Dispatch

Vision: Non-illusory Evidence for Distinct Visual Pathways for Perception and Action

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When visual information about an object's distance is obscured, but its retinal size visible, the object's physical size is ambiguous to vision, however, additional proprioceptive distance information permits physical size to be estimated when grasping the object, but perceptual size estimates remain inaccurate, adding to that evidence for distinct visual pathways for perception and action.

Is visual information that is used to guide action towards an object processed in a different way from visual information that gives rise to conscious experience of the identity of objects in the world? The influential two-visual-systems hypothesis of Milner and Goodale [1] suggests that this is the case. This hypothesis is based to a great extent on evidence from experiments with animals and work with neuropsychological patients having damage in one of two distinct pathways that project forward from the primary visual cortex into the parietal or temporal lobes. A number of studies have tested for functional dissociations consistent with the two-visual-systems hypothesis in neurotypical observers using a variety of tasks based on visual illusions. In these studies, stimuli that were subject to perceptual size illusions were, nevertheless, grasped nearly veridically. These studies have, however, been the subject of ongoing controversy about the relative demands of the grasping and perceptual estimation, tasks. A new study by Chen *et al.* [2], reported in this issue of *Current Biology*, demonstrates dissociation between grasping and perceptual size estimation using a quite different approach that is not subject to these issues, based on the effect of proprioceptive distance information on size constancy when visual information about the distance to an object is restricted.

Milner and Goodale's [1] two-visual-systems hypothesis has had a central place in our understanding of the functional and anatomical organisation of the human visual system for over twenty years. The notion that distinct functional roles of visual information are reflected in anatomically distinct pathways arose from animal studies in the 1960s and 70s by Schneider [3] and Ingle [4], and culminated in the suggestion by Ungerleider and Mishkin [5] that the primate visual system could be divided into a dorsal stream passing from primary visual cortex to parietal cortex in which information about objects' locations is coded, and a ventral stream passing from primary visual cortex to temporal cortex in which information about objects' identity is coded.

Milner and Goodale [1] refined these ideas into a hypothesis stating that the dorsal stream is not simply responsible for coding location, but rather more generally for extracting information useful in the visual guidance of goal-directed action. Furthermore, only ventral stream processes gave rise to conscious experience. Much of the impetus for this position came from studies of patients with visual form agnosia and optic ataxia. The visual form agnosic patient DF, with ventral stream lesions, could not identify objects, or even discriminate their shapes, but her goal-directed actions — such as grasping an object with appropriate grip or posting a letter through an oriented slot — were unimpaired, despite her inability consciously to report the size, orientation and shape of objects. In contrast, patients with optic ataxia, with dorsal stream lesions, could identify objects but were very poor at making appropriate goal-directed actions.

A number of studies [6–8] have shown that procedures that cause the position of targets to be misperceived do not affect the accuracy with which normal observers localise targets through pointing or eye-movements. In 1995, Aglioti *et al*. [9] published a study using the 'Titchener circles' illusion which showed a similar dissociation between inaccuracy in perceptual estimates of targets' sizes and more accurate scaling of grip when the same targets were grasped (Figure 1). At first sight, these results appeared to provide clear evidence for functionally distinct systems for perception and goal-directed action in normal observers, consistent with the two-visual-systems hypothesis. This study and its successors have, however, proved controversial, with new experiments, aimed towards either supporting or refuting the distinction between performance in grasping and perceptual estimation, continuing to be published and debated to this day [10,11]. With criticisms also being raised about aspects of the neuropsychological evidence for the two-visual-systems hypothesis [12], new lines of evidence which might contribute to the debate should be welcomed.

In their 1995 paper, Aglioti *et al.* [9] discussed why perceptual size estimation might be subject to illusions that grasping was not. One possibility suggested was that illusions involve exploiting visual cues to distance from relations between objects in a scene that may, in some circumstances, be invalid — for example, retinal size comparisons in which implicit assumptions are made about size-distance relations — whereas grasping, being focused on a single target, is less susceptible those relational cues. The new paper of Chen *et al*. [2] returns to this theme and is explicitly directed at assessing size constancy in perception and grasping — that is, the estimation of an object's physical size regardless of the angular size it subtends on the retina — without the complexities of design and interpretation associated with illusions.

