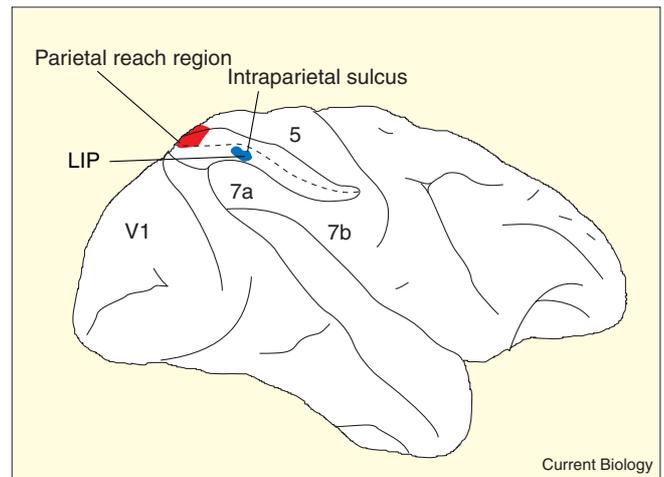
Some parietal lobe regions in the macaque monkey brain. The intraparietal sulcus (opened out) is a critical region, separating the superior parietal lobe from the inferior parietal lobe. Area LIP (blue) lies in the lateral bank of the sulcus and is an important region for integrating visual information with eye position and eye movement signals. The parietal reach region (red) probably includes a number of visual areas where visual information is integrated with eye and hand signals.

turn the remembered locations of two sequentially flashed targets. Both targets disappear before the first saccade, so the second saccade begins from a different eye position than that from which the second target was seen. Normal subjects saccade accurately to the second position, taking into account the new eye position after the first saccade. But although parietal patients make the first saccade accurately, they fail to encode the location of the second target accurately, often making saccades commensurate with the original retinal position of the second target. Thus, they fail to take account of the new eye position, and this may account for one component of the hemispatial neglect syndrome which follows parietal damage [18]. Taken together, these finding suggest that area LIP in monkeys, and homologous regions in the intraparietal sulcus of humans, may be responsible for the perceptual 'compressive' effects observed at around the time of a saccade in healthy humans. But what about the compression seen in visually-guided pointing movements?

Recent electrophysiological studies of the superior parietal lobe (SPL) have demonstrated the existence of a 'parietal reach region' (Figure 1). In this area, representations associated with reaching movements appear to be eye-centred, rather than body-centred [12] — just as the representations in LIP associated with saccades are eye-centred. Several groups have shown that visual signals are combined with hand position and movement signals, as well as eye position and movement signals, in the parietal reach

Figure X
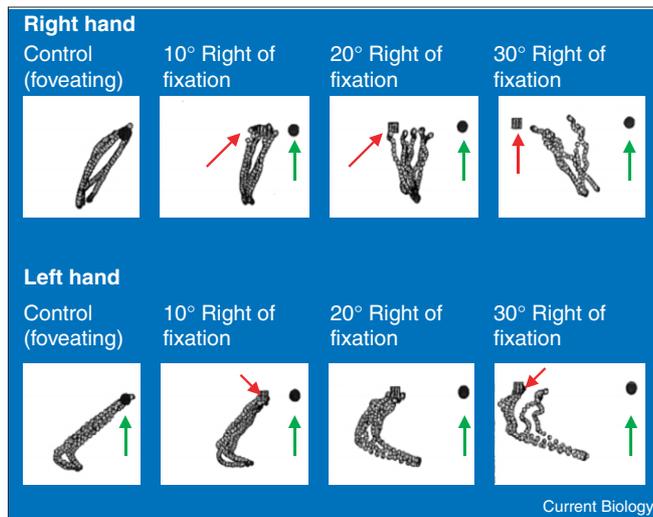
Magnetic misreaching in a patient (Mrs D) presenting with bilateral parietal damage. The panel depicts reach paths for movements executed using the right or left hands. The red arrows indicate the fixation stimulus on each trial, and the green arrows the location of the target stimulus (the point the patient was required to reach to).

region [19,20]. Furthermore, by comparison to other visual areas, this area may have a more prominent representation of the peripheral visual field [21].

In humans, lesions of the SPL lead to misreaching to peripheral visual targets — optic ataxia. While such patients can correctly and accurately execute reaching movements directed to proprioceptively-defined targets — targets defined by the positions of body parts — they mislocalise targets when pointing to visual stimuli, particularly when executing movements directed toward targets located in peripheral vision. Furthermore, when reaching to peripheral visual targets while fixating centrally, these patients tend to err in their reaches towards the direction of gaze [22,23]. This is illustrated in Figure 2, which presents data from a recent case report of an extreme pathological form of this tendency: 'magnetic misreaching' towards the direction of gaze, rather than the location of the peripheral target [23]. It is plausible that the extreme compression of space toward the point of fixation observed in this case of optic ataxia may result from an imbalance between visual representations arising from the fovea and those originating from the peripheral retina.

Finally, what about the veridical reaching seen by Burr *et al.* [1] when healthy individuals had to point without vision to the remembered location of the probe which was flashed just before they made their saccade. We would anticipate that such movements would not be coded in eye-centred coordinates, but rather in body-centred (proprioceptive) coordinates such as those found in parietal areas 5 and 7b. Consistent with this view, lesions of these parietal regions lead to misreaching in the dark, but not when vision is available [7].

In conclusion, behavioural findings in healthy and brain-damaged humans, combined with physiological studies in monkeys, are beginning to shed light on how the brain actively reconstructs space from the retinal image. Current evidence suggests an important role for the posterior parietal cortex, where there are multiple representations of space, each associated with different types or combinations of action.

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