*J Physiol* 587.12 (2009) pp 2825–2835

# In praise of subjective truths

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> **'To determine orientation we occasionally used a PDP-12 computer to produce a graph of average response vs orientation, generating the slit electronically on a television screen. This method took much longer, and the usual minute-to-minute variations in responsiveness of the cell tended to make the curves broader and noisier. We concluded that for both speed and for precision it is hard to beat judgments based on the human ear. Certainly [our curves] could not have been obtained with computer averaging methods before the authors reached the age of mandatory retirement.' (Hubel & Wiesel, 1974)**

(Received 5 February 2009; accepted 23 February 2009)

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David Hubel and Torsten Wiesel had an uncommonly healthy respect for the brain, or at least for subjective truths that their own brains signalled. And the truths revealed to them were perceptual truths, ones in which they could have considerable confidence. With the machinery in their brains reporting unfailingly both the characteristics of the stimulus and the cellular response to it, they had little need for elaborate machines and sophisticated computers. Others perhaps placed too great a reliance on fancy machines, and got nowhere. One of them, Richard Jung, reported later with dismay but also with disarming honesty: 'When I was asked ... why we missed the orientation specificity during five years' work on cortical neurons, I used to ... remark that we might have found them in one experiment if we had used the stick with its easy movements in all orientations instead of the quantifying machine' (Jung, 1975). To be sure, Hubel and Wiesel put in some measurements to soothe and pacify anxious referees and readers, following Steve Kuffler's advice to 'stick in some measurements' to make the papers appear more scientific. The advice would have been bizarre had it not been a frank recognition that, collectively, measurements derived from subjective experiences are wholly or partially suspect to us while those delivered by dispassionate computers soothe our suspicions. Hence the common description of Hubel and Wiesel's work as 'impressionistic', a description to which they no doubt contributed by commonly saying, and writing, of the 'impression' that they gained of one aspect or another of the organization of the visual cortex. But there is nothing wrong with being 'impressionistic', especially when using eye and ear to chart simple visual properties like ocular dominances and orientation selectivities. Judgments based on the human ear are, of course, judgments based on a perceptual system, and the perceptual system is finely tuned enough to be able to determine with an accuracy approaching, and even surpassing, that of a computer, the optimal noise produced by the discharge of the cell. As well, the visual system is sensitive enough to be able to determine with a remarkable accuracy the orientation of a line. So, for measurements of this type, reliance on one's brain is sufficient. Indeed, given what a reliable measuring device the eye and the ear are, it is perverse that so many have placed so much more reliance on measuring instruments.

It is almost certain that many of Hubel and Wiesel's papers would not find easy acceptance for publication today, assuming them to be accepted at all. This is a pity. In an age when the study of subjective truths is becoming increasingly accessible, our intoxication with measurement should not blind us to the fact that subjective truths are the only ones that we can be sure of, that the brain is a superb measuring device, and that it continually executes measurements, be they measurements of light intensity or the degree of hate or desire. We are often more sure of such subjective truths than of objective ones. In this somewhat speculative essay, I argue that it is subjective truths, even those like love and hate, that are the easy ones to study and that it is objective truths that, perversely, are much more difficult to characterize in neural terms. There is thus a direct line that links studies such as those of Hubel and Wiesel and modern human imaging studies that probe more deeply into subjective truths. The essay is not intended to be an exhaustive review, but only an outline of my views at a time when we are celebrating the publication of the first paper in what turned out to be a major contribution to understanding the functioning of the primary visual cortex of the brain, area V1 – a paper that documented objective facts largely through subjective truths.

DOI: 10.1113/jphysiol.2009.170415

## Subjective and objective truths

Let us start with the proposition that subjective truths, being experienced by an individual, are truthful in the sense that the individual experiencing these truths can be certain of them. No one who experiences a line of a certain size or orientation can doubt the truth of their experience, any more than they can doubt the truth of their experience when passionately in love or when ravished by beauty. Objective truths, by contrast, are ones that are not always necessarily directly experienced, and I give an example of this from colour vision below. Hence, we cannot be as certain of them as we can of subjective truths, at least not experientially. Moreover, developments in brain imaging have made the study of subjective truths more accessible, even quantifiable. There are, in fact, gradations between subjective truths that are related directly, in a measurable and verifiable way, to objective facts and those that are entirely divorced from any measurable objective reality, at least at present. But there is one feature that encompasses all these gradations, namely that they are all either actually or potentially objectively quantifiable, even in spite of the fact that many of the experienced, subjective, truths have no physical counterpart which can be easily determined.

## 'Illusory' figures and higher cognitive factors

Perhaps the simplest example to begin with is *Enigma*, the creation of the French artist Isia Leviant (1996) (Fig. 1). A significant percentage of people perceive rapid movement in the rings, the motion reversing direction with prolonged viewing, although there is no objective motion there. The motion, being absent, cannot even be measured objectively. But the absence of objective motion does not mean that there is not a real, though subjective, motion there. For those who perceive the motion, the knowledge that it is not there objectively, that it is created in the brain, and more specifically in the visual motion area V5 (Zeki *et al.* 1993; Fermuller *et al.* 1997; Kumar & Glaser, 2006) cannot in any way abolish the motion and return the stimulus to its 'objective', non-moving, state. Hence objective knowledge cannot override the perceptual, subjective, experience in this instance. To those who see motion, the experience is objective and they can be certain of it. It is the 'objective' absence of motion that is unreal, perceptually at least. What is created here, by mechanisms that remain largely unknown, is a brain reality whose experience is as powerful as any objectively measured reality and indeed more powerful than many.

