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The neurology of ambiguity

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Abstract

One of the primordial functions of the brain is the acquisition of knowledge. The apparatus that it has evolved to do so is flexible enough to allow it to acquire knowledge about unambiguous conditions on the one hand (colour vision being a good example), and about situations that are capable of two or more interpretations, each one of which has equal validity with the others. However, in the latter instance, we can only be conscious of one interpretation at any given moment. The study of ambiguity thus gives us some insights into how activity at different stations of the brain can result in a micro-consciousness for an attribute, and also tell us something about interactions between different cerebral areas that result in several potential micro-conscious correlates, though only one predominates at any given time. Finally, the study of ambiguity also gives us insights into the neurological machinery that artists have tapped to create the ambiguity that is commonly a hallmark of great works of art.

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1. Introduction

In this essay, I use the term ambiguity in the sense that it is understood by most people and as it is defined in the *Oxford English Dictionary*: “uncertain, open to more than one interpretation, of doubtful position.” To this, I will add below a neurobiological definition. I consider ambiguity to be a characteristic of much great art, an attribute that heightens substantially the artistic and aesthetic merit of a work. In accordance with my general view that we should seek to understand the reasons underlying aesthetic appreciation and evaluation in the organization and functioning

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of the brain (Zeki, 1999), I try to explore here some of the neurobiological foundations of ambiguity. I restrict myself to the visual brain and thus to visual art, not because I know more about the visual system but because I know less about other systems. My aim is twofold: first, to explore what ambiguity tells us about conscious processes in the visual brain. The relationship of ambiguity to consciousness is critical; ambiguous states would indeed not be possible without consciousness. Correspondingly, a discussion of the relationship of consciousness to ambiguity may provide not only material for new experiments but also insights into how the brain is organized to acquire knowledge. My second aim is to show that the characteristic of ambiguity in art is not special to art. It is rather, a general property of the brain which is often confronted with situations or views that are open to more than one, and sometimes to several, interpretations. The artist, rather than creating ambiguity, thus uses, sometimes to exquisite effect, this potential of the brain. Equally, the viewer uses this same potential in providing different interpretations.

Of necessity, in the present highly incomplete state of our knowledge about the functions and functioning of the brain, the exploration of the relationship of ambiguity to conscious processes in the brain that I give here is nothing more than a sketch designed to stimulate further experimentation. Similarly, the neurobiologically based explanation of ambiguity in art that I give cannot be anything near complete and may even turn out to be wrong in the end. But I hope that it will nevertheless constitute the basis of further artistic explorations of how ambiguity works in neurological terms.

2. The brain and the acquisition of knowledge

To understand the neural basis of ambiguity requires us first to understand that the brain is not a mere passive chronicler of external events and that perceiving is not therefore something that the brain does passively (Zeki, 1984, 1993). Rather, the brain is an active participant in constructing what we see, through which it instils meaning into the many signals that it receives and thus gains knowledge about the world which, of course, it can only do in the conscious state. The percepts that the brain creates are the result of an interaction between the signals that it receives and what it does to them. To understand perception, and the knowledge that we acquire through it, we must therefore enquire not only into the nature of the signals that the brain receives but also into the contribution that the brain makes to, and the limitations that its characteristics impose upon, the acquisition of knowledge (Kant, 1781; Schopenhauer, 1859; Zeki, 2001).

The primary law dictating what the brain does to the signals that it receives is the law of constancy. This law is rooted in the fact that the brain is only interested in the constant, essential and non-changing properties of objects, surfaces, situations and much else besides, when the information reaching it is never constant from moment to moment. Thus the imperative for the brain is to eliminate all that is unnecessary for it in its role of identifying objects and situations according to their essential and constant features. The search for the constant is relatively simple when the choice itself is limited, as in colour vision. It becomes more complex when, in trying to instil meaning into this world and extract the essentials, the brain is confronted with several possible solutions. Here, it must first ascertain what the possible solutions are and decide which is the most likely. True ambiguity results when no single solution is more likely than other solutions, leaving the brain with the only option left, of treating them all as equally likely and giving each a

place on the conscious stage, one at a time, so that we are only conscious of one of the interpretations at any given time. *Thus a neurobiologically based definition of ambiguity is the opposite of the dictionary definition; it is not uncertainty, but certainty—the certainty of many, equally plausible interpretations, each one of which is sovereign when it occupies the conscious stage* (Zeki, 1999). Each interpretation therefore is as valid as the other interpretations, and there is no correct interpretation. Ambiguity therefore is the obverse of constancy. For here, the information reaching the brain is constant from moment to moment (assuming a constant viewing distance, lighting conditions, and so on) while the percept shifts and is inconstant. In a sense, the brain accepts that there is no single essential and constant feature, but several instead.

In fact, whether the choice available to the brain is limited (as in colour vision) or not, many have sought to account for both perceptual constancy and the ambiguity resulting from perceptual inconstancy by appealing to a ‘top-down’ influence of higher cognitive factors and centres, and especially the frontal and prefrontal cortex. Such an influence implies a separation between processing and perception. To account for colour constancy, for example, both Helmholtz and Hering invoked higher (cerebral) factors such as judgment, learning, and memory. Similar higher factors have been invoked to account for ambiguous figures such as the Rubin vase. But the mandatory involvement of ‘higher centres’ in colour vision or in the perception of illusory figures is doubtful, since all imaging studies of colour vision and illusory figures are united in showing that there is no involvement of frontal or prefrontal cortex (Bartels & Zeki, 2000; ffytche & Zeki, 1996; Hirsch et al., 1995; Larsson et al., 1999). In fact a discussion of ambiguity and its relationship to (micro)conscious processes leads us to conclude that, in some if not all instances, ambiguity may result from a fluctuation in the state of micro-consciousness within an area, without involving higher cognitive factors. This is of course not to say that higher areas are not involved in the perception of certain ambiguous figures, and as we shall see they may well play a critical role in determining which of the interpretations of an ambiguous stimulus we are conscious of.

It is self evident that such a scenario, of many possible solutions, is closely linked to a condition in which some work or scene or narrative is left unfinished. Here again, the brain can complete the work in a variety of different ways, each one of which is as plausible as the others. But in this instance probably greater demands are made of higher cognitive factors, including memory, learning, and experience. In art, the importance of this capacity to provide multiple solutions means that the importance of the work becomes more general and can cover a whole range of situations. My aim here is to show that there are different levels of ambiguity dictated by neurological necessity and built into the physiology of the brain. These different levels may involve a single cortical area or set of areas; they may involve different cortical areas, with different perceptual specialization or they may involve, in addition, higher cognitive factors such as learning, judgment, memory, and experience. Whether the result of activity in a single area or in different areas, these different levels are tied together by a metaphoric thread whose purpose is the acquisition of knowledge about the world and of making sense of the many signals that the brain receives.

