

Turning points

A visible difference Melvyn A. Goodale

Thirty years ago I was a young postdoc working with Larry Weiskrantz at the Department of Experimental Psychology in Oxford. The laboratory (or cubbyhole) where I worked was some distance from the main department and, perhaps because of this, our little group of postdocs and graduate students developed a strong sense of camaraderie. We spent many of our lunch hours arguing science, politics and the human condition — usually in the nearby Lamb and Flag pub.

New publications in visual neuroscience, particularly theoretical papers, provided much of the fodder for our discussions. One of the papers that got us worked up was Gerald Schneider's on "Two visual systems", which appeared in *Science* in 1969 [1]. The paper was remarkable partly because Schneider was a young scientist who had only just finished his PhD, but mainly because it offered a clear and apparently straightforward account of the functional differences between the two main visual pathways in the mammalian brain.

Other researchers had already suggested the ancient visual pathway that runs from the eye to the midbrain in mammals has different functions from the newer visual pathway to the cerebral cortex, but it was the elegant simplicity of Schneider's distinction between the two that resonated with many scientists — including the discussion group at the Lamb and Flag. According to Schneider, the older pathway from the eye to the midbrain enables the animal to *localize* a visual stimulus, whereas the phylogenetically newer pathway to the cerebral cortex enables the animal to *identify* that stimulus. Schneider's evidence for this distinction came largely from his thesis work in which

he showed that hamsters with lesions of the midbrain (in a structure called the optic tectum) were unable to localize visual targets, even though they could identify them, whereas hamsters with lesions in the cerebral cortex (in a region called area V1 or primary visual cortex) could localize visual targets but could not identify them. This distinction between identification and localization — often referred to as the distinction between 'what' and 'where' — was to gain wide currency over the next 20 years.

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The original 'two visual systems' model put forward by Schneider (and its later reincarnation in monkeys by Ungerleider and Mishkin [2]) represented a significant departure from earlier descriptions of visual function, which had tended to treat the visual system as a single, albeit complex, entity. But even though Schneider took a more modular approach, the notion of 'localization' he proposed was poorly defined and it seemed to me that there was something not quite right about his story. Indeed, on reflection, I now realize that it was his failure to ground the term in observable behaviour that disturbed my Calvinistic soul back in 1969. I had come to Oxford from the University of Western Ontario, where I had been taught to be deeply suspicious of attempts to map psychological terms like 'localization' or 'attention' onto specific brain regions. People like Case Vanderwolf and Doreen Kimura emphasized, instead, the importance of studying the relationship between brain and observable behaviour — and by 'behaviour' they meant the actual movements made by the animal, not hypothetical psychological concepts like localization.

Schneider's 'two visual systems' theory (as well as Ungerleider and Mishkin's) lumped together all kinds of spatially organized behaviour under the general heading of 'localization'. Behaviours such as turning the head and eyes towards a sudden movement, running away from a looming shadow, deciding which of two holes is closer, running towards the closer hole and avoiding obstacles on the way, were all seen as depending on the same localization mechanisms. (As we know now, only some of these patterns of behaviour depend on the optic tectum.) These distinctions between different kinds of spatially organized behaviour were never apparent in Schneider's account. The implicit assumption seemed to be that once a stimulus is 'localized' the information can be used to direct any behavioural output. In other words, it was assumed that localization is a process that is quite independent of the behaviour it might elicit or control.

Two years later, I moved to the University of St Andrews in Scotland. Still musing about two visual systems, I began to explore the question in my own lab. Our experiments showed that lesions of the optic tectum in rats affected one kind of 'localization' behaviour — quickly turning the head to look at an unexpected flashing light — but left another kind of localization behaviour — running towards a lighted door — intact. In other words, our experiment showed that localization is not a unitary process: different classes of behaviour use different localization mechanisms, only some of which rely on the optic tectum [3]. Just before we published our findings, however, another 'two visual systems' paper appeared in *Science* [4]. This paper, by David Ingle, was on frogs — on 're-wired' frogs to be exact. For me, it was a revelation.

Ingle's experiments took advantage of the fact that the amphibian brain is capable of far more regeneration following damage than the mammalian brain. He removed

the optic tectum on one side of the brain and found that the axons from the retina that were severed in the surgery sprouted new projections which crossed over to terminate in the optic tectum on the same side of the frog's brain. When he examined the visually guided behaviour of these unfortunate creatures, Ingle found that they showed 'mirror-image' feeding — directing their snapping movements to positions in space that were mirror-symmetrical to the location of the prey objects. They also showed mirror-image predator avoidance. These results provided pretty clear evidence that the optic tectum has a critical role in the visual control of these patterns of behavior in the frog — and also converged nicely with our own findings in rats.

But, remarkably, not all the visually guided behaviour in the re-wired frogs was mirror-imaged. Ingle found that the same frogs showed quite normal avoidance of obstacles as they hopped from one place to another. As it turns out, the reason they showed normal visual control of obstacle avoidance is quite straightforward; the retinal projections to the pre-ectum, a structure in the thalamus just in front of the optic tectum, were still intact and had not been redirected to the opposite side of the brain. (Not surprisingly, lesion studies in frogs and rodents have since shown that this structure has a critical role in the visual control of obstacle avoidance.) Thus, Ingle argued, there are at least two independent visual pathways in the frog: a tectal pathway, which mediates visually elicited prey-catching and predator avoidance, and a pre-ectal pathway which mediates visually guided locomotion around barriers.

Ingle's experiments, like Schneider's before him, suggested that there is modularity in the organization of the visual pathways of the vertebrate brain. But the modularity that Ingle was talking about is very different from the 'what' versus 'where' story. In short, Ingle had demonstrated the existence of

different 'visuomotor' modules, not simply visual modules. In fact, it turns out that there are five or more visuomotor modules in the amphibian brain, each with its own set of retinal inputs and each controlling different arrays of motor outputs. There is no single 'multi-purpose' representation of space residing somewhere in the animal's brain; instead, visual input about spatial location is transformed in different ways for different purposes.

Ingle's paper was a watershed in my own thinking about the organization of the vertebrate visual system. It made me realize that it was possible to talk about modularity in visually guided behaviour without appealing to psychological abstractions like localization and identification (as Schneider had done). Most importantly, however, Ingle's paper got me thinking about how one could approach the study of vision by looking at the different patterns of behaviour that are

elicited and controlled by visual stimuli, an approach that has characterized much of my own research for the past 25 years.

References

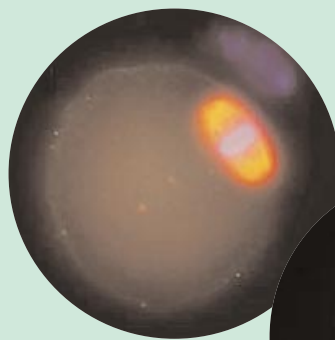
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Biology in pictures

Unravelling the spindle



The kinesin-related protein HSET is essential for microtubule organization in the spindles of mouse oocytes at metaphase II of meiosis. It localizes along the length of the meiotic spindle during both meiosis I and meiosis II. The oocyte at top left

was mock injected and shows a normal metaphase I spindle (DNA is stained blue, tubulin red and HSET green). HSET function has been perturbed in the oocyte at

bottom right by injecting it with antibodies specific for HSET.

This results in dramatic disruption of the spindle and dispersal of the chromosomes. For details see

Mountain V, *et al.*, *J Cell Biol* 1999, **147**:351-365.

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