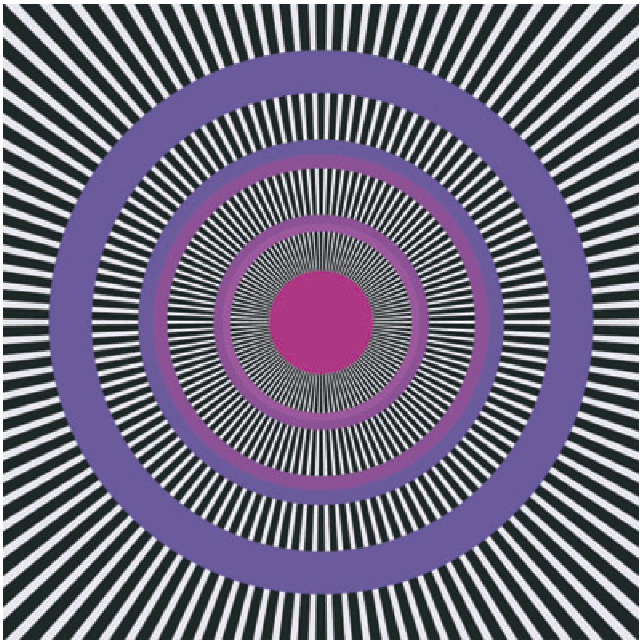

**Figure 1**
'*Enigma*', Isia Leviant

*Enigma* is but one of many examples in which the perceived subjective reality becomes objective, in the sense that it cannot be annulled even in the light of higher cognitive knowledge that the perceived reality is 'illusory', a somewhat perverse term designed to emphasize a separation between objective and subjective reality, without acknowledging the fact that the only perceptual reality the brain has is the subjective brain reality. Another striking example of this is constituted by the so-called bi-stable 'illusory' figures, of which there are many examples. A simple one is the Kanizsa cube (Fig. 2). The cube can be in two recessional planes, and no knowledge that it is actually on a flat surface can modify our bi-stable experience of it. The bi-stability is a brain reality, and that it departs so significantly from the objective reality (since it is a drawing on a flat, two-dimensional surface) does not make it less objective, for it is an experience that we can be certain of, which gives it a reality and therefore an objectivity. More

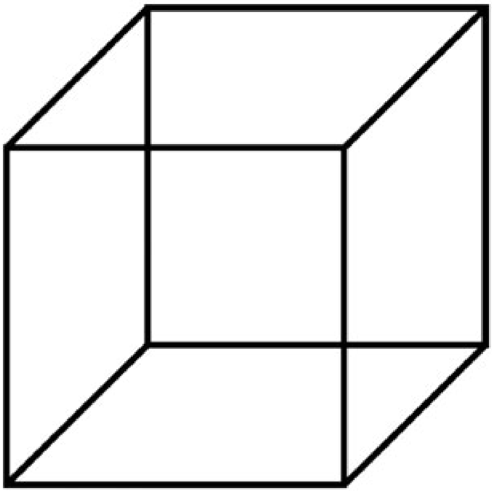

**Figure 2**
The Kanisza cube

impressive are the creations of Patrick Hughes, which rely on flat surfaces on which are sculpted three-dimensional surfaces (http://www.patrickhughes.co.uk/). Here the objects that stick out move with the viewer when seen at a distance, providing what has inappropriately been called a *trompe-l'oeil*. 'Tromper' means to deceive and the implication that Hughes' creations deceive is, in a neurobiological sense, not only pejorative but also inappropriate. Approaching the work suddenly reverses our previous percept and gives away the 'trick'. But knowledge that it is a 'trick' does not in any way reduce the intensity of the experience when we once more view it at a distance. There is no deception here but only the ingenious capacity to exploit the perceptive powers of the visual brain.

The difficulty of over-riding the perceptual experience, and hence the subjective truth, can also be illustrated by the wife and mother-in-law illusion (Fig. 3). Here perception alternates between the two, and it is useless trying to stabilize the percept by forcing it in one direction or the other, for example by adding spectacles to the mother-in-law or earrings and a necklace to the wife. The brain reality maintains this as a bi-stable percept (see Zeki, 2005). There are many other similar examples one could give.

## The subjective nature of colour vision

It is perhaps with colour vision that we face most forcefully the dichotomy between subjective and objective truths. When I first described a specialization for colour in the primate brain, during a meeting at Oxford in September 1972, David Hubel said to me, 'You have discovered the philosopher's stone'. Colour is of course a philosopher's delight. It exemplifies lucidly a central problem for philosophy, often summarised as the Heraclitan doctrine of flux, namely how we can obtain (constant) knowledge in a world that is in constant flux, where nothing remains the same from moment to moment, and how sure we can be of what we know. In spite of fluctuations in the wavelength-energy composition of the light reflected from a surface, we can always be (subjectively) sure of what the colour is, although we can never be certain (unless we are equipped with measuring devices) of the precise, and objectively measurable, wavelength-energy composition of the light reflected from that surface. It is because colour is a subjective experience through which we obtain stable knowledge of which we can be certain about the world, even in spite of wide fluctuations in the wavelength composition of light reflected from surfaces in different viewing conditions, that Arthur Schopenhauer commended the study of colour to students of philosophy, and wrote: 'A more precise knowledge and firmer conviction of the wholly subjective nature of color contributes to a more profound comprehension of the Kantian doctrine of the likewise subjective, intellectual forms of all knowledge and hence serves as a very useful introductory course to philosophy' (Schopenhauer, 1854). Colour, the end product of complex and largely unknown brain mechanisms, can also be both qualified and quantified as a subjective experience.