2.1. Nodes and essential nodes in the visual brain

It is useful to introduce here the concept of nodes and essential nodes (Zeki, 1999; Zeki & Bartels, 1999a) by giving a very rough sketch of the organization of the visual brain (Fig. 1).

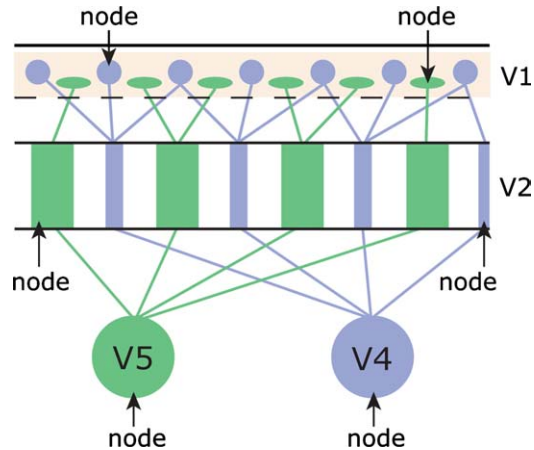


Fig. 1. Diagrammatic illustration of nodes and essential nodes. Signals related to colour (blue) and motion (green) reach distinct compartments in the primary visual cortex (V1) and the area surrounding it (V2). The specialized compartments of V1 and V2 constitute nodes that project to further nodes V4 (for colour) and V5 (for motion). The latter are essential nodes in that the signals in them becomes explicit and does not necessarily need to be processed further. When V4 and V5 are destroyed the nodes in V1 and V2 become essential nodes and the subjects' perceptual capacities in colour and motion now reflect the physiological capacities of cells in V1 and V2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this paper.)

In essence, a very prominent part of the input from the retina reaches the primary visual cortex, known as area V1. Signals belonging to different attributes are distributed to specialized compartments within V1. V1 is surrounded by another visual area, V2, which also has specialized compartments that receive input from their counterparts in V1. V2 itself is surrounded by further visual areas, prominent among them being V3, V3A, V4, and V5, all of them specialized visual areas that receive distinct inputs from the specialized compartments of V1 and V2. These specialized areas have diffuse return anatomical connections with areas V1 and V2 and also reciprocal connections with further visual areas, but the details do not concern us here. There are therefore many visual areas in the brain and each receives input, directly or indirectly, from area V1. By a node I mean a stage in the visual pathway, for example area V4 or area V5, or a specialized sub-compartment within the pathway, for example the compartments of V1 and V2 that feed V4 or V5 (Fig. 1). An example of the latter would be the blobs of V1 and the thin stripes of V2, both of which contain wavelength selective cells and project to area V4 (DeYoe & Van Essen, 1985; Hubel & Livingstone, 1985; Livingstone & Hubel, 1984; Shipp & Zeki, 1985). An essential node is one at which activity becomes perceptually explicit without the need for further processing (Zeki, 1993; Zeki & Bartels, 1999a). In other words, when activity at a node has a conscious correlate, it becomes an essential node. Each node can potentially become an essential node, a supposition that receives support from the work of Logothetis and his colleagues (Logothetis, 1998), who have shown that, in every visual area, including even area V1, there are cells whose responses follow the percept rather than the visual input. I refer to the conscious correlate that is the result of activity at an essential node as a micro-consciousness (Zeki, 2003; Zeki & Bartels, 1999a), since activity at other nodes leads to a micro-conscious correlate for other attributes (Zeki, 2003). Visual consciousness consists therefore of many micro-consciousnesses that are

distributed in space, since they are the correlates of activity in spatially distinct locations. Moreover, different visual areas (nodes) have distinct activity time courses (Bartels & Zeki, 2003), reflecting perhaps the fact that we become conscious of different attributes at different times, because different areas take different times to complete their processings (Arnold, Clifford, & Wenderoth, 2001; Moutoussis & Zeki, 1997a, 1997b; Zeki & Moutoussis, 1997). Hence, the micro-consciousnesses are also distributed in time. Overall, at the level of micro-consciousnesses, there is no such thing as a unified *visual* consciousness. Visual consciousness consists of many micro-consciousnesses that are distributed in time and space.

Area V4 provides a good example of an essential node. Activity in it leads to the conscious perception of colour without the need for further processing. We therefore say that a micro-consciousness for colour is generated as a correlate of activity within the V4 complex. In the intact brain, the nodes that feed V4—the blobs of V1 and the thin stripes of V2—are not necessarily essential nodes as far as colour vision is concerned, in that activity in them is processed further, at the level of V4. They become essential nodes in two conditions: one obtains when activity in them leads to conscious awareness of the fact that the dominant wavelength has changed, as happens when a scene is viewed under two different illuminants, with different wavelength compositions. This is a consequence of the fact that most of their chromatic cells are concerned with wavelength composition and seem to lack the machinery for long-range interactions that generate colours (Moutoussis & Zeki, 2002; Zeki, 1983). The other condition is when V4 is damaged, leading to a perceptual state produced by activity in the blobs of V1 and the thin stripes of V2, and characterized by an inability to construct constant colours (Zeki, Aglioti, McKeefry, & Berlucchi, 1999). In patients rendered achromatopsic (cortically colour blind) by damage to V4, the intensity of lights of different wavebands can be detected, but no colours can be ascribed to them or, if the damage is sub-total, the attributed colour is heavily dependent upon the wavelength composition of the light reflected from a surface (Kennard, Lawden, Morland, & Ruddock, 1995). This is in spite of recent evidence that at least some cells in monkey V1 are influenced strongly enough by their immediate surrounds to suggest a perceptual colour induction (Wachtler, Sejnowski, & Albright, 2003). Assuming a similarity between monkey and man, it is possible that, because of the limited spatial range of these interactions, such cells are not capable of effecting the long-range interactions necessary for constructing constant colours, thus leaving a patient with a damaged V4 essentially incapable of colour constancy. At any rate, present clinical evidence suggests that, when V1–V2 become the essential node for colour vision (in the absence of V4), their physiological capacities are reflected perceptually by an unstable colour vision in which constancy is a primary casualty.

