Blindsight in hindsight

Larry Weiskrantz recalls the conditions surrounding a rare 'discovery' in psychology – response to visual stimuli without conscious perception

It is difficult to pinpoint just when the idea of blindsight first emerged, although, as is perhaps usual in such matters, there are a number of claimants. But we can date the year when the word 'blindsight' was first used – in 1973. Its oxymoronic properties were such that it soon found frequent usage, sufficient to make its entry into the *Oxford Concise Dictionary* – 'a condition in which the sufferer responds to visual stimuli without consciously perceiving them'. That condition is a lesion or removal of the visual cortex (striate cortex, V1) in the occipital lobes of humans.

Historically a more absolute and very persistent conclusion had been held, pithily summarised by William James (1890, p.47):

> The literature is tedious *ad libitum*… The occipital lobes are indispensable for vision in man. Hemiopic disturbance comes from a lesion of either one of them, and total blindness, sensorial as well as psychic, from destruction of both.

Indeed, James also held a similar view for such a condition in the monkey – that the blindness was absolute and permanent. But he did so by ignoring Munk's conclusion, that 'very gradually vision slightly improved so that he will not bump into things' (1881, translation by von Bonin, 1960, p.106). Luciani (1884, p.153) took this much further from his own work, concluding that 'some time…after the extirpation, [monkeys'] visual sensations become perfect again, they are able to see minute objects, what they want is the discernment of things… they are deficient, in a word, of visual perception'. His conclusion was doubted by William James, without citing his evidence, who referred in 1886 only to Luciani's work translated from the original Italian into German, failing strangely to mention an excellent English translation (by one of the editors of *Brain*) of the original Italian that appeared in that journal two years earlier.

That there should be a total loss of visual function after V1 removal has become increasingly paradoxical as it became clear that the retina projects to several targets in the brain other than the major input to V1 (via the thalamic dorsal lateral geniculate nucleus). The largest of these non-striate pathways – the superior colliculus – is larger than the intact auditory nerve in primates. The output from the superior colliculus can, in turn, reach a large number of cortical and other targets. There are also projections from the retina to the pulvinar nucleus in the thalamus, and from the lateral geniculate nucleus to non-V1 cortical regions. There is no way of isolating the rest of the brain from a visual input in the absence of V1.

> "The background to blindsight extends over a long period and there is no unique discoverer"

Experimental work in the first half of the 20th century established that monkeys without striate cortex could respond to light (e.g. Marquis & Hilgard, 1937). Later, Klüver (1942) concluded that they could discriminate only 'total luminous flux', but research by the Pasiks and colleagues (1971) showed that the visual capacity could support simple pattern discrimination and detection of gratings. Humphrey taught monkeys with V1 removal to respond impressively to a variety of 'salient' visual events, by requiring the animal merely to reach out and touch the source of the visual event (Humphrey & Weiskrantz, 1967). He also studied one monkey, Helen, in considerable detail (Humphrey, 1974), and showed that she could navigate herself through an obstacle course.

Despite the animal work, it was commonly and persistently held that humans were rendered completely blind following removal or damage of all visual cortex (although there were some discrepant neurological reports, for example by Teuber and colleagues (1960), Riddoch (1917), and Bard (1905)). The disparity between the human and animal evidence was puzzling and to many seemed unbridgeable. It led to a history of speculations by Marquis and others in the 1930s that there was 'encephalisation of function' as the phylogenetic tree was ascended, although a review of the evidence did not lend support (Weiskrantz, 1961).

It is rare for patients to have damage to the visual cortex in both hemispheres; more commonly the damage is to one hemisphere leading to loss of vision in the contralateral half-field of vision, a hemianopia. But within that region, too, the defect was thought to be absolute, in contrast to the residual visual sensitivity found in the hemianopic field of monkeys definitively established by Cowey (1967). One of the first positive clues with empirical evidence that the field defect of a human was not completely inert, despite the claims of affected people

references

Bard, L. (1905). De la persistance des sensations lumineuses dans le champ aveugle des heminanopsiques. *La Semaine Médicale, 22*(May), 3–255.

Campion, J., Latto, R. & Smith, Y.M. (1983). Is blindsight an effect of scattered light, spared cortex, and near-threshold vision? *Behavioural and Brain Sciences, 6*, 423–448.

Cowey, A. (1967). Perimetric study of field defects in monkeys after cortical and retinal ablations. *Quarterly Journal of Experimental Psychology, 19*, 232–245.