The colour of a surface remains significantly the same in spite of wide, and measurable, variations in the wavelength-energy composition of the light reflected from it, a phenomenon known as colour constancy. At dawn or dusk, a green leaf can (and often does) reflect significantly more red than green light, and yet we perceive it as being green, though a darker shade of green than the green perceived at noon time. No amount of knowledge about the excess of long-wave (red) light reflected from

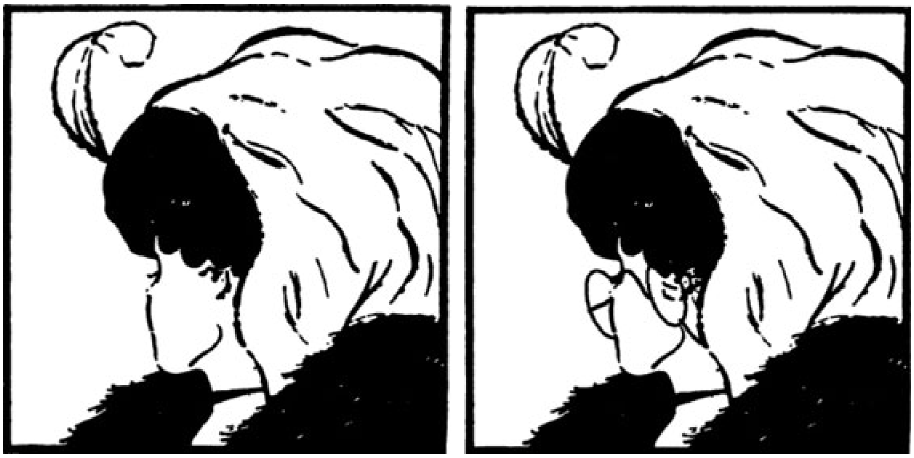

**Figure 3**
Left, bi-stable figure: wife/mother-in-law. Right, an attempt to dis-ambiguate the same figure. Despite the spectacles and eyeshades to stabilize the perception of the 'mother-in-law', the figure remains unstable.

the leaf – derived from objective measurements – can possibly modify our experience of it as green, except in the damaged brain. This is important to emphasize, because both Helmholtz and Hering invoked explanations based on judgment, learning and memory to account for colour constancy, supposing that the sensory experience is somehow modified by previous experience. They were both explicit about this, Helmholtz supposing that colour is due to 'an act of judgment' (von Helmholtz, 1911) and Hering writing that, 'All the colours that we know or think we know we see through the spectacles of our memory colours and therefore quite differently from the way we should see them without these' (Hering, 1930). Following Edwin Land, I adhere more to a relatively simple computational process, undertaken without reference to previous experience. Land believed that the computation occurred somewhere between retina and cortex (hence the term *retinex*), while I place the comparison stage that results in colour within the colour centre, the V4 complex (see Bartels & Zeki, 2000), though I also suppose that V4 acts in concert with the earlier visual areas which feed it with signals – V1 and V2 – and with which it is reciprocally connected. Hence I consider the subjective reality of colour to be the result of a brain process apparently occurring in a specialized part of the visual brain (Bartels & Zeki, 2000), and one that almost certainly involves the comparison of the wavelength composition of light reflected from a surface and that reflected simultaneously from its surrounds (in the range of 7 to 10 deg in all directions from the borders of the surface) (Wachtler *et al.* 2001 and author's unpublished results). This comparison results in a ratio for the amount of light of all wavebands reflected from the surface and from its surrounds (Land, 1974, 1983). These ratios are taken by the brain and, at least in the Land system, a comparison of these ratios (for light of different wavebands) by the brain results in the construction of colour by it.

When I say that the colour of the leaf or of a surface does not change, I do not imply that its shade or hue remains the same, a fact which some have tried to beat the phenomenon of colour constancy with. Indeed, artists would not have achieved their exhilarating colours without reliance on the fact that hues and shades change by juxtaposition with other colours (Zeki, 2008).

But colour categories do not change. A green surface that is part of a multi-coloured scene does not become red because it reflects an excess of long-wave light. Nor do I imply, as some simplistic minds have tried to make out, that there is no relationship between physical reality and the subjective experience of colour. There obviously is, and it lies in the ratio-taking system of the brain. The constancy arises from the fact that the reflectance of a surface (measured in terms of the per cent of light of any given wavelength reflected from it in relation to light of that waveband incident on it) never changes, even if the actual values reflected change from moment to moment. By taking ratios, the brain is able to establish that a given surface is reflecting more, or less, light of given wavebands compared to its surrounds. But there is no physical law that dictates that these ratios should be taken; it is a brain law that so dictates. In Immanuel Kant's terms, ratio-taking is a brain concept that is applied to the incoming signals. The result is a convincing subjective experience, so convincing that we may call it objective because we can be certain of its result. It is objective but only through the interposition of brain mechanisms. As Kant emphasized, we can never know the thing in itself (*das Ding ans sich*) because our only knowledge is the one obtained through the operations of the mind (for us, the brain). When the specific brain area, V4, is destroyed as a result of stroke or lesions, the brain cannot undertake these comparisons, even though the retina and the optic pathways leading to V4 are intact. The consequence is that the world appears colourless and is perceived in what is usually described as 'dirty shades of grey' (Zeki, 1990).

As with the orientation-selective cells of V1 studied by Hubel and Wiesel, the reaction of monkey V4 cells often correlate with the human (Zeki, 1983*a*; Bartels & Zeki, 2000) and monkey (Kusunoki *et al.* 2004) perception of (constant) colour. Hence they are not that difficult to classify as colour-coded cells, even without the use of elaborate measuring devices, although I and others have done so (Fig. 4). The procedure is simple. Putting a coloured patch of the appropriate size and of the presumed colour preference of the cell (determined by eye and verified by plotting its action spectrum), with the patch-forming part of a complex multi-coloured scene (the Land colour Mondrian), one simply needs to alter the wavelength composition of the light reflected from the patch, without changing its colour category, to determine its response. If it continues to respond to the coloured patch in its receptive field, even after significant variations in the wavelength composition of the light reflected from the patch, it is almost certainly a colour-coded cell. There are in fact even simpler tests that allow one to classify a cell as colour coded with rapidity (Zeki, 1983*b*). That these are indeed colour-coded cells has since been verified with much more sophisticated techniques, in the awake-behaving monkey (Kusunoki *et al.* 2004).