2.2. *Processing sites are perceptual sites*

Strong evidence in favour of essential nodes has recently been obtained by experiments which show directly that processing sites and perceptual sites are one and the same. There has been much evidence that favours such a view or is at least consistent with it (Dehaene, Naccache, Cohen, Bihan, & Mangin, 2001; Rees, Kreiman, & Koch, 2002; Zeki, 1993; Zeki & Bartels, 1999b). But perhaps the most compelling evidence comes from recent psychophysical experiments combined with imaging studies (Moutoussis & Zeki, 2002) (Fig. 2). The use of dichoptic visual stimulation allows us to arrange the sensory input into the visual brain in such a way that it is sometimes seen

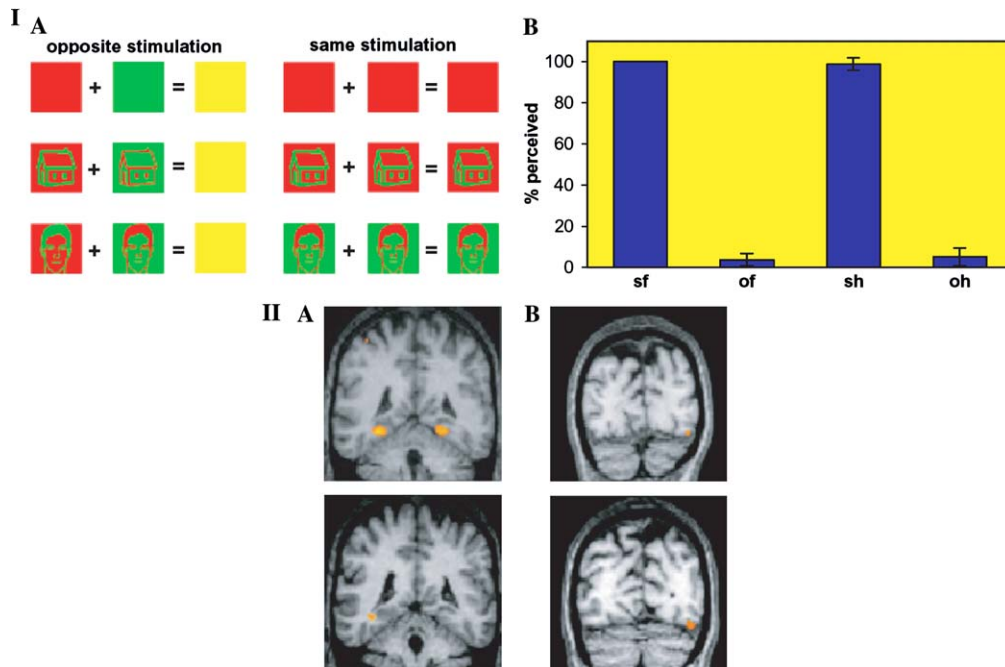


Fig. 2. (I. A.) A schematic presentation of the experiment of Moutoussis and Zeki (2002). Pictures of houses, faces, and uniformly colored controls were used. The input to the two eyes and the expected perceptual output (Upper) and subjects' true psychophysical performance (Lower) are shown. Continuous fusion of the stimuli was achieved by using repetitive brief presentations. Identical stimuli of opposite colour contrast were invisible when presented dichoptically to the two eyes (opposite stimulation), whereas identical stimuli of the same colour contrast (same stimulation) were easily perceived. Control stimuli were never perceived either as a face or a house. (B) The averaged performance of the seven subjects in the face/house/nothing discrimination task. The averaged percentage of the number of stimuli perceived is shown (of a total of 448 per subject per stimulus category) together with the standard error between the subjects. sf, same faces; of, opposite faces; sh, same houses; oh, opposite houses. II. Group results of brain regions showing stimulus-specific activation under conditions of same and opposite stimulation, revealing that such activation correlates with perceived and not-perceived conditions. (A Upper) The contrast same houses-same faces shows bilateral stimulus-specific activation in the parahippocampal gyrus (Talairach coordinates, 230, 244, 212 and 26, 244, 210). (Lower) The contrast opposite houses-opposite faces shows unilateral stimulus-specific activation in the same region (238, 242, and 210). (B Upper) The contrast same faces-same houses reveals stimulus-specific activation in a region of the fusiform gyrus (42, 282, and 212). (Lower) The contrast opposite faces-opposite houses reveals stimulus-specific activation in the same brain region (44, 274, and 214).

and sometimes not, even though the stimulus is identical in both situations. Thus, when an identical stimulus, such as a house or a face, is presented monocularly to each eye in turn, the presentation to one eye alternating with that to the other eye every 100 ms, the two images are fused into a single image and the subject can report consciously and correctly what the stimulus was. But if the same stimulus is presented to each eye in the same way though with opposite colour contrasts, the two colours cancel each other in the fusion; the stimulus is no longer perceived and cannot be recognized by the subject, even though the visual input to the eyes is the same as in the condition when the stimulus was correctly perceived. Brain imaging experiments show that the same stimulus-specific areas are activated regardless of whether the stimulus is perceived or not.

Thus when the stimulus is that of a face, the area in the brain specifically implicated in the perception of faces is specifically activated, regardless of whether the stimulus is perceived or not. A similar result obtains with stimuli depicting houses, which activate a different, specialized, part of the visual brain (Tovée, 1998). This demonstration shows that the cortical perceptual sites, at least for faces and houses, are not separate from the cortical processing sites. This is not to imply that other cortical areas are never involved in the perception of houses and faces. There is little doubt that the memory system would be involved when the identification is that of a particular house or a particular face. The importance of the demonstration lies in showing that there is not a separate site specialized for perceiving, as opposed to processing, an argument that is important in what follows.

To summarize therefore the neurological context within which this article is written: There are many different visual areas in the brain, each one of which receives visual input in stages, each stage constituting a node. These nodes become essential nodes if the activity in them requires no further processing and results in a conscious correlate. An essential node is therefore a processing site as well as a perceptual site. One important conclusion that follows from this in the context of this article is that activity at a given essential node need not necessarily be dependent upon an input from a ‘higher’ area, or what is commonly called a “top–down” influence.

2.2.1. *The non-ambiguous state*

2.2.1.1. *Obligate interpretation—colour vision.* I begin by considering unambiguous conditions, when the brain has no option but to interpret signals in one way and one way alone. Colour vision provides a good example. It is important to emphasize here that when I say that the brain has no option, I mean that it has no option given its genetically determined neurological apparatus and wiring (Zeki, 1999). The question that we ask in colour vision is: what is the formal contribution that the brain makes in acquiring knowledge about colour, what is the ‘concept’ that it applies to the incoming signals, and what are the limitations that it imposes, given its neurological apparatus.

