

# The theory of multistage integration in the visual brain

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The theory of multistage integration is based on evidence that the visual brain consists of several parallel multi-stage processing systems, each specialised for a given attribute such as colour or motion. Each stage of a given system processes information at a distinct level of complexity. Our theory supposes that activity at any stage of a given multistage processing system is perceptually explicit - that is to say it requires no further processing to generate a conscious experience. This activity can be integrated, or bound, with the perceptually explicit activity at any given stage of another or the same multistage processing system. Such binding is therefore not a process that generates a conscious experience, but rather one that brings different conscious experiences together. Many perceptual advantages result from such a flexible and dynamic integrative system. Conversely, there would be disadvantages to limiting perception and binding to hypothetical 'terminal' stages of such processing systems or to hypothetical 'integrator' areas. Although we formulate our hypothesis in terms of the visual brain, we believe it might form a general principle of brain functioning.

## 1. INTRODUCTION

In this paper we revise and extend the theory of multi-stage integration in the visual brain (Zeki 1990b, Zeki 1993), which states that integration can occur between any two stages of one or more processing systems. In this extension we rely on new facts and on our twin theories of the asynchrony of consciousness (Zeki and Bartels 1998) and of the perceptual sites in the visual brain (Bartels and Zeki 1998a and Bartels and Zeki 1998b). The former states that the stages of any processing system generate separate conscious events asynchronously with respect to each other and with respect to the outside world. In other words, that consciousness is not a unitary faculty, but that it consists of many microconsciousnesses. The latter theory supposes that simultaneously presented attributes which are perceived at the same time (in the range of tens of milliseconds) are processed at the same site, and those perceived at different times are processed at different sites. The three hypotheses are intimately linked and rely on substantially common facts.

We base our theory on the following facts and on our interpretations of them:

1. The visual brain consists of many different visual areas (Zeki 1978, Felleman and Van Essen 1991). Of these, the primary visual cortex (area V1) receives the predominant input from the retina and is

surrounded by area V2. Both areas have a detailed map of the retina and hence are said to be topographically organised (Talbot and Marshall 1941, Daniel and Whitteridge 1961, Cragg 1969, Zeki 1969, Allman and Kaas 1974). There are many further areas beyond V1 and V2 in what is known as the prestriate cortex; these have larger receptive fields and relatively cruder topographic organisations (Van Essen and Zeki 1978, Boussaoud et al. 1991, Mountcastle 1995).

2. V1 and V2 have cells representing all the principal submodalities of vision (colour, form, motion and depth), cells concerned with a given submodality being segregated into anatomically identifiable compartments within both areas (DeYoe and Van Essen 1985, Shipp and Zeki 1985, Livingstone and Hubel 1988). Areas beyond V1 and V2 show greater specialisations for processing different attributes of the visual scene such as colour, form, or motion (Zeki 1978, DeYoe and Van Essen 1985, Shipp and Zeki 1985, Livingstone and Hubel 1988). When we speak of a specialized area we do not imply that it is specialized for a single function only. For example, when we speak of V5 as being specialized for motion, we do not mean to imply that it is not also involved in the generation of depth or form from motion. And when we speak of the specialization of V4 for colour we do not mean to imply that it is not also involved in the processing of luminance and of forms, both of which can be

intimately linked to colour. It is worth recording the contrary view, with which we do not agree, that there is no functional segregation in areas V1 (Lennie *et al.* 1990, Leventhal *et al.* 1995) and V2 (Gegenfurtner *et al.* 1996) or in the visual brain at large (Schiller 1997).

