Colour possesses me... It possesses me forever; I know that. That is the meaning of this happy hour: colour and I are one. I am a painter. Paul Klee 16th April 1914

One day after a traffic accident the artist JI woke up to a world without colours. Like Paul Klee, he had always drawn profound pleasure from colours, but now the world suddenly felt empty and meaningless. JI had suddenly become completely colourblind, achromatopic. Not only was his way of earning a living threatened; this radical change in subjective experience brought on a profound depression as insightfully described by Oliver Sacks and Robert Wasserman in the essay "The case of the colorblind painter": "Mr. JI could hardly bear the changed appearances of people ("like animated gray statues") any more than he could bear his own changed appearance in the mirror: he shunned social intercourse and found sexual intercourse impossible. He saw people's flesh, his wife's flesh, his own flesh, as an abhorrent gray; "flesh-colored" now appeared "rat-colored" to him. This was so even when he closed his eyes, for his preternaturally vivid ("eidetic") visual imagery was preserved but now without color, and forced on him images, forced him to "see" but see internally with the wrongness of his achromatopsia. He found foods disgusting in their grayish, dead appearance and had to close his eyes to eat. But this did not help very much, for the mental image of a tomato was as black as its appearance."

Thus, not only had colour totally disappeared from, JI's direct visual impressions; the very *memory* of colour had also disappeared. It was as if colour had been drained from all aspects of JI's life. Music, for example, had given him great pleasure, as a result of the cascade of inner colours stemming from his extremely intense mixing of sensory impressions, *synaesthesia*, whereby individual notes were also immediately and directly experienced as colours. Now, once JI had lost all sense of colour, music suddenly seemed monochromatic and no longer a source of pleasure.

In other words, colour has a deep emotional resonance amplifying and going beyond many of the other qualities of visual impressions. But despite great scientific advances in the field, our conscious experiences, expectations and memories of colour are still fundamentally mysterious.

Qualia

It is hard to imagine what it is like to lack colour in our subjective experience of a colourful world; as if reality were suddenly to be experienced as a blackand-white film. But what is it actually that we see? What is it that we call reality? Normally we assume that everyone else sees the world in the same way as ourselves – that other people experience the same colours. But is this true? The very idea is challenged by colour-blind individuals walking around wearing different-coloured socks without realizing it.

Morten L. Kringelbach & Kristine Rømer Thomsen

Colourful pleasures of the brain

On the whole we rarely think much about the complexity of vision. It is as if 'seeing' is so simple, so straightforward. Visual impressions almost overwhelm us from the moment we first open our eyes, and precisely because of this inevitability we seldom consider how complex it really is to experience the world through the senses.

Our senses are the basis of our subjective experience, and our most fundamental pleasures derive from seeing, hearing, tasting, smelling and feeling the world around us. It is therefore a very effective form of torture to deprive another human being of the possibility of sensing the world, since it quickly gives rise to a strong absence of pleasure.

Neuroscience has dealt in great detail with the sense of sight. It is probably the sense that takes up most space in the human brain, and depending on how you measure it, as much as half of the brain can be said to be dedicated to the processing of visual impressions.

In the following we will try to outline the knowledge that the neurosciences have built up over the past fifty years about how the brain processes visual impressions, and in particular colour. As we shall see, experiencing the world through the senses is not a passive registration, but rather an active construction which is constantly revised by the brain.

Despite these scientific advances it is still an unsolved problem how we become aware of visual impressions. This subjective feeling of conscious experience, *qualia*, is undoubtedly the most difficult scientific problem of consciousness. Why does it have to *feel* like something to be conscious, and how does one measure the quality of subjective experiences of, for example, the colour red? These are profound questions closely related to what makes us human – and can perhaps provide a hint as to why the creation and experience of art are so central to humanity.

Sensory perception

An overwhelming body of scientific data has revealed many of the details of how our senses, and thus our sensory receptors, provide information for the brain to decode and give meaning to the world. The five most important senses are vision, hearing, touch, taste and smell, but they are not the only senses, since there are other sensory receptors providing the brain with important information, such as for example the distension of the stomach (which plays a role in connection with hunger).

There are specialized primary areas in the cerebral cortex for the decoding of sensory information. But as always, the really interesting things take place further on in the brain processing; in the regions called the higher-order association areas. This is where the brain activity is found that helps to determine whether we need to act or to bring about changes in the internal environment of the body.