The colour of a surface remains substantially the same even in spite of wide-ranging variations in the wavelength composition of the light reflected from it, a phenomenon generally known as colour constancy. The brain, in other words, is able to discard all the variations in the wavelength-energy composition of the light reflected from a surface and assign a constant colour to it (Land, 1974; Land & McCann, 1971).¹ To be able to do so, there must be some constant physical feature about the surface. That feature is reflectance. By this is meant that a surface reflects a constant percentage of light of any waveband in terms of the amount of light of that waveband that is incident on it. A green surface will reflect, let us say, 70% of middle-wave (green) light that is incident on it, no matter what the actual amount; it will reflect 20% of incident long-wave (red) light, again no matter what the amount, and so on. In normal conditions, the surrounding

¹ In what follows, I use essentially the description given by Edwin Land. I am aware that there are other algorithms besides his that have been proposed, and also that some have disputed the novelty of Land’s system. These are matters that do not concern us here, for there is broad agreement that constancy is the principle characteristic of the colour system and there is also broad agreement that no one really knows the precise neural mechanism by which constant colours are constructed by the brain.

surfaces will have different reflectances for the same wavebands and will therefore reflect different percentages of the same intensity of these different wavebands that are incident upon them. The ratio of light of any given waveband reflected from a surface and from its surrounds will therefore always remain the same in all illumination conditions. To ascertain the reflectance of a surface, the brain simply has to take the ratio of light of a given waveband reflected from it and from its surrounds, which it must of course do for all wavebands. This provides the brain with a lightness record for the scene at each waveband. The next step consists in comparing its lightness in the three wavebands, and thus determining its colour. This description is based on the Land system and the exact stages involved in the neural implementation are not known. It is possible and even likely that the brain uses a procedure different from the one envisaged in the Land algorithm but the end result of brain operations must be the same, that is the construction of a colour which is independent of the precise wavelength composition of the light reflected from it, since it is significantly a matter of comparison between one surface and surrounding surfaces. By applying a brain-based, genetically inherited ‘concept’ of ratio taking for different wavebands, the brain can determine that a given surface (in our example the green surface) has a high reflectance for middle-wave light, and low reflectances for lights of other wavebands, *compared to surrounding surfaces and without reference to absolute values*. The knowledge that the brain thus acquires, in the strict sense, is not about colour but about the constant property of a surface, namely its reflectance. Colour then becomes a sort of an addition, an interpretation, *a visual language*, that the brain gives to that constant property of reflectance. What is critical to understand here is that the comparison is done by the brain and the result of that comparison, knowledge of the reflectance of a surface for lights of different wavebands, and the tagging of a visual language to that knowledge, belongs to the brain, not the world outside.

There is no ambiguity here, in that surfaces have definite reflectances for lights of different wavebands, and the brain merely has to compare the reflectances of these surfaces and their surrounds for the same wavebands and determine which has the higher reflectance for light of one waveband and of another. Given that reflectances are immutable, the brain has no option but to reach the conclusion that it does. It has developed an efficient and unfailing machinery for doing so, and a significant part of that machinery, related to long-range ratio-taking mechanisms, is vested in the colour centre of the brain, the V4 complex (Bartels & Zeki, 2000; Wade, Brewer, Rieger, & Wandell, 2002). The V4 complex is thus the essential node for both the construction and the perception of colours, without any evidence that it consults other, perhaps ‘higher,’ cortical areas in this endeavour, although it of course becomes an essential node by co-operation with the nodes in V1 and V2, with which it is reciprocally connected. When the colour centre in the brain is damaged, or where the receptors for colour vision are lacking (Bartels & Zeki, 2000; Zeki et al., 1991), such long-range comparisons become either impossible or are much reduced in scope, leading to the condition of achromatopsia, or to conditions in which colour vision is much impoverished (see Zeki, 1990 for a review).

It is interesting to consider the apparent chaos that is caused when, through partial damage to the colour centre, the ratio taking mechanism of the brain becomes imperfect though not completely non-operational. The consequence is to give the brain several options, in that the colour of a surface now becomes hostage to the wavelength composition of the light reflected from it (Kennard et al., 1995; Zeki et al., 1999). But these options are not available simultaneously, in that the colour of a surface will change markedly only when the wavelength composition of the

illuminating light also changes markedly. These options are useless, for they cannot give a correct interpretation of the reflectance of a surface and hence of its colour. The different options do not have equal validity as in truly ambiguous situations. In a healthy brain with an intact colour centre, there is no room for many different interpretations of what the reflectance of a surface and hence its colour is, which is not to say that the colour that one individual sees is the exact replica of what another sees. But for a given individual, there is no luxury of giving different interpretations to the reflectance of a surface, a luxury that in this case would only lead to confusion and false knowledge.

2.2.1.2. The Kanizsa triangle. The same physiological straight-jacket, determined strictly by the rules of the brain, is at play in interpreting other patterns of signals, which are nevertheless not as rigid as colour vision in allowing no options. Orientation selective cells are capable of responding to virtual lines. Such cells are to be found in areas V2 and V3 (Peterhans & von der Heydt, 1989; Von der heydt & Peterhans, 1989) but whether the orientation selective cells of V1 respond to virtual lines of their preferred orientation remains a matter of dispute (see Ramsden, Hung, & Roe, 2001). Whichever area they are located in, these cells, by definition, respond optimally only to their preferred orientation and not at all to the orthogonal orientation. They are therefore not free to respond in other ways, thus forcing only one plausible interpretation. A more complex situation arises with the objectively ‘unfinished’ pattern of Fig. 3. The brain tries to make sense of this, by ‘finishing it off’ in the most plausible way, and interprets the pattern of luminances in this Kanizsa figure as a triangle. There are of course other interpretations that the brain could give in this instance, but they are far less plausible. There are many variants of this Kanizsa figure and their characteristic is that they are all open to only one *plausible* interpretation. The interpretation is probably dictated by the physiology of orientation selective cells in the cortex, and more specifically the orientation selective cells in areas V2 and V3. But the patterns in the Kanizsa figures, though consisting of lines, nevertheless constitute objects. It is not surprising to find therefore that viewing the Kanizsa illusory figures also activates area LOC (Hirsch et al., 1995; Larsson et al.,

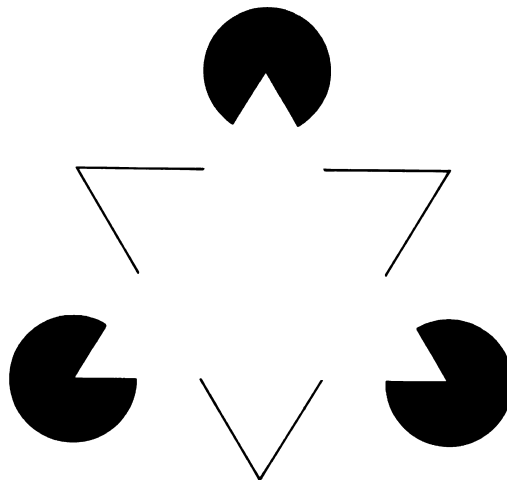


Fig. 3. The Kanizsa triangle.