3. The specialised areas beyond V1 and V2 receive input from different and specialised compartments of V1, either directly or through specialised compartments of V2, as well as from other sites (see below) (Livingstone and Hubel 1984, Shipp and Zeki 1989a, Shipp and Zeki 1989b, Zeki and Shipp 1989, Nakamura *et al.* 1993). We thus speak of specialised processing systems. The cortical part of each processing system consists of the sensory entry sites (such as the specialised cells in V1 that code for wavelength, orientation or motion) and the pathways leading from them to the specialised areas, both directly and indirectly. Each processing system therefore consists of several stages or nodes, at each one of which the visual signals are processed at a certain level of complexity. By 'node' or 'stage' we refer either to a whole area, such as V4 or V5, or to the functional subdivision of an area. Examples of the latter are the blobs and interblobs of V1 and the thin, thick and interstripes of V2. Activity at a node represents unique information, not present explicitly at nodes above or below it. The information generated at a node is rendered explicit not only by virtue of the input to it, but also because of its dedicated physiological capacities. The latter comprise specialised processing circuits that might also have a memory component. The information thus generated at a node may be implicitly represented in activity at other nodes. By implicit we mean information that requires further processing to become perceptually explicit.
4. The components of a processing system can act independently of V1. An example is provided by area V5 which is specialised for motion (Zeki 1974). Its principal characteristic, directional selectivity, survives de-afferentation from V1 (Rodman and Albright 1989, Girard *et al.* 1992). This survival is made possible by another visual input which reaches V5 from a thalamic nucleus - the pulvinar - without passing through V1 (Cragg 1969, Benevento and Rezak 1976). The latter pathway thus constitutes another processing system that shares V5 (Zeki and ffytche 1998). Signals from fast moving objects which have shorter latencies of cortical arrival reach V5 through this pathway while signals from slowly moving objects reach it through V1 (ffytche *et al.* 1995). This suggests that processing systems can converge to share a specialised node (Zeki 1998).
5. Each node has multiple anatomical outputs, as if the results of the operations performed at each are of interest to several further areas. Moreover, there are strong lateral connections that link anatomically the nodes of the different processing systems. For example, lateral connections link the subdivisions of V2 which house cells with different specialisations (Rockland 1985, Levitt *et al.* 1994) and there are also direct links between more specialised areas such as V4 and V5 (Felleman and Van Essen 1991). The latter in turn have feedback connections to all the stripes of V2 (Shipp and Zeki 1989a,b, Zeki and Shipp 1989). The consequence is that a subdivision of V2 that is specialised for, say, motion can be influenced by colour through (a) lateral connections within V2 linking it to subdivisions that are specialised for colour, and (b) through back projections from V4 which is also specialised for colour. But V5 can also be directly influenced by V4. In summary, a stage representing a given level of one processing system has the anatomical opportunity of sending signals to several stages of another.
6. Anatomical evidence shows that there is no single area to which all the specialised visual areas connect, which would enable it to act as an integrator capable of binding signals coming from all the different visual sources. There are in fact examples of common areas to which two different processing systems project. However, it appears that when this happens each input maintains largely its own territory within the common recipient area, with minimal convergence or overlap with other inputs, thus leading us to speak of a *juxtalconvergence* (Shipp and Zeki 1996). Moreover, there is no 'terminal' station in the cortex, in the sense of a cortical area that is recipient only. Each area of the cortex, and indeed each subdivision of each area, receives inputs and sends outputs to both cortical and sub-cortical stations (Zeki 1993). Each is therefore only a part of a more extensive processing system which includes, besides subcortical stations, areas in the temporal, parietal and frontal cortex. The latter areas, too, constitute only parts of the processing system since they all project to further areas and are reciprocally linked with the earlier visual areas from which they receive input.
7. Clinical evidence shows that damage restricted to one processing system leads to an imperception in the attribute for which that system is specialised, and not to a global blindness. Examples are motion imperception (akinetopsia), colour imperception (achromatopsia) and face imperception

(prosopagnosia) (for reviews see Damasio 1985, Zeki 1990a, Zeki 1991). Moreover, damage to different levels of a processing system produces imperceptions of different types and degrees of severity within the attribute for which that processing system is specialised. When one of the higher stages of a processing system is damaged by a lesion, subjects are not rendered blind to the attribute that that system processes; instead their capacities for that attribute reflect the physiological capacities of the parts of the processing system that are left intact by the lesion. For example, patients who become akinetopsic by a damage to area V5 are unable to see objects when in fast motion ( $> 5^{\circ} \text{sec}^{-1}$ ); they can nevertheless perceive them when in slow motion ( $< 5^{\circ} \text{sec}^{-1}$ ), presumably reflecting the capacities of the stages left intact by the lesion (Shipp *et al.* 1994). Another example is provided by the colour processing system. Some subjects with lesions in the human V4 complex (Bartels and Zeki 1998b) are rendered achromatopsic and only able to see the world in shades of grey; they can nevertheless distinguish between different wavelengths of light though with elevated thresholds and without being able to assign colours to them (Vaina 1994, Fries and Zeki unpublished results). For others, the colours that they perceive are unstable and change with changes in the wavelength composition of the illuminating light (Kennard *et al.* 1995). This probably reflects the physiological capacities of the parts of the processing system that are left untouched by the lesion, namely areas V1 and V2 (Zeki 1983a). Finally, a person blinded by a lesion in V1 but with an intact V5 can nevertheless experience, crudely but consciously, fast motion in his field of view (Barbur *et al.* 1993, Weiskrantz *et al.* 1995, Zeki and ffytche 1998), by virtue of the direct pathway reaching V5 through the pulvinar. That this conscious experience correlates with activity in area V5 suggests that the latter pathway can act as a processing system on its own. Activity in it is sufficient to generate a conscious percept, without the participation of the motion processing system that reaches V5 through V1.

