Imagery, art and biological aspects of visual consciousness

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The last 20 years have seen an unprecedented progress in our understanding of the brain. Having come to the end of the decade of the brain, neurobiology has provided an extraordinary wealth of knowledge in complementary and opposite directions. New tools in electrophysiology are making it possible to analyse in minute detail the transmission of signals between neurones. Molecular biology is complementing our understanding of the signalling between cells and how the neurone interacts with its DNA content. At the other end of the spectrum, brain-imaging techniques are making it possible to correlate the activity of whole regions of the brain with subjective conscious experience.

Does this leap in our understanding of the brain necessarily mean that we have achieved a better understanding of consciousness? Our understanding of the anatomy, physiology and psychophysical functions of the visual system is more advanced than other systems and we shall focus on the phenomenon of visual awareness. However, the underlying assumption is that the visual system illustrates features, which will be found in other perceptual modes. Here we shall examine what a biological theory of consciousness might look like and attempt to relate it to issues in vision. We shall not cover the specific issues of visual consciousness which have been examined in depth elsewhere (Zeki and Bartels, 1999) but rather provide an idiosyncratic overview of how general aspects of consciousness might relate to questions of visual perception.

Clearly, one would expect a biological theory of consciousness to include evidence of how brain structure and function relate to visual perceptual phenomena and we shall examine recent findings in this area. One might expect that consciousness does not come into the world ready-made but instead undergoes a period of emergence that we might expect to parallel the development of the brain. By far the most successful theory in biology and intimately related to development in its mechanics is evolution and we shall address theories of the mind and evolutionary psychology. A biological theory of consciousness needs to examine what the limits are of consciousness in non-biological brains. Eliminative materialism having receded, it is again almost politically correct to conceive that the mind exists and we can briefly consider what has been called the hard problem: the question of the relationship of mind and matter. While consciousness is essentially a subjective phenomenon, neural correlates of consciousness have been looked for and found and we shall review some examples of these.

What is consciousness?
The materialist approach to exactly what is consciousness is quite simply not to define it. This contrasts with the approach of Jaynes, who situates consciousness squarely in the realm of subjective experience before proceeding to discuss what consciousness is and what it is not:

O, what a world of unseen voices and heard silences, this insubstantial country of the mind! What ineffable essences, these touchless rememberings and unshovable reveries! And the privacy of it all! A secret theatre of speechless monologues and prevenient counsel, an invisible mansion of all moods, musings, and mysteries, an infinite resort of disappointments and discoveries. A whole kingdom where each of us reigns reclusively alone, questioning what we will, commanding what we can. A hidden hermitage where we may study out the troubled book of what we have done and yet may do. An intercom that is more myself than anything I can find in a mirror. This is consciousness that is myself of selves, that is everything, and yet nothing at all—what is it?

And where did it come from?

And Why?" (Jaynes, 1993)

The question of what is visual consciousness is somewhat more tractable. Richard Gregory and others have explored visual perception and shown that in some very fundamental way it corresponds to a construct, a hypothesis of the world. This is illustrated by certain well known visual illusions where alternating precepts are involuntarily elicited (Gregory, 1998). In the geometrical illusions shown in figure 1, the dimensions of the two lines of the upside-down T appear of different lengths while the horizontal bars in the Ponzo and Müller-Lyer illusion appear of different lengths. These illusions illustrate how big a gap there is between the physical construct of the retinal image and the perceived image. In the words of Richard Gregory: 'The senses do not give us a picture of the world directly; rather they provide evidence for the checking of hypotheses about what lies before us. Indeed we may say that the perception of an object is an hypothesis' (quoted by Narretranders, 1998).
One important idea behind the psychophysics of illusion is that the nature of the illusion instructs us on the underlying neuronal constraints of perception. Vertical lines are important factors in the construction of depth perception and these lines have an impact on the length of the perceived horizontal lines in the Ponzo illusion, so that the top line, which should be in the far distance, is perceived smaller that the nearer line. The fact that a second-order phenomenon such as depth impacts on perceived linear dimensions suggests that top-down process play a central part in visual perception. This is further illustrated by the ambiguous figures illustrated in figure 2. Here, a face or a vase is reported and in the second a young or an old woman. The important thing is that the percepts alternate. The alternation of the perceived images and the difficulty in simultaneously perceiving the face and the vase, the young and the old woman, goes along with a gestalt theory of perception. Viewed in this way, one of the most remarkable illusions to which we are subject is the perception of colour. Presented with a series of surfaces of different spectral reflectance, we perceive each as exhibiting a relatively invariant colour over a wide range of variations of the spectrum of the illuminant.
Since the light that arrives at the eye depends on the product of the illuminant and reflectance spectra, the information available at this level has to co-vary directly with the colour of the illumination. However, quite different spectra give rise to identical perceived colour. This phenomenon of spectral constancy has fascinated students of perception for over three hundred years. Indoor tungsten lamps are yellowish; outdoors, sunlight is bluer. One has only to take photos indoors and outdoors with the same film to be reminded how the world would vary if the visual system did not implement compensatory mechanisms. Clearly, the visual system is taking into account contextual information. However, because changes in illuminant lead to global changes of all surfaces, without the context of several surfaces, the visual system can no longer assign an invariant colour to a single surface.