Chen *et al*. [2] presented their (neurotypical) observers with views of a real sphere which they either had to grasp, or to provide a perceptual estimate of its physical size by matching the distance between their thumb and forefinger to that size. Responses to three different sizes of spheres were analysed. The distance between the sphere and the observer varied so accurate size estimation required information about the retinal size of the image of the sphere *and* an estimate of its distance to be combined. In one condition, the sphere was viewed in normal illumination and a variety of visual cues to its distance were available. In the second condition, the sphere, which was coated in luminescent paint, was viewed in darkness, monocularly, through a pinhole. The sphere was visible by virtue of its luminescence, but the view of its surroundings, including all cues to its distance, was greatly restricted. In a final manipulation subjects either kept their non-grasping hand in their laps, or it was placed directly below the sphere on its supporting pedestal, thereby providing a proprioceptive cue to the sphere's distance.

The results show that both perceptual estimation and grasp size demonstrate size constancy when the lights were on (grasp and perceptual estimate size were unaffected by the distance at which spheres were presented). In the restricted viewing condition, perceptual estimates of size were erroneously significantly reduced at greater distances. Grasping was also affected when proprioceptive cues were unavailable, but with proprioceptive cues the distance to the sphere did not affect grasp size – in other words size constancy was preserved. There appears to be a functional difference between vision for action and perceptual size estimation.

A range of criticisms have been aimed at illusion-based studies purporting to demonstrate such function dissociations. Some of these have been resolved by further experiment, but some remain controversial [13]. Among these criticisms are the following. First, that equating comparative perceptual judgements of the sizes of the central discs in the Titchener circles illusion with grasps directed towards just one of the discs (but see [10,14]) is problematic. Second, that the obstacle avoidance demands of grasping the disc in the centre of the large circles are lower than those of grasping the disc surrounded by small circles which counteracts the perceptual illusion for grasp. Third, that the surrounding circles, which are two dimensional in contrast to the three dimensional central discs, are irrelevant in grasp formation. Fourth, that illusory displays do, in fact, affect grasping. Fifth, that the relationship between disc sizes and perceptual size estimates have a non-unitary slope — for any increase in the size of the disc the perceptual size estimates increase is larger — and this must be taken into account when making comparisons with grasp size. And sixth, that the illusion still affects action components other than that measured (maximum grip aperture).

The Chen *et al.* [2] study aimed to eliminate these concerns: no comparative judgments need be made; there are no obstacle avoidance demands; there are no illusion inducers, flat or otherwise; size constancy is perfect for restricted vision with proprioceptive cues; and a correction is applied to account for differences in the slopes of changes in object size of perceptual estimates and grasp apertures. It remains to be seen whether action parameters other than maximum grip aperture are affected regardless of proprioception, although it would not be at all surprising if, for example, latency or speed slowed in conditions of darkness and it would be hard to argue that such changes undermined the argument for a functional dissociation between vision for action and vision for perception in this experiment.

Recent criticisms of evidence for the two-visual-systems hypothesis highlight the need for new approaches. By devising a design that eschews illusion and demonstrates a functional dissociation between perceptual estimates of size and grasp scaling in normal observers Chen *et al*. [2] have moved the debate on the two-visual-systems hypothesis significantly forward.

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Figure 1. Grasping an illusion: the Titchener circles' task of Aglioti *et al.* [9].

The observer, who grip size is being measured, grasps one of the central discs in this task [9]. The surrounding flat circles induce a perceptual illusion that the disc surrounded by large circles is smaller than the disc surrounded by small circles. In fact both discs are the same size. As reported by Aglioti *et al.* [9], grip size is relatively unaffected by this illusion in contrast to a perceptual comparison of disc sizes, although there is continuing debate as to whether the effect of the illusion on action and on perception truly differs [10].

In Brief:

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Figure 1: