Toward the Where and What of Consciousness in the Brain

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ABSTRACT

We consider here how new results arising especially from brain imaging but also from other areas of brain science (single cell analysis, deficits) are modifying our understanding of the neural representations involved in consciousness. The problem is discussed in terms of the two basic questions: where are the crucial sites for the creation of consciousness in the brain, and what is the appropriate representation involved? A framework is first developed and criteria thereby deduced for a neural site to be regarded as essential for the creation of consciousness. Various sites in the brain are considered, but only few are found to satisfy all the criteria. Past models of consciousness are considered as guides to developing an answer to the 'what' question. The notion of the central representation is then created, regarded as composed of information intrinsic to awareness; this representation is suggested as being in the parietal lobes. The manner in which the central representation can contain the complexity of consciousness is then analysed in terms of the three-stage model of awareness, for which brain imaging support is also presented. This model is then related to the higher-order thought approach. The paper concludes with a summary.

KEYWORDS: consciousness; brain imaging; neural networks; deficits; working memory; attention

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1. INTRODUCTION

The quest for the neural correlates of consciousness in the cerebral cortex (NCC) is now proceeding apace (Taylor, 1999). Many attempts have been made to track down the possible sites that are necessary for consciousness to be present, and whose neural activity is well correlated with conscious experience. Such a search is important: only by more detailed examination of such supposedly circumscribed sites can the 'value added' by consciousness be able to be examined in terms of the relevant neural activity leading to consciousness itself. Uncertainty still remains, however, as to the sufficient conditions that must be observed as neural activity for the network of sites involved in the brain to be claimed as *the* sites of consciousness. Here a framework is developed and related criteria deduced so that neural sites can be selected to give a first approximation to such important areas. The further and much deeper scientific question of how any neural representation can actually support consciousness can then be explored and related to possible philosophical and psychological discussions.

The problem we presently face in the search for the NCC is that the nature of consciousness is subtle, and its characteristics seem to change from moment to moment. Such vacillation has led to the site of the NCC in the brain also being uncertain. To prevent the NCC from wandering all over the brain, be it now in the primary sensory or the unimodal associative cortices (Pollen, 1999) or now in the prefrontal cortex (Crick & Koch, 1998), I will initially explore, in Sec. 2, evidence in support of various possible sitings of the NCC. Certain criteria that must be satisfied by neural activity for it to be a candidate for the NCC will then be discussed in Sec. 3, where I conclude that the lateral parietal lobes are the most appropriate region for the siting of consciousness. Guidance from previous models of consciousness, collected in Sec. 4, is used to help construct in Sec. 5 the notion of the central representation, which contains the crucial contents for consciousness. A general flow of information in the brain is then developed in Sec. 6, which incorporates the central representation. The manner in which this representation can contain the complexity of consciousness is achieved by expanding the central representation in Sec. 7 by means of the 3-stage model of consciousness; some experimental evidence is presented to support this extension. In the next

section I relate this to the higher-order thought approach to consciousness. A brief discussion concludes the paper.

2. EXPERIMENTAL DATA

The data I consider are of a variety of sorts: from single cells, lesion effects on behaviour, and brain imaging (mainly PET and fMRI). The single-cell data involve the presence or absence of significant activity, observed in an animal under anaesthesia, that has little effect on early sensory cortical responses, in V1 and MT (for example see Moutoussis & Zeki [1997]) nor in inferotemporal cortex TE (Tanaka, 1996). Yet, a considerable effect of anaesthesia on parietal lobe single cell responses has been observed, which in the past has led to great difficulty in making measurements of such cells before the advent of the ability to measure from awake behaving monkeys (Milner & Goodale, 1995).

As a start to considering lesion effects, I note the singular lack of loss of consciousness, due to frontal deficits, brought about by either disease or injury. The cases supporting this claim are numerous. One example is the famous case of Phineas Gage (Damasio, 1994), who had a tamping iron blown through his frontal lobes, with considerable loss of frontal cortex but without successive loss of consciousness as he was carried to the local doctor. Another example is the case of the young man who was born bereft of most of his frontal lobes (Damasio, 1994), but yet, apart from great social problems, lived a normal conscious existence.