The capacity of the brain to compensate for fluctuations in information arriving at the eye so as to achieve a valid interpretation of the object properties of the world is not limited to colour. For instance, in the wall-of-blocks image in figure 3 Logvinenko (1999) has modulated the average luminance from top to bottom in a sinusoidal fashion as if the illumination on the blocks varied from light to shadow in this way across the image. In the example in figure 3 the light source would be in the bottom right-hand corner. Under these conditions, one perceives the top surfaces of the blocks in shadow (for example, the diamond-shaped region labelled ‘2’) as being painted with a lighter pigment than those that are well illuminated (for example, the region labelled ‘1’). The priority that such contextual effects take over the sensory coding of light in the interpretation of the image is highlighted by the fact that the actual luminance arriving at the eye from the two regions is in fact identical! This effect is so powerful that the reader may be obliged to view regions 1 and 2 through a mask to convince him/herself that they are indeed the same shade of grey.

It is easy in physical terms to describe the strategy of the brain. Two surfaces of equal luminance on the retina but appearing to be under different illuminants must correspond to surfaces of different reflectance. In order for a surface in shade to produce the same luminance on the retina as one under the light, the surface in shade must be of a much lighter reflectance. The brain does not arrive at this conclusion by reflection, however. The computation is automatic, taking into account the contextual information about the geometry and the lighting seemingly instantaneously. The contextual information renders it impossible to see the image in any other way, despite the fact that the different surfaces are quite close to each other (about one degree at normal viewing distances). The percept remains stable at larger viewing distances which render the retinal distances between the images even smaller and facilitates the visual comparison between them.

The geometrical illusions, the ambiguous figures and the compensatory mechanisms illustrated by transparency illustrate mechanisms that the brain is also using to tackle a very global problem of figure/ground segregation. But segmentation does not just involve separating objects from each other. In fact the visual system performs a much more complex segmentation in separating material from lighting changes. From a 2-D distribution of light in the retinal image, the visual system can separate out opaque surface properties, intervening transparent media (filters and atmospheric conditions like fog), shadows and gradients of illuminance. We have seen the segmentation of illuminance gradients in Logvinenko’s wall-of-blocks (Logvinenko, 1999). These characteristics of the visual image are not simply discounted but are perceived simultaneously. The problem is illustrated nicely with the perceptual transparency generated by a simple filter (figure 4). A transparent colour filter placed on a set of differently coloured surfaces could be interpreted as a new set of opaque surfaces. Instead, the visual system integrates along the boundary of the filter that the changes in colour are characterized by a certain coherence (D’Zmura et al., 1997). This coherence suggests that the change in colours is due to a single process, for example an
direction of change of colour across the boundary of the filter in a random fashion. Now, the square region is not segmented out as a homogeneous layer through which the underlying surfaces can be perceived (despite the fact that the chromatic contrast around the square at each boundary remains locally the same).