1999; Stanley & Rubin, 2003), an area that is critical for object recognition in the human brain (Malach et al., 1995). In terms of our description, LOC could be referred to as a processing-perceptual centre for objects. As with colour vision, LOC works in collaboration with areas V2 and V3 (Murray et al., 2002), with which it is presumably reciprocally connected.

2.2.1.3. Essential nodes and ‘top–down’ influences in resolving ambiguities. To interpret the ‘unfinished’ picture of Fig. 3 as a triangle naturally involves a semantic element, which itself is shaped through experience. This, among other reasons, is probably why many have thought that a ‘top–down’ influence is brought to bear upon the pattern of signals, forcing their interpretation in a certain way. What is meant by ‘top–down’ is vague in neurological terms, but what is implied is that a ‘higher’ thought process influences the way in which we interpret things or that a ‘higher’ area influences neural activity in a ‘lower’ area. The meaning of ‘top–down’ influences becomes clearer when one considers what the proponents of this view had in mind. Both Herman von Helmholtz and Ewald Hering evoked ‘top–down’ influences (though without using the term) in trying to account for the constancy of colours. Helmholtz (1911) thought that factors such as prior knowledge and judgement were important, while Hering (1877) invoked the importance of memory. Implicit in such thinking is the supposition that processing and perception are always entirely separate, that a processing site in the brain is different from a perceptual site or, more accurately, that an interpretation has to be brought to bear upon the result of processing in an area, the interpretation emanating from a different source than the processing site. Effectively, this means that we can only become conscious of the triangle in the Kanizsa triangles, or of a colour, if some ‘higher’ area located, for example, in the frontal lobes, forces the interpretation of the ambiguous figure in a certain way. If this were invariably so, one would expect that, when the brain is constructing colours, cortical areas such as the ones in frontal lobes that have been implicated in thought processes would be engaged and that their activity could be demonstrated with imaging experiments. Yet imaging studies show that the computation of reflectances and the consequent construction of colours by the cerebral cortex is an automatic and autonomous process undertaken by a specific area in the visual brain, the V4 complex (the colour centre) (Bartels & Zeki, 2000), without involving frontal areas or other areas implicated in memory and abstract thought. The V4 complex constructs colours in the abstract, that is to say, it is indifferent to what objects colours belong to. As much can be demonstrated by using, in these experiments, Mondrian scenes which are constituted by an arbitrary assembly of squares and rectangles of different colours, with no recognizable shapes. Additional brain areas are recruited if, in such imaging experiments, subjects are shown colours that are the properties of recognizable (semantic) objects (Zeki & Marini, 1998). The V4 complex, in brief, constitutes an essential node for colour, activity at which has a conscious correlate and does not need to be processed further.

In the same way, it has been supposed that the interpretation that the brain gives to the configuration shown in Fig. 3 is imposed ‘top–down’ (Gregory, 1972). If so, then ‘higher’ areas of the brain should become engaged when subjects view such figures. But imaging experiments show that, when human subjects view and interpret such incomplete figures as triangles, activity in the brain does not involve the frontal lobes. The reason for the absence of any frontal lobe involvement, and hence the absence of ‘top–down’ influences as traditionally understood, is becoming obvious and it entails a major shift in our thinking about perceptual and processing sites in the brain and about consciousness too. While older theories assume, either explicitly or

implicitly, that a processing site is different from a perceptual site, evidence from physiological and imaging experiments, discussed above, shows that this is not necessarily so and that, in many instances relating to the perception of figures with semantic content, such as faces or houses, a processing site is also a perceptual site (Moutoussis & Zeki, 2002). The consequence of this postulate, if true, is important for understanding the neurological basis of ambiguity, for it implies that some categories of ambiguity at least are generated and possibly resolved by activity in given areas, without recourse to other, or higher, areas. As we shall see below, there are other categories of ambiguity that are probably dictated (and resolved) by the intervention of ‘third’ areas.

3. Simple perceptual ambiguity

3.1. Ambiguous bi-stable images

The absence of any real ambiguity in the examples given above is occasioned by the fact that there is no more than one plausible solution to the visual problem, even if it is the brain that constructs what is perceived. The situation is rendered more complex when one considers the Kanizsa cube (Fig. 4). Here there is little information in the intersecting lines. They could all be in the same plane, or some could be in a plane that is closer to the viewer than others. The brain has no means of knowing, and thus allows for all three interpretations. The important point to note is that, at any given time, only one interpretation is possible, *and this interpretation is as valid as the other interpretations*. It is a sort of interpretational flip-flop, one OR the other but not the two simultaneously. It is difficult to tell whether this interpretational flip-flop is due to any ‘top-down’ influences or to the activity of areas beyond the ones that register and combine the oriented lines into particular groupings. Without much evidence to go by, my hunch is that it is due to activity in a single area. If true, such a supposition has important consequences, for it implies that a micro-consciousness that is due to activity at a single essential node can be in several, mutually exclusive, states. One of the reasons that leads me to this conclusion is the obligate nature of the recessional planes seen in other instances, of which a good example is provided by the work of the British artist Nathan Cohen.

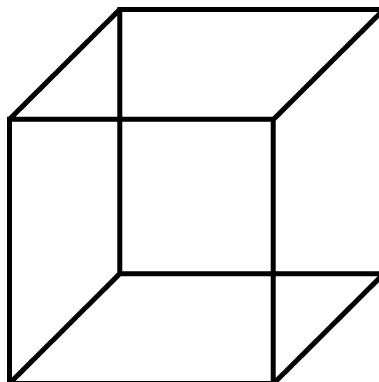


Fig. 4. The Kanizsa cube.

3.2. Obligate metastability

Cohen's abstract compositions make original use of a long-known perceptual effect, namely that juxtaposed rectangular forms can be interpreted by the brain as being in one of two recessional planes, either towards or away from the viewer at the point of juxtaposition, but not in both simultaneously. What Cohen's work shows compellingly is that, with the addition of further elements (rectangular shapes) of the same type, there develops an obligate perceptual relationship in the planes occupied by the contiguous rectangular forms. In the composition shown in Fig. 5, when the plane at the point of convergence of the central rectangles is towards the observer, the two surrounding ones are shifted to a plane away, and vice versa. There is no choice in this obligate relationship, which raises interesting physiological problems that are worthy of study. One would suppose, not unreasonably, that there must be some reciprocal relationship between cells that are capable of signalling recessional planes, and that that relationship depends upon the lateral connections between cells in a given area, assuming of course that there are no 'top-down' influences. Given the strong topographical relations involved, one would also suppose that the metastability is due to activity in an area with a good topographical map in it. Given that many cells in the third visual complex are disparity selective and capable of signalling what occurs in front of, and behind, the fixation plane (Adams & Zeki, 2001; Poggio & Fischer, 1977), and given the topographic representation of the visual field in the V3 complex (Cragg, 1969; Lyon & Kaas, 2002; Zeki, 1969), it becomes reasonable to suppose that this perceptual metastability is due to the instability of the responses of cells in V3, in the sense that the activity of some cells dominate perceptually at one moment and that of others at another. It is important to note here that such perceptual alterations can be attenuated or even abolished if the (ambiguous) visual stimulus is periodically removed from view, suggesting that un-interrupted viewing is necessary for the unstable physiological mechanisms that lead to multistable vision (Leopold, Wilke, Maier, & Logothetis, 2002). While the critical experiments have not been done, it is interesting to note what the consequence of such a demonstration is. It implies that the physiology of a single area, or a