One area of brain lesions that is of particular relevance to the NCC is that of neglect. Patients usually suffer a loss of the right parietal lobe, and subsequently lose awareness of input from their left hemifield. This loss, for example, is observed in the inability to cross out lines on the left of their field of view. Nevertheless, their lot can be ameliorated by vibration of the neck muscles, and in general shows a dependence on body signals. Thus, neglect is a loss of awareness in a body-centred frame of reference, although there may also be object-frame dependence of their loss (Karnath, 1997). Agreement has now been reached that neglect arises specifically from damage to the inferior parietal lobe (Milner, 1997).

Much is also being discovered about the siting in the cortex of buffer working memories. Those for spatial vision are in the right (Jonides & Smith, 1997), those for language and temporal estimation in the left, inferior parietal lobes (Coull & Nobre, 1998). On the other hand, extinction involving loss of awareness of the right hand object of two similar objects, one on the left, one on the right, is sited in the superior parietal lobe (Milner, 1997).

Our recent fMRI data (Schmitz et al., 1998a, 1998b) indicates that activation is most strongly correlated with the experience of the motion after-effect (MAE) in BA 40, the supramarginal gyrus in the inferior parietal lobe. Our experimental paradigm to observe this phenomenon used motion adaptation to a set of horizontal bars moving vertically downward for 21 seconds and then stopping. Subjects exposed to such a display usually experienced the MAE for 9 or so seconds after cessation of the movement of the bars.

Our whole-head fMRI measurements of each subject during this paradigm (Schmitz et al., a, 1998b) showed a network of connected areas, as shown in Fig.1. This network had a posterior group involving especially the motion area MT, which was found to be responsive to all forms of motion, as well as the MAE (Tootell et al., 1995). On the other hand, we observed a set of
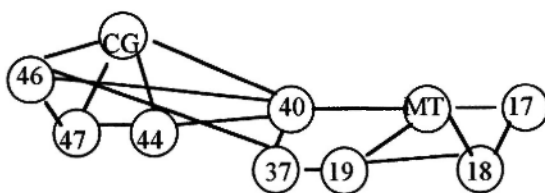

Fig. 1: The network of areas active in the brain during the MAE experiment (Schmitz et al., 1998a, 1998b). The lines joining the various modules denote those for which the correlation coefficient is at least 0.4. MT denotes the middle temporal area, and the other areas are numbered according to Brodmann's numeration.

anterior modules, shown in Fig.1, that were particularly active both during the MAE period and just after the cessation of oscillatory movement of the bars, both up and down (used as a control), and after which no MAE experience was reported. Finally certain inferior parietal regions demonstrated activity almost solely in response to the MAE period.

In all then, the experimental evidence points most strongly to the siting of awareness in the parietal lobe. Possibly the superior parietal lobe is not an essential component of awareness, as claimed in (Milner & Goodale, 1995), as the patient DF lost the ability to make actions (involving the superior parietal lobe) in a conscious manner on oriented objects, although was able to make the correct actions automatically. Such actions, however, can involve a 'motor' version of conscious experience, which is not usually regarded as consciousness. I will not overstep the experimental bounds if I conclude that at least the lateral parietal lobes are essential for awareness.

3. THE CHARACTERISTICS OF CONSCIOUSNESS

In this section I give a list of characteristics of neural activity that I consider essential for consciousness to be present in association with it, together with supporting evidence for my claim. This listing will help guide the process of model assessment and building. The characteristics that I regard crucial are as follows:

A. *Temporal duration.* Neural activity must be present for at least 200 msecs for awareness to arise. This notion is supported by the data of Libet (Libet et al., 1964) and by the duration of activity in buffer working memory sites, suggested by a number of workers as being the sites of creation of consciousness (Taylor, 1999).

B. *Competition for consciousness.* This characteristic is needed for a unique winner to occur and for disambiguation of the interpretations of inputs to be achieved (Taylor, 1996a). Competition for consciousness is related to the attentional characteristic listed next.