8. The perception of a given attribute correlates with activity in the area specialised for processing that attribute. For example the fast circular motion that is perceived by humans when viewing the static work of Leviant entitled *Enigma* correlates with the selective activation of one node of the motion processing system, area V5 (Zeki *et al.* 1993), as does the motion after effect (Tootell *et al.* 1995). Similarly, the perception of afterimages induced by colour correlates with the selective activation of one node of the colour processing system, the V4 complex (Sakai *et al.* 1995, Hadjikhani *et al.* 1998).

Recent direct evidence for this equation of a processing system with a perceptual one is provided by imaging experiments which have shown that the cortical ratio-taking operations that are critical for generating colours occur at the very site which, when damaged, leads to the syndrome of cerebral achromatopsia, namely the human V4 complex (Bartels and Zeki 1998b).

9. A given node may be shared by two processing-perceptual systems. One example is area V5 (see point 4). Another is the area within the fusiform gyrus which is activated when humans recognise objects either in static pictures (form-from-luminance) or from motion (form-from-motion) (Zeki and Bork 1998). In theory, if one of the two processing systems feeding into this node is damaged, patients should suffer a visual imperception related to the damaged processing system only. We interpret the following clinical examples in this light: Brain-damaged subjects who are unable to see stationary objects can nevertheless immediately perceive them when they are set into motion (Botez and Sebranesco 1967, Kertesz 1979, Humphreys and Riddoch 1987). Conversely, brain-damaged subjects who are unable to perceive forms generated from motion can nevertheless perceive them when generated from luminance (Regan *et al.* 1992). In the examples given above, if the damage is restricted to the shared node, one would expect patients not to be able to recognise objects, no matter what processing system is delivering the input to it. There are indeed clinical examples of 'agnosic' patients who have lost the capacity to recognise certain categories of objects. But no study has ever been conducted to show that such patients cannot recognise the same category of objects no matter how they are derived (e.g. from motion or luminance or colour).
10. A processing-perceptual system can be selectively spared, as with the colour processing system following carbon monoxide poisoning or severe cardiac arrest (eg Wechsler 1933, Humphrey *et al.* 1995). When spared, a person who is (legally) blind can nevertheless have a surprisingly good, though far from perfect, capacity to see and understand colours, even if they cannot associate these colours with any form. This shows that for two attributes which are intimately linked in ordinary visual experience (in this case form and colour), the binding of one attribute to another is not the necessary pre-condition for the conscious experience of one of the two only.

11. Psychophysical evidence shows that the different processing systems do not terminate their tasks at the same time with regard to an external event. When different attributes of the visual scene are presented simultaneously (in real time) they are not necessarily perceived at the same time; colour, for example, is perceived before orientation which is in turn perceived before motion, colour having an advantage over motion of 60 to 80 ms (Moutoussis and Zeki 1997). That at the sub-second stage perceptions occur in parallel but not necessarily simultaneously adds to the clinical evidence which suggests that different perceptions are the result of activity in different processing systems. We thus speak of parallel and asynchronous processing-perceptual systems which are asynchronous with respect to one another (Zeki and Bartels 1998, Zeki and ffytche 1998). This is the perceptual reflection of the modularity of the visual brain. We consider these multiple and asynchronous parallel perceptions to be multiple visual micro-consciousnesses which are asynchronous with respect to each other (Zeki and Bartels 1998). Put more briefly, we suppose that the conscious correlates of two attributes such as colour and motion vision differ in space and time.

The above facts and our interpretation of them leads us to our extended theory of multistage integration, which states that each node may have a conscious correlate and that integration may occur between the conscious correlates of any two (or more) nodes belonging to either the same or different processing-perceptual systems. Both the distributed conscious correlates and their integration are necessary, because they ensure that the explicit information unique to each node, which would otherwise be lost, is preserved. The functional specialisation that is so prominent a feature of the brain is thus to be found not only between different processing systems, specialised to process different attributes, but also between the nodes of a given processing system, since each node is specialised to process signals to a unique level of complexity, and one which is perceptually useful.