Fig. 5. Composition by Nathan Cohen.

limited number of what are called ‘early’ visual areas, allows a multiple perceptual interpretation of incoming signals. That interpretation is nevertheless strictly circumscribed by the basic physiology of the cells in the visual area, without involving factors such as memory and learning. Accepting that activity at an essential node can have a micro-conscious correlate, one is naturally led to the conclusion that the micro-consciousness can be in more than one state, though we can only become conscious of one state at any one time. This raises the question of whether what regulates the change from one state to another of the same micro-consciousness (due to activity in the same essential node) is identical to the mechanism that regulates the change from one micro-conscious state to another when the switch is due to activity at two different essential nodes.

4. Resolution of ambiguity by third areas

4.1. Ambiguous interpretations of the same category

In the above examples, I have hypothesized that the same cortical area is engaged during the bi-stability or metastability where the metastability involves the same object or attribute. I may be wrong in this supposition and only further experiments will clarify the picture. My reason for doing so is to be found in the principle of functional specialization in the visual brain (Livingstone & Hubel, 1988; Zeki, 1978), which tells us that the processing of distinct visual attributes is the privilege of distinct visual areas. A cube is a cube, whether one of its planes is closer to the viewer or further away; hence one supposes that it is differences in processing *in the same area* that leads to different versions of the cube. The same reasoning holds for other and more complex bi-stable images, such as the ‘wife–mother-in-law’ image (Fig. 6), though with a difference. Since each one of the two images seen in this bi-stable image is that of a face, I assume (though without much direct evidence to support my assumption) that the bi-stability involves activity in the same area. But here the two faces differ substantially in other attributes, principally that of age but also in viewing angle, making it plausible to suppose that other influences will be brought into play in giving one of two different interpretations. The involvement of other areas is even more plausible in examples such as the Rubin vase (Fig. 7) where the two images, faces and a vase, belong to different categories. One supposes that two different areas are involved and that, as perception



Fig. 6. (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.

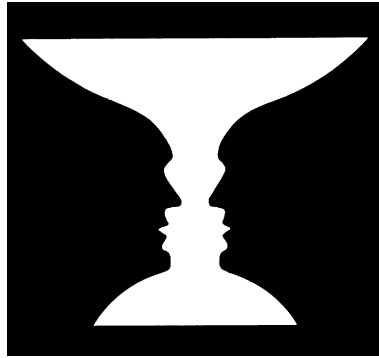


Fig. 7. Bi-stable figure: vase/faces.

shifts from one to the other, from the area concerned with face recognition to the one involved with object recognition, ‘third’ areas may become engaged.

Imaging experiments (Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998; Lumer, Friston, & Rees, 1998) have shown that the switch from one percept to another during the presentation of bi-stable images (when the stimulus remains the same but the percept changes) is indeed accompanied by a shift in the activated areas. For example, a shift from faces to vases entails a shift in the site of activation within the fusiform gyrus, a region of the visual brain that contains areas for object recognition. However, they have also shown that the fronto-parietal cortex is engaged whenever a percept changes from one condition to another. The intervention of a higher ‘third area’ distinguishes this kind of ambiguity from the more straightforward ambiguity that is due to activity within a single area alone and renders the interpretation of these experiments awkward. One interpretation might be that the fronto-parietal cortex is the ‘higher’ area dictating the percept and hence that we only become conscious of the interpretation through the intervention of the fronto-parietal cortex. This would be tantamount to saying that the areas in the fusiform gyrus that are activated are not sovereign in dictating what is perceived, and hence that a processing site is not really a perceptual site. But such an interpretation sits uneasily with the experiments of Moutoussis and Zeki (2002), referred to above, in which there is no demonstrable involvement of the fronto-parietal cortex. In these experiments, two conditions prevail: (a) when the stimulus remains the same but the percept changes and (b) when the percept remains the same but the stimulus changes. Collectively, they show that a processing site is a perceptual site. How is one to resolve this difficulty? Recent experiments (Sterzer, Russ, & Preibisch, 2002) have shown that where the reversal is that of a single attribute—the change in the direction of motion that is perceived—the activity is restricted mainly to V5 and to V3B, the former an area that is critical for motion perception and the latter an area that is important in extracting contours (Zeki et al., 2003). But here again the fronto-parietal cortex is engaged. One conclusion that can be drawn from these studies is that the fronto-parietal cortex is involved when there is a perceptual *change* of which we become aware, without being involved in the percept that we are conscious of. The experiments of Lumer et al. (1998) and Kleinschmidt et al. (1998), referred to above, are consistent with this explanation, which leads to the following conclusion: that activity in the parieto-frontal cortex is critical for us to become aware of a change, without necessarily knowing what has

changed. To become aware of what has been processed or what has changed, (heightened) activity at a specialized processing site (essential node) is critical.

5. The stability of perceptual instability

The extent to which the machinery of the brain is programmed to allow of different interpretations, and the seeming poverty of any ‘top–down’ influences, can be demonstrated by showing that it is not easy to dis-ambiguate these ambiguous figures. This may be readily ascertained by examining the so-called staircase illusion (Fig. 8). Adding features to the illusion which, one might have thought, would oblige the brain to perceive the figures in only one way does not lead to perceptual results that can only be interpreted in one way. The same is true of the ‘wife–mother-in-law’ illusion (Fig. 6). Adding a number of features to the figure, to force the brain to interpret it in one way only, is never successful. The brain retains the options of interpreting it in two ways. This suggests that the brain does not have much choice in the multi-interpretations that its organization makes possible. *The ambiguity, in other words, is stable.* It also argues against ubiquitous ‘top–down’ influences, even when coupled with direct visual stimulation. For the addition of further visual features that, top–down wise, would have imposed a single interpretation on the figure, fails to do so. This stability in the ambiguity, together with the fact that ambiguity may reside in a single object belonging to one category (for example, the cube), leads one to ask whether the multiple interpretations that the brain gives to a figure may not, at least with some figures, be the result of reciprocal fluctuations in the responses of cells in a single area.