C *Attention.* Impressive evidence shows that awareness arises only of inputs which are being attended (Mack & Rock, 1998).

D. *Bodily inputs available.* Such inputs are needed to give a perspectival character to inputs, following detailed investigations by psychologists (Bermudez, Marcel & Eilan, 1995).

E. *Salience of inputs available.* Coded in the limbic system, salience is needed to give a suitable level of importance to a given input. This salience can arise, for example, from the cingulate cortex, as involving motivational activation. Salience is important for the attentional competitive process.

F. *Past experience.* This characteristic is to make use of previous relevant experience and arises initially from hippocampus. Evidence for such memory involvement is presented in Taylor (1999).

G. *Awareness of awareness.* Introspection is a separate facility from 'simple' awareness, in that it gives one the ability to be aware that one is actually being aware of a given input or of a thought (Rosenthal, 1986). This reflexive quality may be possessed by animals lower than ourselves, without language.

All these inputs are available, it would seem almost uniquely, for the lateral parietal lobes, except for that involved with G. Thus the buffer working-memory sites for space and time (and language) have been noted as being there (Paulesu et al., 1993; Salmon et al., 1996; Jonides & Smith, 1997; Coull & Nobre, 1998; Smith et al., 1998), as is a competition for consciousness associated with these sites (Taylor, 1996b). Attention involves a network of parietal, cingulate, and frontal modules (Corbetta et al., 1998; Nobre et al., 1997), but only the former are considered directly involved with awareness of inputs. Bodily inputs are also available there, as noted from effects of manipulation of the body in neglect, as well as from known neuroanatomy (connections with the vestibular apparatus and the cerebellum are well known). The limbic system is also well connected to the lateral parietal lobes (Stein, 1992) and so is episodic memory. For example, in rats, the parietal lobe has been shown to be the final resting place for memories built during step-down inhibition learning (Izquierda et al., 1997). The inputs to grant powers of introspection are not clear, and indeed the problem of how such a facility could be implemented neurally is very problematic. Leaving this difficult question aside for the moment will therefore be necessary, and assuming that it can be solved at a later stage; I will return to it in Sec. 8.

I conclude, modulo the question of implementing inputs for G, that the lateral parietal lobes are suitably connected and structured to satisfy all criteria A to F above. Given the site of the NCC, with a set of characteristics of consciousness delineated, of what is the neural activity composed? In other words, what is the flow of information in the cortex that leads to consciousness?

4. PAST MODELS OF CONSCIOUSNESS

Numerous models have been presented in the past to explain consciousness. The models are of a variety of types. A broad class of models uses a descriptive account, but with a limited relation to brain activity (Marcel & Bisiach, 1992); such models are of value to give a broad-brush approach to the problem. Another class attempts to delineate in a more detailed manner how the activity of the brain could give rise to consciousness (Taylor & Freeman, 1997). The former class is of value in giving general guidance to model-building; they can usefully inform the latter class as to what function brain structures are performing to achieve consciousness in the mind of their possessor. The latter class will be considered here in detail (although supported by general ideas from the former). These ideas give guidance to help build a model of consciousness that encompasses the experimental data presented on the siting of the NCC in Sec. 2, and containing the characteristics A to G of Sec. 3. To develop this topic, I will give a brief summary of some relevant models, and their relation to the comments made earlier, before using insights gained to develop further. The models I consider are as follows:

1. *Gray's Hippocampal Predictor* (Gray, 1995) suggests that the hippo-campus enables predictions to be made of future experiences, so creating consciousness. Various amnesic subjects, without hippocampus, still respond in a conscious manner in conversation, despite severe long-term memory deficits. Their conscious experience is compromised, however so supporting the presence of characteristic F in the previous section.

2. *Shallice's Supervisory Attentional System* (Shallice, 1988) assumes total control of neural activity by the frontal 'supervisory attentional system'; nevertheless, evidence for the NCC not being sited in the frontal lobes

was given in Sec. 2. Yet evidence for frontal involvement in endogenous attention is strong; I will later discuss such evidence in detail as part of the three-stage model (in Sec. 7). This also supports characteristic C above.