In evolutionary terms the senses of taste, smell and touch are likely to be the oldest, while both vision and hearing are of later origin and function over long distances. Taste and smell are both chemically active senses that permit us to gather information about the vital food needed to provide sufficient energy for survival. Even very primitive organisms have similar chemical senses, which allow them to register potential problems with their food before it is ingested. As such these chemical senses function best at short distances; however, it is a great advantage also to be able to pick up early danger signals from more remote surroundings. The sooner an organism obtains information about potential dangers, the faster and better the organism can plan and execute the appropriate behaviour.

The sense of vision permits us to retrieve quick, accurate information from the visible world even at very great distances. This information is complemented by the sense of hearing, which provides further information about the non-visible surroundings, and can for example work rather like 'eyes in the back of your head' by giving us information about what is behind us, and thus cannot be seen.

The sense of vision

Sight is thus just one of many senses, each of which of course rarely stands alone; each interacts with the other senses. Here we will concentrate on the sense of vision. Very briefly, the eye registers visible light that reaches the visual receptors (the 'rods' and 'cones' of the retina), where it is converted into neural impulses. These move along the optic nerve through the thalamus to the primary visual cortex in the posterior parts of the brain (Fig. 1).

In the classic model of the sense of vision there is a well ordered flow of activity in the brain's processing of visual information. From the posterior parts of the brain visual impressions flow back to the frontal parts through a hierarchy of brain areas, each of which contains an increasingly high level of detailed information about the visual impressions, such as the luminance, colour, shape, depth and motion of the various elements.

When we look around, we have the feeling that all details in the field of vision are equally in focus at the same time. This is an amazingly powerful illusion, given that we have a blind spot in each eye and a visual angle such that fewer than two degrees of our retina are in focus at any one time. Yet, this is also a good example of how limited insight we have into the way our brain functions. Very few of us are aware that our eyes engage in small, imperceptible movements four times a second. These movements are called *saccades* and help us to maintain the illusion of retaining focus throughout the field of vision.

The saccades demonstrate how vision is an active process. We register the saccadic eye movements, for example, when we look at faces. The saccades follow the shape of the image and can be said to 'touch' the face, just as a blind person would touch the real face. It is therefore possible that seeing can be thought of 'touching at a distance' – as already proposed by the Anglican bishop and philosopher George Berkeley in the eighteenth century and later elaborated by the late Danish-English neuroscientist Rodney Cotterill. The sense of sight permits us to react very quickly if a lion leaps in through the door. Instead of having to wait until the lion gets up so close that we can feel the sharp fangs, we see the lion from a distance and can jump to safety. The sense of vision has therefore been of great evolutionary importance, and perhaps functions somewhat like the sense of touch – but from a distance.

It is interesting to note that the left hemisphere of the brain processes visual impressions from the right field of vision, while the left field of vision supplies the right hemisphere. The visual impressions are further reversed in the primary visual areas, such that the images the brain has to process are both mirror images and reversed in relation to the sense impressions that the retina receives from the world, and the brain subsequently has to reverse this.

There are many different types of information processing in the visual areas, which decode luminance, colour, shape, depth and motion. These systems do not function independently of one another, but share information, which becomes ever more sophisticated and closer to an invariant representation of objects as it moves away from the primary areas to the secondary and higher areas.

Take, for example, faces which are first seen as mixtures of colour and shape, which are only later integrated in the so-called invariant face area in the fusiform cortex on the ventral surface of the brain. Neurons in this area are most active for real faces, but not for example when shown manipulated faces where ear, nose and mouth have been moved into unnatural positions. This face-specific activity is in contrast to areas closer to the primary visual areas, which have the same volume of activity for both types of face. This means that humans can lose the ability to see faces if the invariant face area in the fusiform cortex is lesioned, and they may come to mistake their wife, for example, for a hat.

Colour impressions

The ability to see colour can also be lost. But compared with faces, colours are much simpler, and thus, paradoxically, much more complex to process. Whereas the ability to see faces is a higher-order phenomenon that requires complex processing and integration of very different kinds of visual information, colour information is a completely integrated part of our visual impressions. Colour is a natural part of the visual spectrum of light and is processed all the way from the rods and cones of the retina to the specialized higher-order brain areas.