## Objective truths can be deceptive

The difficulty does not lie in characterizing cells whose responses correspond so well to perceived colour, in both human and monkey. Rather the difficulty arises when trying to detect and quantify cells whose activity does not correlate with the perceptual experience but departs from it and obeys the objective reality instead. In broad terms, the work of Nikos Logothetis (1998) and his colleagues has shown that all visual areas of the brain, including even area V1, contain cells whose responses correlate with percepts and others that do not. In V1, the responses of wavelength-selective cells are often counter-intuitive, if only because they correlate with objective facts that may lie outside the realm of our experience, at least if our brains are undamaged (see below). We cannot assume, for example, that because there are cells in the V4 complex whose responses correlate with the perceptual experience of colour, that the responses of antecedent cells that lead to the emergence of the V4 cells necessarily also do so. This can be dramatically illustrated by the wavelength-selective cells of V1 which connect with V4, either through the thin stripes of V2 or directly. These cells commonly respond indifferently to the colour of the stimulus and obey its wavelength composition alone (Zeki, 1983*a*). Thus, a cell of a narrow action spectrum restricted to middle-wave (green) light, may or may not respond to a green surface that is part of a complex multi-coloured scene, depending upon the amount of green light reflected from it, in relation to light of other wavebands (Fig. 5). This does not correspond to our experience of colour because, in a complex, multi-coloured world, we perceive a green surface that reflects more red light as green. Equally, a red-on, green-off cell may respond with an on or off to a patch of any colour placed in its receptive field, depending upon whether the patch is made to reflect more middle-wave or long-wave light (Fig. 6). Present evidence shows that, in both monkey and human, cells whose responses correlate with monkey or human perception of colour predominate in area V4.

It is interesting to note that patients with total or partial damage to V4 seem to experience the world of colour in a manner that is entirely dependent upon wavelength composition. This has interesting consequences if we assume (as Hubel and Wiesel did implicitly in their reliance on their own perceptual systems and as I do explicitly here and elsewhere) that the responses of cells in the brain have a conscious, perceptual, correlate. V4 is an essential node for colour vision (Zeki & Bartels, 1999); when damaged, subjects no longer see the world in colour but in shades of grey. But it is interesting to note that patients with total or partial damage to V4 seem to experience the world of colour in a manner that is entirely

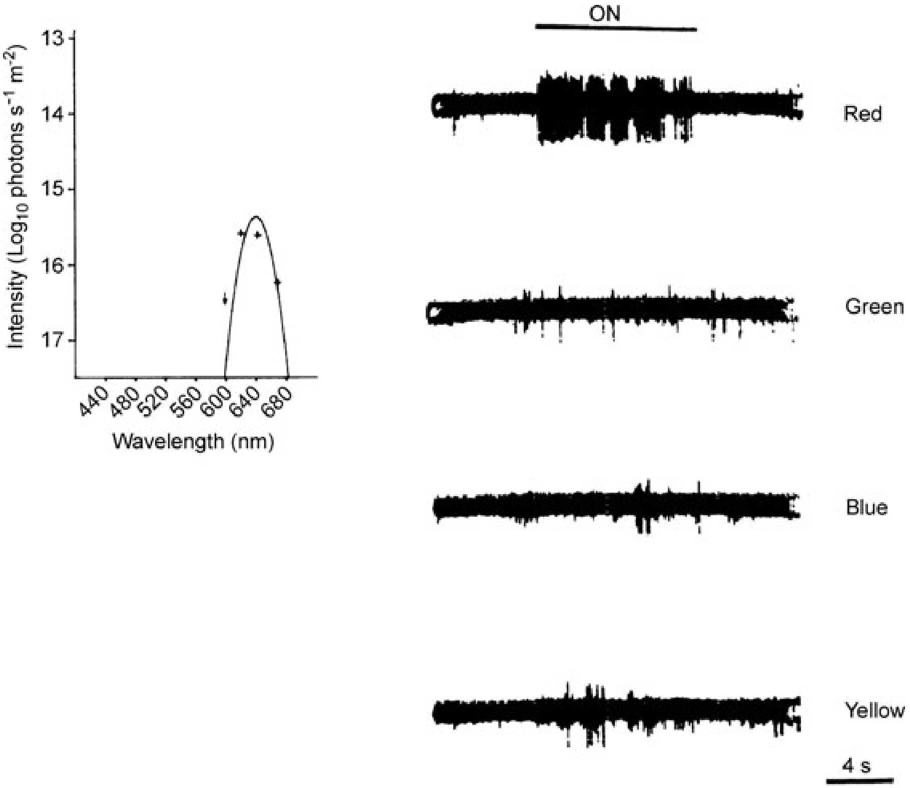

**Figure 4. The responses of a long-wave-selective cell in V4 to areas of different colour of a multicoloured Mondrian display**

Its action spectrum is shown in the inset (where downward arrows indicate there was no response at the highest available intensities). Each area, when put in the cell's receptive field, was made to reflect a standard triplet of energies (60, 30 and 10 mW sr$^{-1}$ m$^{-2}$ of long-, middle- and short-wave light, respectively). The receptive field size of this binocularly driven cell was 3.5 deg × 5 deg and was situated within the central 7 deg. It was stimulated through the ipsilateral eye (Zeki, 1983*a*).

dependent upon wavelength composition. Here we come across a paradoxical and highly interesting fact, derived from clinical studies: where the damage to V4 is sub-total, the subjective experience follows the physical reality and in the process becomes meaningless (Kennard *et al.* 1995). Now the colour of a surface is determined by the dominant wavelength in the light reflected from it, the patient now perceiving it as red, and now as green, depending on which is the dominant wavelength reaching the eye. Hence the patient ascribes an inconstant colour to a surface, and comes closer to perceiving Kant's 'thing-in-itself', the price being paid is that colour ceases to be stable and can