Quite subtle alterations in an image suffice to produce powerful changes in its layered segmentation (Adelson, 1993). Figure 5 shows two versions of the wall-of-blocks (Adelson, 2000). One readily sees in the image on the left that the blocks are painted grey with the exception of four white stripes. There are differences in the dark-grey surfaces, which appear to be due to lighting and shade. The colour that the grey surfaces are painted appears the same, except for the diamond-shaped regions that form the tops of the cubes marked (a) and (b). When they are surrounded by white — see (a), they appear darker than when surrounded by the grey surfaces — see (b). This might be explained by contrast phenomena that are considered to be mediated at low levels in the visual system. Consider what happens when the junctions between the light and dark regions are modified. This is shown in Figure 5 where the 'Ps' junctions on the left-hand panel are converted into 'X' junctions in the right-hand panel (compare (c) in both panels). Now the dark greyness of this region is attributed to an intervening transparent filter and is not seen as a characteristic of its surface. However, this rather subtle alteration of the local geometry produces a global alteration in the layered segmentation of the image. If the lowered luminance coming from the dark grey region is due to an intervening filter, then the brain computes that the surfaces below it must be painted in a lighter colour. Now comparing the equivalent surfaces (i.e. the a and b diamonds in both left and right panels) between the two images reveals that the top surfaces of the blocks display a greater difference in lightness when the dark-grey region is perceived to be transparent. Again looking at these diamonds through a mask will convince the reader that the grey of each is in fact invariant!

**Visuo-motor integration**

The perceptual stability issue referred to above becomes even more acute when one considers the basic function of vision: to explore the environment. Exploring implies an active process and indeed the eyes are equipped with extraocular muscles that allow them to probe the environment. However, the motor activity of the eyes introduces an extraordinarily complex issue of visual stability. This is illustrated by the eye-pen experiment, which has been referred to since Descartes. If you visually fixate and press gently on the eyeball the visual scene moves with the movement of the eyeball. Yet when the eyes move in what are referred to as saccadic eye-movements the visual environment remains stable. One powerful hypothesis for explaining visual stability during voluntary movement is that the motor command from the motor to the extraocular eye muscles is doubled by a signal from the motor cortex to the
visual system. This corollary discharge is thought of as either being an evaluation signal or possibly acting as a subtractive factor (Jeannerod et al., 1979).

Conceptually the corollary discharge has important implications. It implies that there is a motor-to-sensory pathway and that motor signals should be detectable at early levels of the visual pathways. Indeed this has been shown to be the case (Kennedy and Magnin, 1977). This changes concepts of how the brain is organized where it was traditionally considered a fundamental constraint that there is a flow of sensory towards motor. The motor-to-sensory signals and a more general concept of corollary discharge have recently been given new vigour and a wider scope from the work of Marc Jeannerod’s group, who, along with others, have shown that corollary discharge mechanisms could play an important role in maintaining a stable notion of self, despite perceptual fluctuations resulting from voluntary exploration of the physical and social environment (Franck et al., 2001).

Motor commands are not the only form of non-visual activity to be found in the visual cortex. Integration of the senses was until a few years ago considered to be relegated to higher levels of the visual pathways (Stein and Meredith, 1993). However, it is becoming increasingly clear that multisensory integration occurs at very early stages in the visual cortical pathway (Giard and Peronnet, 1999). Given the projection of the auditory cortex onto the visual cortex one can question how an auditory stimulus might impact on visual processing. One possibility is of course synaesthesia and the perception of coloured sounds, which might be of developmental origin (Kennedy et al., 1996). Pathways linking the visual cortex to other sensory pathways have important consequences for the functional reorganization of the brain after early lesions and must play an important role in the sensory and cognitive capacities of the congenitally blind and deaf (Cohen et al., 1997; Neville et al., 1998).