Gazzaniga, M.S., Fendrich, R. & Wessinger, C.M. (1994). Blindsight reconsidered. *Current Directions in Psychological Science, 3*, 93–96.

Humphrey, N.K. (1974). Vision in a monkey without striate cortex: A case study. *Perception, 3*, 241–255.

Humphrey, N. & Weiskrantz, L. (1967). Vision in monkeys after removal of the striate cortex. *Nature, 215*, 595–597.

James, W. (1890). *Principles of psychology*. London: Macmillan.

Klüver, H. (1942). Functional significance of the geniculo-striate system. *Biological Symposia, 7*, 253–299.

Leh, S.E., Mullen, K.T. & Ptito, A. (2006). Absence of S-cone input in human blindsight following hemispherectomy. *European Journal of Neuroscience, 24*, 2954–2960.

Luciani, L. (1884). On the sensorial localisations in the cortex cerebri. *Brain, 7*, 145–160.

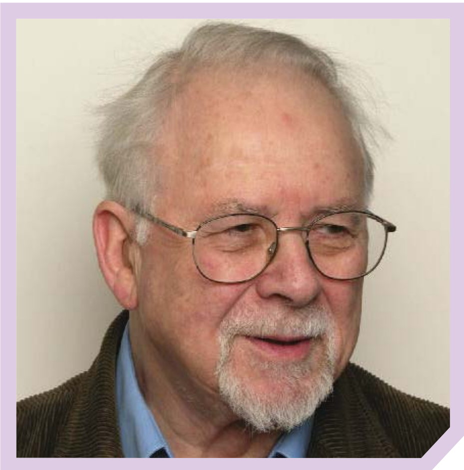
Marquis, D.B. & Hilgard, E.R. (1937). Conditioned responses to light in monkeys after removal of the occipital lobes. *Brain, 60*, 1–12.

Marzi, C.A., Tassinari, & Lutzemberger, L. (1986). Spatial summation across the vertical meridian in hemianopes. *Neuropsychologia, 30*, 783–785.

themselves, came from a study by Pöppel and colleagues (1973), who were interested in whether visual stimuli directed to the blind hemifield could exercise a control over eye movements, given the animal evidence that the superior colliculus played a role in the control of eye movements. They flashed a light briefly in different locations in the field defects of war veterans and asked them to look in the direction in which the flash had occurred. With encouragement, the subjects played the game, even though they said they could not actually *see* the flash. There was a weak but positive correlation between the target and the eye positions, at least for eccentricities out to about 25°. Alas, these investigators stopped with eye position as their dependent variable.

Soon afterwards a patient, D.B., came to our attention. His right visual cortex had been removed surgically to excise a non-malignant tumour, causing a left hemianopia. There was evidence in a clinical setting that he could locate visual stimuli in his blind field. For example the ophthalmic surgeon at the National Hospital, Michael Sanders, noted that D.B. could find his outstretched hand rather more accurately than one might have expected, and told his colleague Elizabeth Warrington, who then contacted me, knowing of my interest in the animal evidence. We repeated the study of Pöppel et al., and confirmed their evidence regarding eye positions. But with the testing methodology one is forced to use with animals for selective discriminations – forced-choice responding to alternative visual stimuli – we also found evidence for a number of other visual capacities (Weiskrantz et al., 1974).

The rest has become reasonably well known to workers in visual neuroscience. Elizabeth Warrington (whose major contribution has received little publicity) and I followed D.B. over a 10-year period, leading up to the *Blindsight* book in 1986, during which time a variety of visual capacities were demonstrated to the surprise not only of the experimenters but also to D.B. himself – evidence of reaching for targets, orientation discrimination, visual acuity using gratings, movement, simple shapes, etc., in the absence of acknowledged awareness by him. Since then colleagues and I have continued to follow him over another 25-year period, recently summarised in a new edition of *Blindsight* (Weiskrantz, 2009) spanning the entire 35 years. A number of other patients have also been studied by others and us.