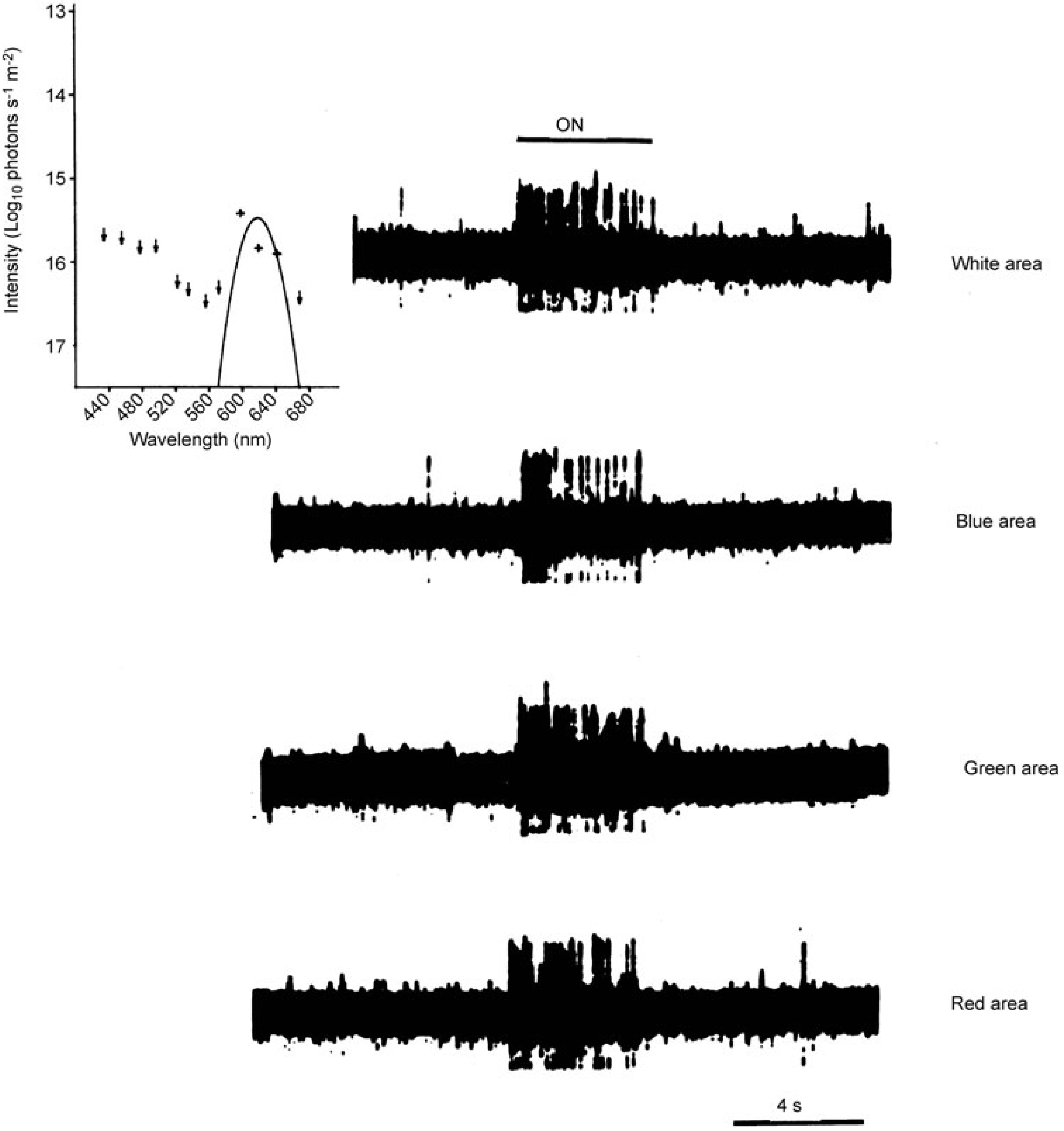

**Figure 5. The responses of a V1 cell selective for long wavelengths (see inset for its action spectrum) to areas of different colour of a multicoloured Mondrian display**

When each area was made to reflect 83, 33 and 7 mW $sr^{-1}$ $m^{-2}$ of long-, middle- and short-wave light the cell responded to each with approximately the same vigour. The horizontal line above the trace indicates that the projector shutters were open. The receptive field of this cell was 1 deg × 0.5 deg in size and situated within the central 1 deg. It was stimulated through the contralateral eye only. Each area when put in its receptive field covered it completely. In the action spectrum, downward arrows indicate that there was no response at the highest intensities available (Zeki, 1983*a*).

no longer signal an invariant and constant property of surfaces; colour, in short, ceases to be a biological signalling mechanism (see also Zeki *et al.* 1999). In a sense the subjective reality that the brain creates through its ratio-taking operation allows for a more stable and objective percept – that of colour – than the objective reality is capable of doing when not submitted to the brain's ratio-taking operation.

Much the same is true of a patient who became blind after a severe cardiac arrest but was still able to see and experience colours (Zeki *et al.* 1999). He had lost the capacity to construct constant colour, his perception of colour now being very much wavelength based. That this wavelength-based perception is based on the activity in V1 is strongly suggested by the fact that, when he viewed different colours (with high phosphor purity) on a screen in a scanner, the activity in his brain was confined to the territory of V1. This seemingly supports the view that his subjective experience of colour was limited and reflected the physiological capacities of cells in V1 that had been uncompromised by the widespread damage (Zeki *et al.* 1999).

Other evidence, but this time derived from imaging experiments, suggests that the responses of some cells in other visual areas also correlate better with the objective, physical properties of the stimulus than with the subjective experience. V5 provides a good example. Evidence shows that cells in this area, in both monkey and man, are strongly directionally selective, that is to say they respond to motion in one direction but not in the opposite, null, direction (Zeki, 1974; Moutoussis & Zeki, 2008). Correspondingly, responses in V5 show a strong correlation with the strength of the motion signal (measured in terms of the number of elements that are moving coherently). In a display consisting of dots in motion, it is easier to experience motion when many elements move together (coherently) than when they do not, leading to the widely accepted suggestion that activity in V5 correlates with perceived motion. Such a conclusion requires qualification, however, because it might lead one mistakenly to the conclusion that