Architecture of the visual brain

The visual cortex is subdivided into 30 or so separate areas which are organized in an ascending hierarchy going from visual area V1, V2, V3, ... etc. Successive levels of the hierarchy are thought to extract progressively more complex aspects of visual information and each area is specialized in a particular attribute (e.g. colour in V4, movement in V5). The hierarchical organization of the visual system is reflected in the changing nature of the receptive fields, which are to be found at successive levels. This is illustrated by a famous diagram of Hubel and Wiesel showing the emergence of orientation selectivity in the primary visual area, area V1 (figure 6A). Their work suggested that the projections from the thalamus to the cortex converge on single neurons and that the geometry of this convergence underlines the transformation of the circular receptive field of the thalamus to the orientated receptive field.
of the cortex. This introduces the concept that the successive changes in receptive field reflect feedforward processes occurring in a hierarchical system.

The concept of feedforward mechanisms in the visual system has been amply proved since Hubel and Wiesel's original suggestion. The work of numerous neurophysiologists showed that there is a progressive increase in complexity in the response of single neurons at successive levels in the visual system. More importantly, it has been shown that inactivation of one level in the visual hierarchy inactivates the neurons at the following level.

While feedforward mechanisms certainly account for a lot of the physiology of the visual system, they fall short on one important criterion. They do not take into account the overall architecture of the system. For example, the projection of the thalamus on to area 17 shown in figure 6B illustrates clearly defined feedforward processes. However, what needs to be taken into account to understand the pathway is that considerably more projections go from the cortex to the thalamus (i.e. feedback projections) than in the ascending direction. Further, while the thalamus provides the major input to the cortex, it turns out that in area V1 synapses from the principal thalamic relay constitute a small fraction (less than 3%) of the synaptic machinery of area 17.

Our work in Lyon has focused on quantifying the relative proportions of feedforward and feedback and show that the relationship alluded to in figure 6C is repeated at all successive levels. Visual cortical areas are functionally interconnected in a hierarchical order (figure 7). Descending and ascending connections are equally numerous and the input from one level to the next constitutes a small fraction of the total synaptic connectivity, which largely originates from lateral and descending connections.

Until recently, the physiology of feedback connections was largely ignored by physiologists. However, a number of studies have begun to show that feedback pathways play an important role in the visual system. Inactivation experiments show that feedback pathways are involved in distinguishing objects from background, a phenomenon known as segmentation. One aspect of the higher-order processes that is illustrated in the ambiguous figures shown in figure 2 is that shape recognition involves segmentation. This ties in the top-down processes described in psychology with feedback connections in the brain.

There are a number of intriguing consequences of the hypothesis that feedback projections relay higher-order processes to lower stages of the visual system. One such higher-order process that has been identified at early stages is visual mental imagery (Koslow et al., 1999). In the early 1970s,
numerous experiments had shown that there is a clear distinction between visual imagery (based on an array format) and verbal thought (propositional in format) (Kosslyn, 1994). Numerous neuropsychological studies of brain-damaged patients have shown that localized damage to the cortex leads to localized damage to the mental image (Farah, 1985). Work at the beginning of the last century suggested that visual imagery uses the same neuronal machinery as visual perception. Modern techniques have confirmed and extended this. Together these results have profound implications for our understanding of the cortical architecture shown in figure 7. Activation of the early stages of the cortical pathway by visual imagery implies a massive activation of feedback pathways.

**Natural vision**

Berkeley’s *New Theory of Vision* written in 1709 questioned how brain function and structure in the light of experience constrains visual perception (Berkeley, 1910). So far we have examined how neural mechanisms in the brain can enlighten our understanding of perception. Do issues of perception illuminate our understanding of neural mechanisms? Recent results in a field known as natural vision suggest that they will. Up to the 1980s recordings from single neurons were carried out in anaesthetized and paralyzed animals. More recently behaving animals have been studied, where a trained animal learns to fixate and single neurons are recorded using microelectrodes. While the behaving animal provides an improved preparation, it continues to look at the response of neurons to meaningless stimuli. Recently however, single-unit recordings have been used to study responses to perceived stimuli. Here neurons are recorded while the animal uses explorative eye movements. Strikingly different results are obtained. While classical recordings show strong neuron responses, during active exploration of meaningful stimuli single neurons give much weaker responses. This has led Malcolm Young to hypothesize that ‘expectation’ is an important component of the physiology of single neurons and that the latter is shaped by Bayesian statistics (Young,
2000). While for psychophysicists this is not an altogether surprising possibility, for physiologists it suggests a very different way of looking at neural networks. It suggests that the physiology of visual cortical neurons is not entirely encapsulated by the concept of the receptive field and Young has suggested that we need to think in terms of the perceptive fields. It suggests that the full repertoire of inputs to the single neuron is not revealed by its response to meaningless stimuli. It suggests for example, that the role of the huge silent majority — the feedback pathways, corollary discharge, proprioception from the extraocular muscles of the eye etc. — are not being investigated by the visual stimuli, which are empty of perceptual significance. The field of natural vision could put Locke and Berkeley back at centre stage suggesting, as it does, that our knowledge of the world and the physiology of single neurons are intimately intermeshed. Clearly, the wheel turns.