6. Ambiguity and the micro-consciousnesses

We have argued elsewhere (Zeki, 2003; Zeki & Bartels, 1999a) that there are many micro-consciousnesses, each the correlate of activity in a specific brain area (a processing-perceptual site). Micro-consciousnesses are therefore distributed in space. Micro-consciousnesses are,

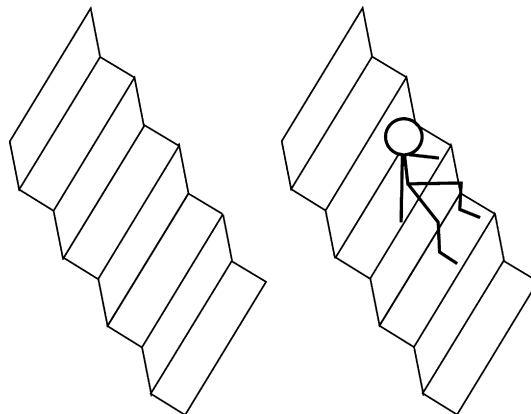


Fig. 8. (Left) The staircase illusion. (Right) It is difficult to stabilize the staircase by placing a figure on the stairs.

however, also distributed in time, because we become conscious of some visual attributes (e.g., colour) before others (e.g., motion) (Moutoussis & Zeki, 1997a, 1997b). In general, it would be reasonable to suppose that attributes that are perceived at different times are processed at different sites (or essential nodes).

The arguments I have given can be summarized by saying that activity of different groups of cells in the same area can result in different micro-consciousnesses for the same figure (for example of the different recessional planes in the Kanizsa cube) or that two different micro-consciousnesses for the same figure might be the consequence of activity in two different areas (as in the face–vase figure). Either way, one must suppose a shift in strength of activity, either from one group of cells to another within a single area, or from cells in one area to those in another. This also applies in cases of binocular rivalry. Logothetis and his colleagues have argued convincingly that binocular rivalry is the consequence of two rivalrous perceptions rather than eye dominance (Logothetis, 1998). Where the rivalry is between two gratings of different orientation or of two colours, one presented to each eye, one can conjecture that one group of cells holds sway over the other because of a shift in strength of activity. Where the rivalry is between two stimuli of different category, for example a face and a house, one can conjecture that the fluctuation in strength is between cells in different areas. This leads to an interesting problem: that there is a mechanism in the brain that can work on a single area or on two (or more areas) to alter the balance of the strength of activity between cells, whether the cells themselves are located in the same or in different areas. Such a mechanism would allow one micro-consciousness to dominate over the other, regardless of whether the two micro-consciousnesses are the correlates of activity in the same area or in two different areas. In the former, it gives activity of one set of cells conscious primacy, while in the latter it gives one area perceptual primacy over the other. Given our conjecture and demonstration that the shift from the unconscious to the conscious state involves an increase of activity within an area (Moutoussis & Zeki, 2002; Zeki & ffytche, 1998), we can now go further and conjecture that, where the shift in micro-consciousness during the perception of an ambiguous figure such as the Kanizsa cube is due to activity within a single area, then the relative activity of one set of cells will be higher than that of another. It goes without saying that the demonstration that activity in a processing-perceptual site acquires a conscious correlate only when the activity at that site becomes more intense (otherwise it remains a processing site alone) does not give insights into the question whether the heightened activity is due to the recruitment of previously unresponsive cells or to the increased activity of already active cells.

7. Higher levels of ambiguity

One of the functions of the brain, as emphasized earlier, is to instil meaning into this world, into the signals that it receives. Instilling meaning amounts to finding a solution. But the brain commonly finds itself in conditions where this is not easy, because it is confronted with several meanings of equal validity. Where one solution is not obviously better than the others, the only option is to allow of several interpretations, all of equal validity. Such a higher level of ambiguity is to be found in the multiple narrative interpretations that can be given, for example, to Vermeer's painting entitled *The Pearl Earring* (Fig. 9). Note that this is a single stable image, and the only variable is that the brain of the beholder can offer several equally valid interpretations of the



Fig. 9. The Pearl Earring by Johannes Vermeer (1632–75).

expression on her face. She is at once inviting, yet distant, erotically charged but chaste, resentful and yet pleased. These interpretations must all involve memory and experience, of what a face that is expressing these sentiments would look like. The genius of Vermeer is that he does not provide an answer but, by a brilliant subtlety, manages to convey all the expressions, although the viewer is only conscious of one interpretation at any given moment. Because there is no correct solution, the work of art itself becomes a problem that engages the mind. “Something, and indeed the ultimate thing, must be left over for the mind to do,” wrote Schopenhauer. There could be no better illustration of this than the work of Vermeer, where nothing is explicit. Vermeer’s *The Music Lesson* provides another interesting example (Fig. 10). This revolves around the relationship between the man and the woman. Many interpretations are possible. He could be her teacher, or brother, or husband or a suitor. They could be discussing something quite banal, like the quality of her playing or something a good deal more serious, such as a separation or a reconciliation. All these interpretations have equal force and validity. The brain must entertain them all and try to find the correct solution, except that in this instance there is no correct solution. It is this that led me to offer a neurological definition of ambiguity, namely it that it is not vagueness or uncertainty, but rather certainty, the certainty of different scenarios each one of which has equal validity with the others (Zeki, 1999). There is no correct answer, because all answers are correct. Schopenhauer wrote, “. . .through the work of art, everything must not be directly given to the senses, but rather only so much as is demanded to lead the fancy on to the right path. . .for Voltaire has very rightly said, “*Le secret d’être ennuyeux, c’est de tout dire*” [the secret of being boring is to tell everything]. But besides this, in art the best of all is too spiritual to be given directly to the senses; it must be born in the imagination of the beholder, although begotten by the



Fig. 10. The music lesson by Johannes Vermeer (1632–75).

work of art. It depends upon this that the sketches of great masters often effect more than their finished pictures.”