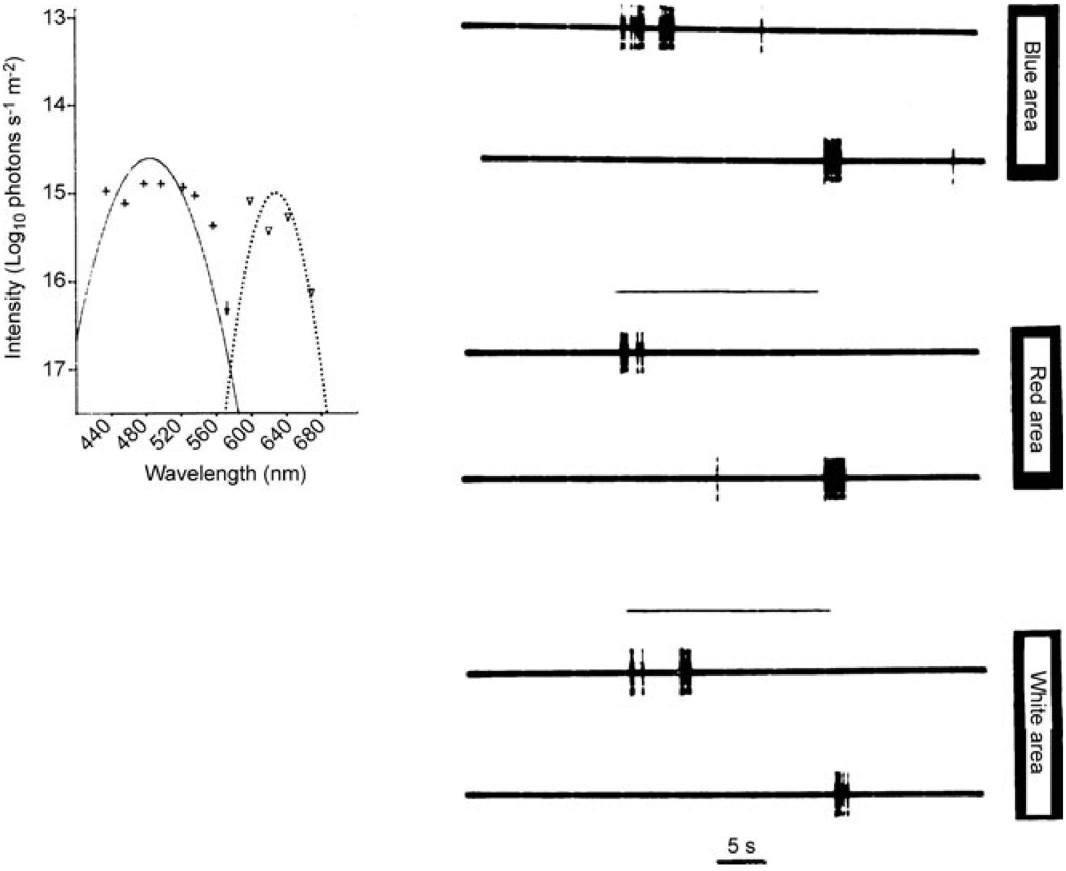

**Figure 6. The responses of an opponent input cell in V1 to the blue, red and white areas of a multicoloured display**

Inset shows its action spectrum. This cell gave an ON or OFF response to an area of any perceived natural (constant) colour, depending upon the relative amounts of long-, middle- and short-wave light reflected from the area. Receptive field size was 0.5 deg × 0.5 deg. Stimulation through ipsilateral eye (Zeki, 1983*a*).

perception correlates directly with the strength of cortical activation (Rees *et al.*, 2000). In fact, we have shown in recent experiments using dichoptic stimulation that a weakly perceived motion stimulus (that is one in which the motion is in opposite directions in the two eyes) is more effective in activating area V5 (as well as area V3) than a robustly perceived but weaker motion stimulus (in which the motion direction is the same in each eye (Moutoussis & Zeki, 2008). In the first condition, twice the number of directionally selective cells are stimulated, compared to the second condition. Given the widely accepted view that activity in V5 correlates with the perception of visual motion, this result raises the question whether there is a more specialized group of cells within V5 whose activity results in a conscious experience of motion, cells whose activity cannot be easily detected through changes in the BOLD signal. Whatever the explanation for it, the result is counterintuitive since, given all that has been written about V5, one would have hardly expected it to be more responsive to a strong stimulus that is weakly perceived than to a weak stimulus that is robustly perceived.

## Nodes and essential nodes in vision

Implicit in the argument made above is that the activity of some visual areas, or that of the cells in them, can have a perceptual correlate. We refer to such areas and cells as essential nodes, the definition of the term being that activity in them does not require further processing before becoming perceptually explicit. Thus, V4 constitutes an essential node for colour vision and V5 for motion vision, which is not to imply that the activity of every cell in V4 correlates with the conscious perception of motion or that the activity of every cell in V5 with that of visual motion. But here arises a problem. Orientation-selective cells are not confined to V1. They are also found in V2, V3 and V3A (Zeki, 1978). In the Hubel–Wiesel hypothesis, the orientation-selective cells of V1 are but one stage in the hierarchical elaboration of form, and have been often interpreted to be the physiological building forms of form. If this were so, then the activity of orientation-selective cells in V1 would perhaps not constitute an end point, in that the responses of cells there would require further processing before their activity acquired a conscious correlate. Hence their responses would be perceptually occult. Had this been so, Hubel and Wiesel would not have been able to use their perceptual system to chart the organization of V1. But it would seem unlikely to be so. It is not clear that the orientation-selective cells of V1 are used to construct form and indeed whether such cells are necessarily the physiological building blocks of form. In recent experiments using brain imaging techniques, we have shown that viewing simple oriented lines and increasingly complex forms consisting of assemblies of oriented lines, does not lead to a sequential activation of visual areas, with V1 being most strongly activated by simple lines and the areas constituting the lateral occipital complex (LOC) (Grill-Spector, 2003) being best activated by complex form constituted from many lines (Cardin & Zeki, unpublished results). Instead, we find that there are several, parallel form systems in each of which complex forms give a more robust response than simple forms. Given the strong correlations between cell responses and perceptual reactions – the basis of much of Hubel and Wiesel's work – it seems reasonable to conclude that V1 is an essential node for the perception of oriented lines, that is to say that activity of such cells in it can have a perceptual correlate without the necessity for further processing. This is not to say that the outputs of these cells are not subject to further processing, which results in a perceptual correlate of a different kind.