Larry Weiskrantz *is Emeritus Professor of Psychology at the University of Oxford*
Larry.Weiskrantz@psy.ox.ac.uk

The evidence for unconscious visual discrimination was counterintuitive and challenged directly by critics (e.g. Campion et al., 1983; Gazzaniga et al., 1994) who suggested various possible artefacts, such as stray light, or residual islands of cortex. Even more dismissively, because of signal detection theory considerations, it was claimed (Campion et al., 1983, p.427) that 'from the theoretical point of view the unconscious aspect of blindsight is hence essentially trivial, and from the practical point of view it is impossible to treat scientifically'. There have also been disclosures of even more subtle possible artefacts, and so the guard must remain up. That there should be criticisms is to be expected and even welcomed, although they were sometimes administered with excessive zeal and persistence. On the whole, the early serious criticisms have been addressed and the original position bolstered (reviewed in Weiskrantz, 2009).

It is rare for a 'discovery' to take place in this area of science, like finding a new continent or a previously unseen butterfly, but it was immediately obvious that the phenomenon of successful performance without awareness in D.B. across a startlingly broad range of visual tasks must have a bearing on the neural and philosophical aspects of consciousness. It is equally obvious that the background to blindsight extends over a long period and there is no unique single discoverer. Indeed, I have always resisted any such label. There have been major contributions from multiple sources: from animal studies and the ever-strengthening evidence for residual function in them; from neuroanatomy; from the acknowledged complexities of neurological clinical examination and purported exceptions to the cortical blindness rule in humans; from behavioural studies of patients like D.B. together with functional MRI imaging; and the prompt given, restricted as it was to eye position, by the evidence from Pöppel et al. (1973). More immediately for me there were richly fruitful discussions with colleagues, especially Elizabeth Warrington and graduate students (subsequently senior colleagues), especially Alan Cowey and Nicholas Humphrey. In fact, it was easier for me personally to accept the evidence about 'unconscious' vision given the earlier findings of successful storage without 'remembering' in amnesic patients

Mohler, C.W. & Wurtz, R.H. (1977). Role of striate cortex and superior colliculus in visual guidance of saccadic eye movements in monkeys. *Journal of Neurophysiology, 40*, 70–94.
Munk, H. (1881). *Über die Funktionen der Großhirnrinde*. Berlin: Hirschwald.
Pasik, P. & Pasik, T. (1971) The visual world of monkeys deprived of visual cortex. In T. Shipley & J.E. Dowling (Eds.) *Visual processes in vertebrates. Vision Research Supplement no.3* (pp.419–435). Oxford: Pergamon Press.
Pöppel, E., Held, R. & Frost, D. (1973). Residual visual function after brain wounds involving the central visual pathways in man. *Nature, 243*, 295–296.
Riddoch, G. (1917). Dissociation of visual perceptions due to occipital injuries, with especial reference to appreciation of movement. *Brain, 40*, 15–17.
Sahraie, A., Weiskrantz, L., Barbur, J.L. et al. (1997). Pattern of neuronal activity associated with conscious and unconscious processing of visual signals. *Proceedings of the National Academy of Sciences USA, 94*, 9406–9411.
Sahraie, A., Trevethan, C.T., MacLeod, M.J. et al. (2006). Increased sensitivity after repeated stimulation of residual spatial channels in blindsight. *Proceedings of the National Academy of Sciences USA, 103*, 14971–14976.
Sanders, M.D., Warrington, E.K., Marshall, J. & Weiskrantz, L. (1974). 'Blindsight': Vision in a field defect. *The Lancet, 1*(7860), 707–708.
Stoerig, P. (2007). Functional rehabilitation of partial cortical blindness. *Restorative Neurology and*

(Warrington & Weiskrantz, 1968), and similar dissociations from awareness in unilateral neglect, aphasia, dyslexia and agnosia (for a review, see Weiskrantz, 1997). Even earlier there was a valuable sabbatical period in the early 1960s with Lucas Teuber in New York, which exposed me to the studies by of him and his colleagues of war veterans with brain damage to visual cortex.

If the fixing of a date for blindsight is inherently difficult, at least the invention of the word itself can be dated. In 1973, I was invited to give a talk about our unpublished evidence on D.B. to the Oxford Neurology Department. Shortly before the occasion I was hurriedly asked for a title, and out popped 'Blindsight and Hindsight'. Soon afterwards 'blindsight' appeared in print in a short paper with colleagues (Sanders et al., 1974). (In fact, hindsight in the title of the talk was and is just as important – given the strategic role of the superior colliculus.)

So much for 'Looking back': what does the future hold for blindsight research? In general, attention is likely to be focused on five main questions, to which I now turn.