However, even so-called natural vision tends to view 'the visual system' as its field of enquiry, leaving aside the obvious fact that visual objects make noises, have physical textures and may well smell. It is becoming increasingly well documented that the merging of the senses is a central feature of what consciousness has to chew on. For instance, cross-modal links have been shown to play an important role in visual attention. For some time the dogma of localization led researchers to expect inter-modal integration at higher associative levels. Recent brain-imaging studies show that visual stimuli with a simultaneous tactile stimulus leads to an enhancement of activity in the primary visual cortex (area 17 or V1) (Macaluso et al., 2000). These results implicate directly feedback projections, which are likely to include direct projections from the auditory cortex (A1) (Falchier et al., 2002). While these results lead one to question the localist's dogma and lead ultimately to a rethink on the neural basis of consciousness they also have profound implications regarding the sort of functional reorganization that one can expect after early lesions. For example, in the congenitally blind Braille, but not touch, has been shown to activate area 17 (Sadato et al., 1996; Weeks et al., 2000). Likewise in a recent study Helen Neville has shown that in the congenitally deaf and native signers there is a linguistic activation of visual areas, leading one to wonder what exactly the linguistic function of the visual image would be in these subjects.

**Development of the visual brain**

Although it has been considered that the cortex develops from a uniform structure that entirely depends on being shaped by epigenetic forces relayed from the sensory periphery, recent findings show that there is in fact an important genetic determination of individual areas. Similarly it was thought that early-formed connections between cortical areas were largely random and that the adult pattern of connectivity emerges by a process of selective elimination. Recently, it has been shown that ascending pathways (involved in construction of receptive fields) emerge early in development and are controlled by molecular mechanisms (Batardiere et al., 2002) (figure 8). This contrasts with the late development of descending pathways (involved in segmentation and visual imagery) (Kennedy and Dehay, 1993, 1997). These findings correlate with what is known of the cognitive development of children.

**Evolution of mind**

This constitutes a major challenge for biological theories of consciousness, given on the one hand the huge conceptual significance of theories of evolution and on the other the absence of a fossil record of the mind.

Jaynes argues that consciousness evolved after language. Complex behaviour can occur independently of consciousness (e.g. driving a car, resolving a problem, changing one's behaviour etc.). This author suggests that consciousness evolved relatively recently. He claims that the heroes of the Iliad used non-reflective language, which contrasts with the use of the analogue 'I' in later writings. This would situate the emergence of consciousness between 800 and 1500 BC. There is also evidence of more recent and subtle changes in consciousness. For example reading aloud was the rule until the late Middle Ages, when reading to oneself with the inner voice was developed.

A more controversial approach to this issue is the recent study of evolutionary psychology. This field is based on a number of suppositions, which although partially accepted in the USA and UK are strongly contested in France: (1) genes influence behaviour (see monozygotic twin studies); (2) human nature is universal and cultural determinism has been grossly overstated (e.g. Eskimos do not have thousands of words for snow—they have about as many as people who go skiing; Margaret Mead was hopelessly fooled by Polynesian teenagers); (3) the human mind is modular and general intelligence is a myth propagated by the US army; (4) the different modules of human intelligence have emerged during prehistory according to a Darwinian process of selection.