## Quantification of the experience of complex visual stimuli

Where visual stimuli are easily quantifiable, for example in terms of their intensity or rate of motion, a correlation between the subjective, perceptual, experience and the responses of cells can readily be determined. Much more difficult to quantify are stimuli such as faces or houses. But whether easy or difficult, the intensity of the *subjective experience* that such stimuli evoke is relatively easy to detect and measure. It would, for example, be difficult to know how to quantify the many images – of faces, colours, movement – that constitute the opening scene of the James Bond movie *Tomorrow Never Dies* (Bartels & Zeki, 2004*a*). Such a quantification could well take me, at any rate, until well beyond the mandatory retirement age. But when subjects view such a complex scene and are asked to rate the intensity of their experience of different attributes (for example of colour or faces) at any given moment, one finds that the intensity of blood flow change in the relevant specialized brain area correlates directly with the intensity of the declared experience at that moment (Fig. 7), the change in blood flow being an index of cellular activity in the area. This allows us to give an objective measurement for their declared subjective states, which otherwise remains private and occult.

## The quantification of reward, pain, desire and hate

We can further illustrate this by two examples taken from very different domains, physical pain and monetary reward. They both share the common property that (a) the stimulus inducing the changes in brain activity can be readily quantified and (b) that the brain activity produced by the presence of the stimulus correlates linearly with the measurable intensity of the stimulus, in either a positive or negative direction. Several areas in the brain, both

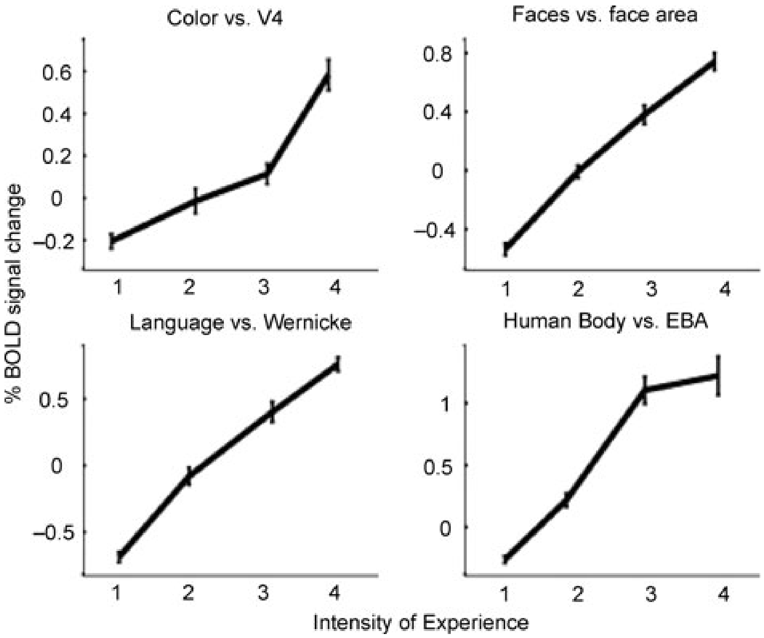

**Figure 7. Linear correlation between the intensity of subjective experience of a given feature with the activity in the areas specialized for it**
The perceived feature-intensities (as rated on a scale from 1–4) for colour, faces, language and human bodies are plotted against the blood oxygen level-dependent (BOLD) signal taken from V4, the face-selective region in the superior temporal cortex, Wernicke's area, and extrastriate brain area (EBA) from all subjects. Corresponding graphs for V4 and fusiform face area were virtually identical and omitted for graphical simplicity (Bartels & Zeki, 2004*a*).

cortical and sub-cortical, show increased activation that is proportional to the declared intensity of pain, in response to increasing temperatures applied to the skin, and hence to measurable factors (Coghill *et al.*). It is one step from this to the supposition, or the hope, that, given the evidence reviewed below, emotional pain, for which there is no present external objective criterion, will also soon be titrated against the declared intensity of it experienced by