There are therefore many ways in which we can lose parts or all of our colour vision. The rods and cones of the eye absorb visible light. There are three different types of cone receptors, each with its own optimal response to different parts of the light spectrum: red, green and blue.

This processing forms the basis of our trichromatic experience of colour, which is created by processing the information from the cone cells. Colour-blindness is thus typically a hereditary condition, where one of these cone receptors is missing. Depending on the type that is absent, colour-blind people have problems distinguishing between different colours. Typically they have problems with distinguishing between red and green as a result of the absence of either the red or the green cone receptors.

Colour processing does not stop with the cones; it continues with activity at the next stage in the *retinal ganglion cells*, whose activity is intensified in opposition to the activity of the cone receptors. Later in the primary visual cortex there are so-called *double-opponent* cells that create local colour contrast in the processing of the retina's information, and this is the basis of the experience of *colour constancy*. In the secondary visual cortex there are so-called "glob" cells, which add important information for the experience of *tint*. There are also cells in the fusiform cortex that integrate colour perception and behaviour.

Damage to or changes in parts of this complex network can lead to subjective changes in the experience of colour. Damage to the cortex is typically called cerebral achromatopsia, as in the example with the colour-blind painter JI from the beginning of the article.

JI's story is both excellently written and rather moving, but his case is not a typical example of achromatopsia. Scans of JI's brain do not reveal typical lesions, and while other patients with cerebral achromatopsia have been thoroughly tested, oddly enough there is no scientific evidence of JI's problems.

For example JI reports that he has gained better night vision, but this claim is not supported by scientific data. That is problematic, given the existing lack of other patients for whom achromatopsia has improved night vision.

Most patients with achromatopsia typically have very diffuse lesions, but if the lesions are combined across patients, one can see that they form a 'hotspot' in a part of the fusiform cortex. This part of the cortex overlaps with the part of the brain changing activity when shown different colour stimuli during brain scanning of normal people.

As it happens, there are a number of higher human brain areas that exhibit colour-related activity, and some of these areas have also been demonstrated in other animals. But at the same time it has been shown that these areas also process other aspects of the visual impression, for example shape, visual attention and stereoscopic vision.

Synaesthesia

As shown the blending of colour with other visual qualities happens naturally. But sometimes the

sense of vision can also blend with other senses, as in JI's synaesthesia of music and colours.

The word synaesthesia comes from the Greek compound of syn- (together) and *aisthesis* (sensation), and was first used in English in 1891. However, the phenomenon was known long before that – one of the first written accounts comes from the English philosopher John Locke in 1690.

One of the first scientists to describe synaesthesia was Francis Galton, in the journal *Nature* in 1880. Like much of Galton's research, which included dubious eugenic ideas, there were mixed, and often strong opinions about the significance of the phenomenon.

Many people have later written off synaesthesia as a side effect of drug abuse, since drugs such as LSD can produce similar experiences of blending of vision, taste, hearing, smell and touch in the transitional zone between imagination and reality. Despite this, very few people take LSD and other hallucinogens on a regular basis, so this explanation is not particularly convincing. Yet, it is only recently that scientists have begun to take synaesthesia seriously and used scientific methods to study the phenomenon.

Over time some have attempted to explain synaesthesia as an experience of associations and memories from early childhood. Perhaps synaesthetes have played a lot with certain types of toys in early childhood, and formed strong memories and associations between sensory aspects of these toys, where for example their toy alphabet letters have had different colours. But this does not explain why only some people have this very direct blending of sensory impressions.

Other possible explanations have tried to reduce the phenomenon to a metaphorical way of describing sensory qualities. Our language is full of sensory metaphors, such as "I can see what you mean". Much good poetry uses sensory metaphors to extend the precision of language, with good examples in poems by among others the American Edgar Allan



Figure 1. Visual sensation. Sketch of how visual information is processed in the brain showing some of the most important elements in the brain (viewed from below). Visual information moves from the eye via the optic nerve through the thalamus to the primary visual cortex in the back brain. Note how the left hemisphere of the brain processes visual impressions from the right field of vision (blue), while the left field (pink) supplies the right hemisphere. (Figure modified from Purves and Lotto, 2003).