It is obvious that there is a relation between works that display such ambiguity and unfinished works, because in both instances the brain is able to give multiple interpretations that are of equal validity to the same work. I have written elsewhere of the unfinished sculptures of Michelangelo as an example (Zeki, 1999, 2002). Even in spite of their unfinished status, they have commonly led to interpretations that are so self-contained that one is left with the conclusion that they must have been ‘finished off’ by the viewer. Charles De Tolnay’s (1934) lyrical description of the Rondanini *Pietà* (Fig. 11) as a work which “comes to represent in the personal life of the artist that state of beatitude to which his unsatisfied soul aspired” could as well be a description of a finished work except that in this instance it refers to an unfinished work. It is thus interesting to compare the unfinished triangles of Kanizsa with the unfinished sculptures of Michelangelo, although many might regard such a comparison as demeaning to the great sculptor. In trying to make sense of the Kanizsa pattern that constitutes a Kanizsa triangle, the brain “finishes it off” in the only way possible; when trying to make sense of the pattern that constitutes the Kanizsa cube, the brain can interpret the intersecting lines as being in one of three planes. In Michelangelo’s Rondanini *Pietà*, the capacity to give multi interpretations is taken yet a step further. Now the solutions are, by comparison, large in number. Hence the capacity to give multiple interpretations is not a separate faculty invented or used by the artist. It is instead tied to a general capacity of the brain to give several interpretations, a capacity that is important for it in its role of acquiring knowledge. It is on this physiological basis that the prized quality of ambiguity in art is built.



Fig. 11. Rondanini Pietà by Michelangelo.

One can therefore conjecture that there are graded steps, not only from non-ambiguous to ambiguous stimuli, but also in the number of areas or distinct cortical sites that may be involved. At the simplest level, I am suggesting that the ambiguity may be due to activity in a single area in which the micro-conscious correlate of activity may be in more than one state. Obviously, there is

no ‘top–down’ influence here. At a higher level, the ambiguity may involve more than one area, as in the Rubin vase. This may or may not involve higher areas in the frontal lobe. At a higher level still, the ambiguous state may involve several distinct areas that are able to bring their influence. The Vermeer paintings referred to above provide a good example. Here, memory, experience, learning and much else besides can influence what is perceived at any given moment. This almost certainly involves a ‘top–down’ influence, from diverse sources, not just the frontal lobes. Thus, opening up the capacity for a given brain area to be influenced by another area is merely one step in opening up the capacity to be influenced by multiple other areas. Hence, the artist exploits this potential of the brain that allows multiple areas to influence what is perceived. It is not ambiguity itself, therefore, that is aesthetically pleasing, even though some artists such as Arcimboldo and Salvador Dali deliberately made of ambiguity an artistic form. It is rather the capacity of multiple experiences, even though we are conscious of only one at any given moment, that a stimulus can provide.

8. Ambiguity and contradictions

In the examples given above, of Vermeer’s work, the possible interpretations are not only many but are also sometimes contradictory. Some will see the girl in Vermeer’s masterpiece as being alternately chaste and erotically charged, or approachable and resentful. These of course are interpretations that my brain is giving to this composition, and it is not implausible though not certain that others will see similar contradictions or other ones. Yet we do possess a work which is in a highly incomplete state and which allowed Johann Winckelmann to perceive as embodying contradictory elements. Winckelmann, often regarded as the father of art history, had a very definite view, one might say a concept, of beauty as reflected in Greek sculpture, which he related to his view of Greek culture in general. For him, Greek art was born out of, and in, a free social and political setting, yet one that was beset by a contradiction or tension that, he thought, was reflected in its art. That tension was between “an ‘active’ manly freedom realized in the violent struggles of the early phases of Greek culture...and a free sensual enjoyment of things.” Winckelmann, of whom Goethe interestingly wrote that “his gift was to search in the outer world what nature had laid in his inner world” chose the Belvedere Torso (also known as the Belvedere Hercules) (Fig. 12), an “unfinished” work, as representative of the highest beauty in Greek art and as one depicting most forcefully this apparent tension. In fact, of course, the Torso, which occupied a very privileged position in Winckelmann’s writings on art (Potts, 1994), is not unfinished but is now, and when Winckelmann saw it, badly damaged and a very incomplete fragment, so that only parts of the torso and thighs remain. It is this incomplete status that allowed Winckelmann to read so much into it and, what is more, so much that is visually compelling, at least to anyone who may not be acquainted with the history of the torso. He thought of it as “the high ideal of a body raised above nature, a nature of mature manly years, as it would appear when elevated to a state of divine contentment” (Winckelmann, 1764). The Belvedere Torso is thus characterized as being actively heroic and passively contended. And these contradictory interpretations, united in a single figure, can compellingly become, or become acceptable, as the interpretations of the spectator as well even though we are only conscious of one interpretation at any given moment. That Winckelmann himself attributed a primary role to the imagination (to us, the brain) in this



Fig. 12. The Belvedere Torso.

instability becomes evident in his description of the Belvedere Hercules, which he asked the viewer to admire for its continuous flow of one form into another. As the viewer interprets these ever changing forms “er wird finden, dass sich niemand im Nachzeichnen der Richtigkeit versichern kann, indem der Schwung, dessen Richtung man nachzugehen glaubt, sich unvermerkt ablenket, und durch einen andern Gang, welchen er nimmt, das Auge und die Hand irre machet” ([the artist] will then find that it is not possible to reproduce this accurately by drawing since the curve that the drawer believes himself to be following changes its direction imperceptibly and confuses both eye and hand with its new direction” (Winckelmann, 1764, *Geisichte*, Vol. 6, p. 98)—quoted by Potts, 1994). To him, “The apparent calm and stillness, which recall the blissful self-absorption of ideal youth, are charged by intimations of the naked physical power of a hero laying waste all that came in his way” (Potts, 1994).

The important point to note here is that it is to some considerable extent, visually at least, the incomplete status of the Belvedere Hercules that allowed him to make, and allows us to consider, contradictory interpretations that are visually convincing. It is perhaps not entirely fortuitous, then, that Winckelman chose an incomplete work to represent his highest ideal of Greek beauty. To generalize what Langerholc (1986) has said, these artists, “relied on ancient laws of perspective and tonality *deriving from the nature of our perceptive mechanisms* [our brain] to draft their illusions. Otherwise they would not have worked” (my emphasis). This applies as much to the Kanizsa cube as to the progression of the Tristan chord in Wagner’s work (Zeki, 2002) and to the Belvedere Hercules.

9. Conclusion

The general point that I make in this article is that there is a continuum in the operations of the brain, the basis of which is to seek knowledge and to instil meaning. In this continuum, we

proceed on the one hand from conditions where the brain has no option in its interpretation of the signals that it receives, as in colour vision, to ones in which there are two equally plausible interpretations and, finally, ones in which there are many interpretations. On the other hand, we also have a continuum in which activity in an area is almost sovereign in this context, to ones in which activity in an area is open to one or multiple influences from other areas. If, as I have written elsewhere, the function of art is an extension of the function of the brain, namely the acquisition of knowledge about the world, then it stands to reason to suppose that the mechanisms used to instil meaning into this world are the very ones used to instil meanings into works of art. It is those basic mechanisms that artists have used so successfully.

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