## 2. THE THEORY OF MULTISTAGE INTEGRATION

Within the context of this and our other two related theories (Bartels and Zeki 1998c, Zeki and Bartels 1998), we propose the following:

I. The activity at each node of a processing-perceptual system leads to a perceptually explicit result, that is to say one that requires no further processing to create a conscious experience (Zeki 1993) and is accompanied by a conscious correlate (Zeki and Bartels 1998). Thus we perceive a given scene

through several perceptual layers. As an example, we perceive a green area within a coloured scene as green under different illuminants, when the wavelength composition of the light reflected from the green surface, and from every other surface in the field of view, changes; we suppose this colour constancy to be the perceptually explicit result of activity within the human V4 complex (Bartels and Zeki 1998b). But we also perceive changes in the wavelength composition and intensity of the illuminant, when these occur. This is probably made perceptually explicit by the activity of cells in V1 and V2 which are sensitive to changes in wavelength composition (Zeki 1983a,b).

II. Activity at each stage or node of a processing-perceptual system has a conscious correlate. Binding cellular activity at different nodes is therefore not a process preceding or even facilitating conscious experience, but rather bringing different conscious experiences together (Zeki and Bartels 1998). This binding of the micro-consciousnesses does not need to, and cannot, wait for a final stage, because there is no final stage in the cortex. Instead, it can occur between micro-consciousnesses generated at any two stages of any two processing-perceptual systems or between two different stages within one processing-perceptual system.

III. A consequence of parallel, modular, processing systems in the visual brain is an increased number of possible different combinations and thus of perceptual repertoires. This would be reduced if the processing systems had to report to a 'terminal' station - either a common one or individual ones - for integration to occur. Such an hypothetical integration area would have to code in a perceptually explicit way the results of the processing at each node separately and in the required combinations. The more economical way that we propose would be to render the activity at each processing site perceptually explicit, which can then be bound. The number of pairwise connections between  $N$  nodes equals  $N*(N-1)/2$ . Even given the constraints of cortical connectivity, this would still create a vast repertoire which would not be possible if integration could only occur between hypothetical 'terminal' stages or hypothetical 'integrator' areas. Our conjecture that each node corresponds to a perceptual site means effectively that there are far more such sites in the cortex than would be possible if there were only a "terminal" perceptual site for each processing system.

IV. If the result of activity at a given stage is not made perceptually explicit, it would be lost in later

processing stages and would no longer be perceptually accessible. The function of many nodes in a processing system is to discard some information in order to extract more global information. For example a picture of a face composed of small dots will activate areas whose cells respond to dots and other areas whose cells respond to faces. Neither of the two stages codes explicitly information that the other stage explicitly codes for. The only way to preserve both types of information - both the dots and the face - is to make activity in both areas perceptually explicit. It would be wasteful for the brain to make only the information of the anthropomorphically defined 'final stage' - the face area - perceptually explicit. Another example is colour vision. The cells in V1 and V2 which are sensitive to wavelength composition cannot code for colour, which, by definition, remains stable despite changes in wavelength composition. It is the activity of cells in V4 that correlates with colour. The information that the cells in V1 and V2 code for excludes them from coding simultaneously for the information coded for by cells in V4 (and *vice versa*). Nevertheless we are aware of what each set of cells codes for - the constant colour of a surface as well as the changes in the illumination condition.

- V. Since different and often mutually exclusive types of information are made explicit at different processing stages, it is necessary that percepts created at each stage of a processing-perceptual system can be bound to other percepts, created independently by the activity of cells at other stages within a given processing-perceptual stream. This is especially so when activity in a single area is important for seeing an attribute, no matter how that attribute is derived. For example, recent experiments show that the same area in the fusiform gyrus is activated when humans view forms generated from luminance and from motion (Zeki and Bork 1998). But once generated from motion, for example, the form has to be re-integrated with an earlier stage of the motion pathway to bind the form to the characteristics of the motion.
- VI. Each processing-perceptual system has a certain hierarchical structure, by which we mean that the visual attribute is processed at a more complex level at a given stage than at the antecedent one. The theory of multi-stage integration nevertheless supposes that there is no perceptual hierarchy in binding since the perceptually explicit activity of cells at a relatively "low" level in one processing-perceptual system can be bound with the perceptually explicit activity of cells at a relatively "high" level of another, or the same, processing-

perceptual system. Nodes which are active and bound together at a given time therefore constitute what we call a functional unit. Any given node may form part of one functional unit or another. The functional units are formed in a dynamic fashion and can criss-cross between different stages of different processing-perceptual systems (Zeki and ffytche 1998).

This theory may turn out to be right or wrong; it will almost certainly have to be modified in the light of new results. We nevertheless hope that something of its basis will remain.

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