Figure 2. Popout. Left: An example of how synaesthesia can help the viewer to find the twos among the fives – in the same way as they appear to everyone with normal colour vision on the right-hand side of the figure.



Figure 3. Synaesthesia in the brain. Comparison between neural activity (in red) in a synaesthete and in controls. Note how the red activity in the synaesthete covers parts of the mauve area corresponding to colour areas in the human brain (yellow circle), while this is not the case with the controls (orange circle). (*Prom Hubbard et al. 2004*).

Poe, the Frenchman Arthur Rimbaud, the Dane Henrik Nordbrandt and many other poets.

One obvious route is to ask people with synaesthesia how they experience the blending of the senses. Interestingly, very few are sure whether they experience the blending of the senses directly or as something they remember. This could mean that we have to take their word for it – that they really experience this blending of the senses.

But one can in fact test whether a person has synaesthesia in a very simple way using the idea of pop-outs. For example, a group of diagonal and straight lines can be constructed such that the diagonal lines form a figure five which immediately popout. This test can be made harder by making the individual elements more identical. A similar principle is used for testing colour-blindness by making the form elements identical and only making the differences in colours form the pop-out pattern.

In a similar way individualized pop-out figures can be made for synaesthesia using the visual elements that a particular person associates with other senses. For example someone with synaesthesia may associate the figures 2 and 5 with very different sensory qualities, and therefore immediately see the popout shape that is formed by the 2s mixed with the 5s, which is much harder for the rest of us (Fig. 2).

A brain-scanning technique called functional MRI has been used to study synaesthetes who experience letters of the alphabet in different colours. It turns out that unlike normal people the synaesthetes do in fact exhibit activity in the colour areas when presented with black-and-white letter stimuli (Fig. 3). It is more difficult to test blind synaesthetes, who might experience colours in connection with hearing certain words. Visual separation tests cannot be used, so instead it is important to try to carefully check that there is consistency over time in the sensory qualities that they report.

We investigated a blind man, JF, who consistently reports that the names of months evoke colours for him. JF was not born blind, but became blind at an early age. We were also able to show with several types of brain scans that there was activity in the colour areas when he heard the names of the months such as March – but not when he heard these in different contexts (such as "going on a march").

It is therefore highly likely that synaesthesia is a genuine phenomenon found in some people. No systematic studies have yet been conducted, but at least 1 out of 2000 people in the general population appears to experience some degree of synaesthesia. Synaesthesia may thus tell us something very interesting about our subjective experiences; about how colours add aesthetic spice to other sensory impressions.

Culture

Even more generally, colour vision is an example of the interaction between culture and nature across scientific disciplines. For colour does not exist in nature. At least not in the form we think we see. Visible light consists of continuous wavelengths, but as shown here before light can be experienced as colour, it takes an intact, complex brain network – from the rods and cones of the eye to activity in specific brain areas.

It seems so obvious to us that we all experience the same colours that we do not normally think for example of those who are colour-blind. As mentioned before, the eyes or brain of colour-blind people work slightly differently; often because of an alteration in their genes, so that they do not see certain colours. The same goes for other animals such as insects, that do not see the same colours as us because they have different receptors in their eyes.

Linguistic studies have shown that humanity universally classifies colours in four main categories corresponding to blue, green, yellow and red. This accords with the fact that all human beings have the same basic genetic structure and therefore have the same fundamental sensory access to nature. An interesting further question then becomes whether the genetic basis of colour vision affects the way in which different cultures have named the colours.

It turns out that there exists a hierarchy of colour words, such that if a culture has three colour words, they are always red, black and white; and of these black and white first and foremost have to do with the intensity of light rather than colour. Cultures with four colour words add either green or yellow to these. This hierarchy continues up to the eleven fundamental colour words. A very small number of cultures only distinguish in their language between light and dark, but are perfectly capable of distinguishing visually among more colours.So our genes lead to a unified human way of seeing visible light. Our natural propensity for organizing the world into elements and naming them has in turn led us to colour words whose order appears to be partly genetically determined. At the same time, most of us would not settle for such a simple description of our subjective experience of colour. Colour words have other sensory qualities attached such as texture. freshness and brilliance. An example is the classical Greek word chloros which is often translated as green, but is perhaps better translated as the freshness or moistness of green foliage.