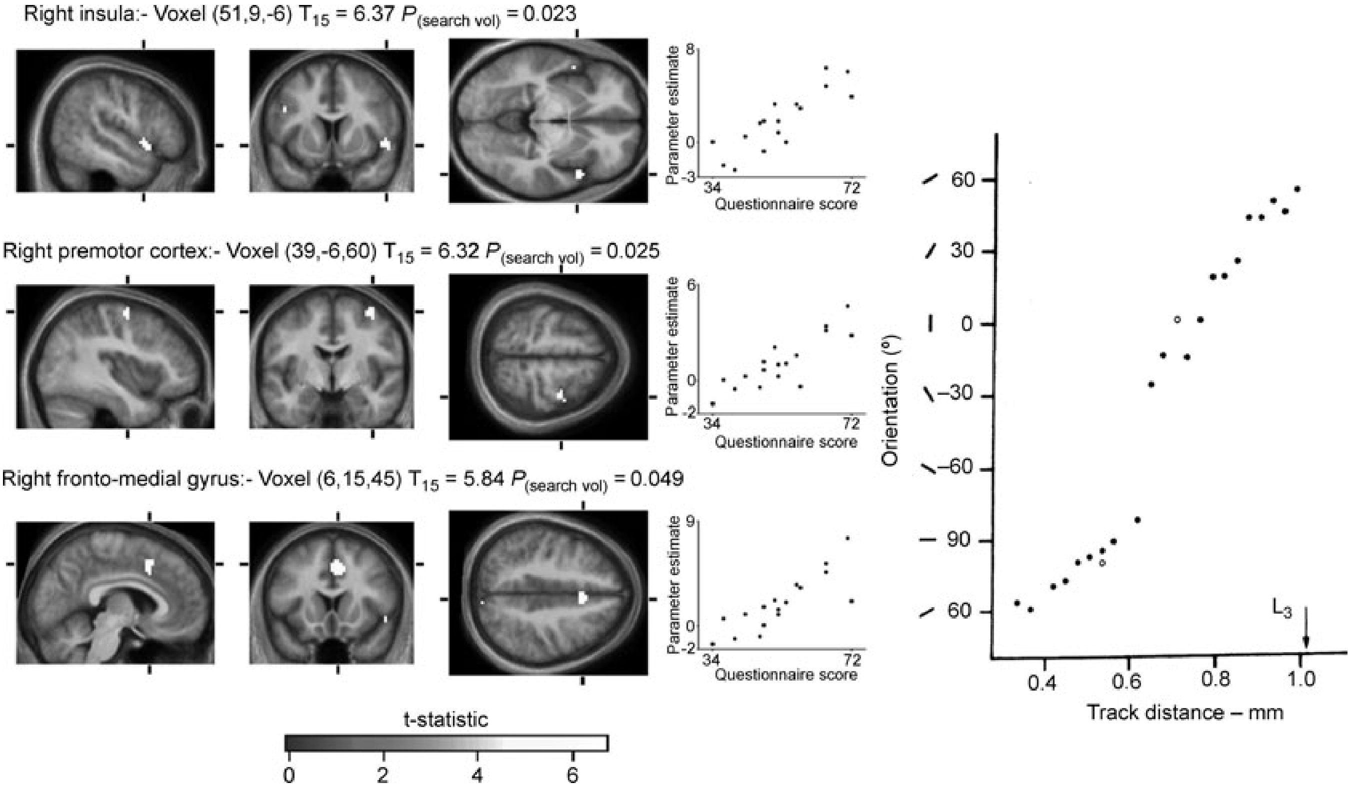

**Figure 8**
A comparison of the graphs of orientation selectivity (judged by ear) *versus* track distance along the cortex of V1, taken from Hubel & Wiesel (1974) (right) and the graphs produced by relating cortical activity measured by the BOLD signal in three brain areas (left) and hate scores obtained from questionnaires (centre) (Zeki & Romaya, 2008). The right-hand panel reprinted with permission of Wiley-Liss, Inc. a subsidiary of John Wiley & Sons, Inc.

the subject. Another example of the relationship between a verifiable objective reality, the subjective mental state that it produces and the proportional change in brain activity is to be found in recent studies of reward (Breiter *et al.* 2001; O'Doherty *et al.* 2001; Elliott *et al.* 2003). Reward and its expectation can be quantified, both objectively and subjectively. A reward, such as a monetary reward, can have a value as can its expectation – high or low. Activation in premotor cortex produced by expectation of a reward is linearly related to the (objective) value of the reward expected. Expectation of reward also produces activity in the amygdala and striatum, but the activity is unrelated to the monetary value of the reward. There are other areas, notably in the oribito-frontal cortex, which give an enhanced response to the lowest and highest values compared to intermediate ones, as if they register extremes only.

This general subdivision of cortical responses in terms of subjective states into three broad categories – areas in which the magnitude of the response correlates with the magnitude of the subjective state, those in which the correlation is for high and low values and not to intermediate states, and those in which activity simply correlates with the subjective state – seems to be true for other subjective states, such as the experience of desire or of hate, as well. Activity in the orbito-frontal cortex correlates linearly with declared intensity of desire whereas activity in the mid-cingular cortex correlates better with stimuli declared to be desirable or undesirable rather than with stimuli to which subjects are indifferent. By contrast, activity in the anterior cingulate cortex simply correlates better with desirable than with indifferent stimuli (Kawabata & Zeki, 2008).

A study of hate shows a remarkable correlation between activity in certain brain areas and the declared intensity of hate (Zeki & Romaya, 2008). The activity in the right insula, the right orbito-frontal and the right premotor cortex reveals a strong correlation, producing a graph that is not dissimilar to the one obtained for orientation *versus* track distance in a paper by Hubel & Wiesel (1974) (see Fig. 8). In time, the graphs produced by studying subjective mental states may end up being as good as the graphs of orientation *versus* track distance, which are also ultimately dependent upon subjective or, at any rate, perceptual truths.

There is thus a line linking the work of Hubel and Wiesel with its heavy dependence on perceptual truths signalled by eye and ear rather than by sophisticated machines, to modern work that uses sophisticated machinery to probe subjective states. Ultimately, they both are critically dependent upon our subjective truths which, with or without sophisticated machinery, remain the only truths that we can be certain of. Perhaps in the future the current sophisticated machineries will be supplemented with ones that are infinitely more complex than today's, but with the purpose of charting subjective truths that are increasingly remote from the simple truths that eye and ear and even the brain's emotional system enable.

Perhaps we should defer to subjective truths far more than we ever defer to objectives ones, for there is a truth to them that is not always easy to find in the objective truth, and they may even lead to unsuspected objective truths. Michael Atiyah has written of a remarkable story in which the experienced beauty of a mathematical solution – a deeply felt subjective truth – triumphed even over objective realities as then seen. The great German mathematician, Hermann Weyl is often quoted as saying, 'My work always tried to unite the truth with the beautiful, but when I had to choose the one or the other, I usually chose the beautiful'. Atiyah explains that Weyl tried to combine Einstein's general theory of relativity with Maxwell's theory of electromagnetism. 'His idea was a beautiful piece of mathematics but unfortunately, as Einstein himself pointed out, it contradicted physical reality. Despite this, Weyl's paper was published with Einstein's objections as an appendix. A few years later, after the appearance of quantum mechanics, Weyl's idea was modified slightly and now Einstein's objection disappeared. Weyl's theory now became accepted and has subsequently underpinned all further work in theoretical physics, a major triumph for beauty over truth' – or perhaps a major triumph of subjective states over 'objective' ones.

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