Pinker, building on themes developed by Dawkins and others, claims that reverse engineering makes it possible to identify the evolutionary pressures encountered by man during his prehistory. He also gives examples of trivial evolutionary explanations (why do men as opposed to women avoid asking for directions? Our male ancestors might have been killed if they approached strangers. What is the purpose of music? It brings people together. Why did happiness evolve? Happy people are more pleasant to be with and therefore attract more allies).

However, Pinker argues that evolutionary explanations that are consistent with objective phenomena are considerably more powerful. For example, why do women become nauseated and avoid certain foods during the early stages of pregnancy? Freudian interpretations are that pregnant women loathe their child and unconsciously desire to abort the foetus...
orally. However, Profet provides an alternative explanation. She notes that pregnancy sickness is stable across human cultures and suggests that it provides a defence against eating toxic poisons common in certain vegetables: (1) hence, plant toxins in dosages which are tolerated by adults cause defects in embryos; (2) pregnancy sickness begins during the period of foetal organogenesis, when foetal susceptibility is maximum but where growth is minimal; (3) women with pregnancy sickness avoid bitter, pungent-flavoured foods, that is to say those most likely to contain toxins; (4) women with severe pregnancy sickness are less likely to have foetuses with defects (Pinker, 1997).

Artificial intelligence
The idea that man-made creatures can be conscious has been around at least since Mary Shelley wrote Frankenstein at the beginning of the nineteenth century. More recently, the advent of computer technology has made us much more familiar with the concept of inanimate cognition, and films like *Blade Runner* and *RoboCop* (50% man, 100% cop) reveal a deep-seated anguish regarding the specificity of human consciousness.

Strong AI (Artificial Intelligence) contends that the human brain is an ideal Turing machine and that as such will be indistinguishable from such a machine. Searle argues that Turing machines merely manipulate symbols and cannot experience the subjectivity of consciousness. He points out that strong AI requires hardware (the brain-computer) and software (the program). Modern students of mind–brain relations mostly avoid such dualism. Undoubtedly, one of the most useful aspects of AI is it gives valuable insight into understanding the neural circuits underlying brain operations. Computational neuroscience makes it possible to simulate neural functions on computers and holds the promise of an improved understanding of the algorithm used by the brain (Searle, 1995).

The mind–body problem
Pushed to its extremes the question is whether consciousness, although produced by the brain, is in some way independent of it (dualism) or whether consciousness is the experience of having a brain (monism). Extreme dualism sees consciousness as acting on the brain (Popper and Eccles, 1977). Extreme monism views consciousness as an unprovable hypothesis.
These two positions, although possibly philosophical in nature, are believed by some (e.g. Dennet) to be resolvable by science (however, see Pinker for a more balanced view). It is, after all, debatable whether science can resolve issues such as dualism versus monism and whether God exists.

Up to here we have considered only brain mechanisms involved in perception. However, although perception is necessary for consciousness, it is not sufficient. A fundamental issue of consciousness is its subjectivity and its primacy. It cannot be reduced to something else. When asked the question 'what is consciousness?' we become conscious of consciousness. However, there is here the risk of an extraordinarily powerful illusion leading to a fatal error. As Jaynes puts it:

In being conscious of consciousness we feel it is the most self-evident thing imaginable. We feel it is the defining attribute of all our waking states, our moods and affections, our memories, our thoughts, attention and volitions. We feel comfortably certain that consciousness is the basis of concepts, of learning and reasoning, of thought and judgement, and that it is so because it stores our experiences as they happen, allowing us to introspect on them and learn them at will.

Just how powerful an illusion the stream of consciousness is, is illustrated by the experiments of Benjamin Libet (Libet, 1983). Electrophysiological recordings from the human brain during surgery allowed him to correlate the subjective experience of time and neural activity. This suggested that subjects, when asked to make a voluntary movement, had neural activity 0.5 sec prior to the conscious decision to act. This finding is disturbing for notions of free will. It shows that there is brain activity prior to the initiation of voluntary motion, indicating that the trigger to act is in fact unconscious. This suggests that conscious acts be controlled by brain activity which itself is not conscious. This relegates consciousness to a veto and could be an explanation of why self-awareness leads to increased levels of inhibition and frequently deterioration in physical performance.