A colourful world

Green is thus not just green; it is almost always associated with an emotional experience: a meal without colours provides nothing like the same pleasure as one with colours. But at the same time we lack a basic understanding of why colour gives us such pleasure and why the absence of colours can cause so intense an absence of pleasure as in the case of the colour-blind painter JI from the beginning of this article. The scientific study of pleasure has given us profound insights into the underlying neural mechanisms for the basic sensory, sexual and social stimuli. This pleasure is subject to the evolutionary imperatives of survival and reproduction. We have identified the most important networks for pleasure, which include the orbitofrontal cortex. There is no doubt that colour contributes to activity in this network, but it is not yet clear exactly how this happens.

Colour is, as we have seen, an integral part of the sense of vision, and undoubtedly has an important evolutionary function. For example the colour of fresh fruit gives us important information that potentially helps us to survive.

Colour can also aid reproduction. The red hindquarters of female monkeys are an important signal to male monkeys. In a number of elegant experiments the American ethologist Michael Platt made male monkeys look at a screen with two types of images. If they looked at one type, they were given more fruit juice than if they looked at the other, which on the other hand afforded them a glimpse of a red perineum, as it is called a little more decorously in Latin. But the male monkeys are connoisseurs of such red things, which are of course not just red, but also have a specific colouration and suppleness as a signal for the responsiveness and ovulation of the female.

It emerges that male monkeys will pay the most fruit juice to see the females' red hindquarters, and that they can only be distracted by nasty, threatening images, such as snakes.

Our knowledge of colour vision is thus greater than ever before. But fundamentally we still know surprisingly little. Just because we have measured changes in the activity of individual neurons or in the blood flow through large regions of the brain, this does not mean that these areas are causally related to the conscious experience of colour.

It was therefore particularly interesting when neuroscientists were recently able for the first time to stimulate brain activity locally with an electrode in a patient with severe epilepsy. Using functional MRI to identify a colour area, the neurosurgeon then inserted an electrode that could both stimulate the brain electrically and measure the changes in the electromagnetic fields in this local area of the brain.

It turned out that sufficiently strong electrical stimulation in this part of the brain gave the patient a conscious sensation of colour. This is strong evidence linking these higher visual brain areas to the conscious sensation of colour. But as always, good research raises as many questions as it answers. For what is sufficient and necessary for the conscious sensation of colour? Where in the brain is colour associated with other sensory impressions like motion and shape?

As always, there are many unresolved questions. Basically, it has become clear that vision is an active process where we constantly ask questions of the surrounding world and regularly revise our subjective experience. Perhaps this world is in the profoundest sense *maya*: an illusion or perhaps rather a 'veil' that is constantly being constructed, as suggested for example in the Buddhist tradition.

Colour art

If we are constantly constructing and creating meaning, and yet barely understand how the brain processes our visual impressions, how can we have any hope of studying something much more complex like art with scientific methods?

Yet there is nothing particularly magical about our aesthetic preferences for visual art, for example. In the best of cases, art uses elements like colour to focus on the most important elements of existence and can function as a mirror for our self-understanding and pleasure.

Neuroscience has just begun to examine what happens in the brain in the encounter with art, but it is already clear that art uses the brain's pleasure network in the same way as the basic sensory, sexual and social pleasures. Art is a higher-order pleasure, but in the same ways as with other higher-order pleasures, it makes use of the same pleasure mechanisms as the basic pleasures.

Art in its many forms, from painting and sculpture to music and literature, plays an almost indispensable role for almost all our pleasures, and a life without colours would be like a dreary party that very few people would want to attend.

Yet some people have had difficulty seeing the point of art, and have therefore gone so far as to suggest that art is an accidental by-product of the brain's evolutionary history. For these scientists art is hedonism without purpose, something with which we can therefore dispense.

Other researchers have reacted strongly against such arguments and pointed out how, for example, cave art clearly was with us from the beginning, when we became *Homo sapiens sapiens*, and that art has played a major role in terms of giving meaning to the world.

The great bulk of scientific data thus shows that art is irreplaceable and of great importance to social interaction and our sense of community. Even if it were true that art is a random by-product of our species-specific abilities, it would be foolish not to try to enjoy this perfect and often colourful companion to life's other sensory, sexual and social pleasures.

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