First, what specific varieties of visual capacity are possible in the field defect, and what bearing might they have on psychological issues? A large variety of visual capacities in the cortically blind field have been revealed recently, among them positive evidence for depth perception, attention enhancement, and luminance contrast (but not colour contrast, thus showing the importance of V1 for colour constancy). One question that has attracted interest is whether emotionally charged visual events might be processed in the cortically blind field ('affective blindsight'), and if so what anatomical routes might be involved – especially to the amygdala, given its well-established role in emotional processing. In one study (Tamietto et al., 2009a) not only were the blindsight subjects able to discriminate between happy and fearful faces in the blind field, but they themselves displayed muscular facial patterns appropriate to the two contrasting sets of emotional stimuli.

Second, what are the anatomical routes over which such capacities might depend in specific instances? This question is being examined using a variety of methods, and both cortical as well as midbrain routes have been implicated. Future studies of blindsight are likely to try to find out which of these multiple pathways will be involved given the specific processing demands being placed upon them.

Third, what diagnostic tools are available for predicting whether or not blindsight will be found in a region of blindness? Marzi and colleagues (1986) have demonstrated that stimuli in the blind hemifield can influence the behavioural and pupillary responses to consciously perceived stimuli in the intact hemifield: the 'redundant target effect'. This has been used not only to demonstrate evidence of blindsight, for example in hemispherectomy (Leh et al., 2006), but also to differentiate various possible anatomical routes. For example, when stimuli were of a colour to which the superior colliculus is known to be physiologically insensitive, the redundant target effect in a blindsight subject diminished, as well as neural activation in the superior colliculus (Tamietto et al., 2009b). Also, pupillary constriction, pioneered in this context by John Barbur at City University, has been found to follow closely the psychophysical profiles for discrimination of stimuli in the blind field (Weiskrantz et al., 1998), and of course also shows a sensitivity to emotional events. Both redundant target effect and pupillometry are likely to be valuable diagnostically in the assessment of various brain lesions in human subjects.

Fourth, what are the prospects for rehabilitation, both for increasing sensitivity and also for bringing discriminations into awareness? The evidence from animal research that practice can lead to recovery of visual function following visual cortical lesions (e.g. Cowey, 1967; Mohler & Wurtz, 1977) has spurred similar enterprises with human subjects (e.g. Sahraie et al., 2006). Practical rehabilitation programmes have now been established (see review by Stoerig, 2007).

Finally, what differences in brain activity are found between good performance with and without accompanying awareness? In comparing conscious vs. unconscious visual processing, it is essential that the two levels of performance be closely matched. This was satisfied in the first such study for blindsight (Sahraie et al., 1997) implicating frontal lobe foci in fMRI during the conscious accompaniment. Future studies will, no doubt, feed into alternative theoretical and philosophical accounts.

Thus, the study of blindsight seems likely to continue to make contributions to psychological phenomena, to anatomy, to rehabilitation, as well as making further inroads into considerations of philosophical and neural underpinnings of consciousness.

Neuroscience, 25, 1-14.

Tamietto, M., Castelli, L., Vighetti, S. et al. (2009a). Unseen facial and bodily expressions trigger fast emotional reactions. *Proceedings of the National Academy of Sciences USA, 106*, 17661–17666.

Tamietto, M., Cauda, F., Latini Corazzini, L. et al. (2009b). Collicular vision guides non-conscious behavior. *Journal of Cognitive Neuroscience.* doi: 10.1162/jocn.2009.21225

Teuber, H-L, Battersby, W.S. & Bender, M.B. (1960). *Visual field defects after penetrating missile wounds of the brain*. Cambridge, MA: Harvard University Press.

von Bonin, G. (1960). *Some papers on the cerebral cortex*. Springfield, IL: Charles T. Thomas.

Warrington, E.K. & Weiskrantz, L. (1968). New method of testing long-term retention with special referenced to amnesic patients. *Nature, 217*, 972–974.

Weiskrantz, L. (1961). Encephalisation and the scotoma. In W.H. Thorpe & O.L. Zangwill (Eds.) *Current problems in animal behaviour* (pp.30–58). Cambridge: Cambridge University Press.

Weiskrantz, L. (1997). *Consciousness lost and found.* Oxford: Oxford University Press.

Weiskrantz, L. (2009). *Blindsight*. Oxford: Oxford University Press.

Weiskrantz, L., Warrington, E.K., Sanders, M.D. & Marshall, J. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain, 97*, 709–728.

Weiskrantz, L., Cowey, A. & LeMare, C. (1998). Learning from the pupil. *Brain, 121*, 1065–1072.