Libet showed that there are large-scale distortions of the timing of sensory awareness. Stimulation of the skin at low intensities can lead to evoked response of the brain in 100 msec without awareness (revealing that subliminal stimulation can lead to non-perceived brain activity). Direct stimulation of the brain, however, leads to awareness only after a duration of 500 msec. This leads to the concept of backward referral of subjective experience. Hence, experience is projected back in time in exactly the same way as a stimulation is projected out onto the body (Norretranders, 1998).

Electrical stimulation of the brain can also evoke strong visual memories. Penfield showed that stimulation of the temporal lobe evoked powerful visual memories. The patients reported vivid visual imagery whereby they were able to contemplate in minute detail that far away sunny afternoon watching their mother baking a cake in the familiar surroundings of the family kitchen of their childhood. Interestingly, it was the combination of the vividness of the imagery that eventually led Penfield — a hardened surgeon — to take up the position of a dualist: despite the intensity of the imagery the patient never relived the memory but instead was only able to contemplate the spectacle of his past life.

Conclusion

It would seem that feedback pathways have a lot in fact to do with visual perception, including imagery, and therefore with learning and visual memory (figure 9). Likewise, imagery must have a lot to do with art. Zeki has argued that the physiology of cortical areas is in some respects a key to understanding abstract art (Zeki, 1999). Perhaps the divide between what is being suggested here and what Zeki is suggesting is the difference between 'representational' art and 'abstract' art. The cave drawings are strongly representational and are only abstract in the sense that they feel so contemporary. The artist would almost certainly have had to rely on visual memory and therefore imagery. How could the abstract solicit visual imagery? Picasso might be an example where the imagery process is not directly solicited. One can doubt that Picasso started a painting with a clearly defined mental image of the end product. This is suggested by Henri Langlois's beautiful filming of Picasso painting. His film shows an initial constructive process, which establishes a representational image, followed by a prolonged reworking leading to the abstract finished product. On the other hand, painters such as Klee almost certainly started off with the abstraction.

We have seen that visual imagery has a neuronal basis, which is involved in top-down processes but which solicits neuronal mechanisms involved in perception. This alone suggests that one might expect cultural constraints on perceptual processes. We have also suggested that the cortical pathways that might be preferentially solicited by imagery develop by a prolonged process of refinement, and therefore are more likely to be shaped by epigenetic factors. Learning to perceive could be highlighted by the artist who shows us, for example, that up to the Renaissance the representation of perspective (along with concepts of zero and infinity) was not required for his interpretation of the physical world. Of course this does not mean that his perception of depth differed in anyway from that in the twenty-first century. It could, however, reflect a deep-seated difference in attitudes to distance and proximity.

Here we have tried to show that perceptual processes are understandable in terms of the architecture of the brain and that they can be directly related to physiological processes of imagery, which in turn underlie visual memory and learning. Clearly, these considerations touch on concepts of mind and artistic creation. Perhaps thought of in this way it will help put art in perspective, not as the prerogative of the happy few, but as conceived by Jung — an archetypal process essential to the human condition.
Figure 9. Summary of the different role of feedback and feedforward pathways. Feedforward pathways are clearly involved in the construction of receptive field properties (on the left this is illustrated by the construction of orientation, colour and movement). Feedback pathways have been shown by our laboratory in Lyon to be as numerous as the feedforward pathways. Their physiological role is less well documented. Recent results suggest they are involved in saliency, segmentation and visual imagery.

In the early part of the eighteenth century, Haydn's Seven Stages of the Cross was drawing huge crowds. Berkeley's idealistic philosophy put in doubt the existence of matter. Art was essentially representational and visual scientists had been scrutinizing the retinal image for a number of years. Dualism ruled. Several hundred years later we have Madonna (Material Girl), postmodern philosophy, abstract art, and the visual neuroscientist can for example localize different attributes of visual information processing in diverse parts of the cortex. Monism has taken centre stage — at least amongst the biologists. Overall one might speculate that something has been gained and something has been lost. Clearly we are not in the same place. However, the complexity of the issues of consciousness and the necessity to survive makes it necessary to bridge this gap.

REFERENCES