3. *Aleksander's MAGNUS* (1996) is based on a set of attractors, built by learning in a recurrent net in RAM-based hardware. Activation of an attractor is claimed to be the 'artificial consciousness' for the system of the related input. The criticism that no 'internal experience' is involved with long-duration attractor activity is strong, however; more generally, features D, E, F, and G above seem completely absent. But attractors are persistent neural states, so involve characteristic A above, and hence cannot be neglected.

4. *Baar's Global Workspace* (1988) regards consciousness as gaining access to a 'global workspace' (GW), after competition between input sensors. The GW is an incompletely defined concept, especially as it does not necessarily have features A to G explicitly involved in its activity. Identifying the GW with the Central Representation (to be developed in the next section) gives more precision, however, and allows much of the GW approach to be taken over into the present development.

5. *Crick & Koch's 40 Hz* (1990) That gamma-band oscillations are important for binding and segmenting is now well-established, both experimentally in the brain and by computation. Because such oscillations are observed in anaesthetised as well as in awake animals (Gray & Singer, 1987), however, such activity cannot be regarded as sufficient for consciousness. Yet, synchronised oscillations are strong candidates for binding low-level features, a process that will be found important in incorporating such features into consciousness (itself produced by activity coded at a much higher level).

6. *Pollen's Early Model* (1999) supposes that consciousness arises from feedback and relaxation to a fixed point of an attractor dynamics. Yet such re-entrance occurs at many levels in the brain, such as between LGN and VI. The activity in the LGN is not in consciousness, so indicating that the existence of such feedback is not sufficient for consciousness to be created. Attractors arising in neural dynamics do have their relevance to consciousness, however; as noted under item 3 above; they need extra features to emerge into it.

7. *Zeki's 'Local Homunculus'* (Moutoussis & Zeki, 1997) proposes that micro-consciousnesses arise in numerous early cortical areas. Not only does this proliferation of homunculi add to the difficulties of consciousness, it is contradicted by the experimental results presented in Sec. 2. But local processing is still important and must be properly incorporated in any further model of consciousness.

8. *Edeleman's Re-entrant Theory* (1989) is based on the special use of re-entrant circuits and so suffers from the difficulties of #6 above but is important for the ultimate creation of consciousness.

9. *Roll's Higher-Order Theory* (1997) uses language to enable higher-order thoughts of lower-order experienced inputs. The perspectival nature of experience is not considered, however, so leaving out the reason for the linguistic system to be able to comment "I feel that X". The approach is still incomplete, although the HOT approach must arise in any high-level conscious system. This approach will be discussed in more detail later (in Sec. 8).

10. *Harth's Inner Sketchpad Model* (1997) is based on the use of the re-entry of a global scalar quantity, the degree of overlap between the input and activation, to achieve hill-climbing or attractor relaxation. The model has the same defect as that of #6 above, being involved in much dynamical processing in the brain, but not just that specifically producing consciousness. The model is still relevant, in terms of the response to item #3.

11. *The Competitive Relational Mind Model* (Taylor, 1999). That a competitive process occurs in and between working memory sites for the emergence of consciousness is now becoming clear, but is still insufficient for the production of any HOT account of introspective awareness. Further circuitry is needed to build on this approach, as will be done later in Secs. 5 and 6, and extended to the three-stage model in Sec. 7 and to the HOT approach in Sec. 8.

All the above models contain several important features: (a) synchronisation and feedback/feedforward dynamics for binding low-level features into high-level concepts, (b) involvement of episodic memory to 'fill out' content, (c) attractor dynamics to build working memories with suitable temporal duration, as well as informational content, and (d) competitive processes between working-memory activations to provide attentional processing acting

as a filter on many interpretations of ambiguous inputs. All models still must be fleshed out and related to the further characteristics of Sec. 3 that have been left out: bodily input to give perspectivalness (D), salience (E), and introspection (G). The first two items can be added relatively easily, at least in principle: inputs from amygdala (for salience) and from proprioception/ vestibular apparatus (for bodily inputs). The last (item G) cannot, so again will be left until later. I will now develop a general neural representation that will allow these various features to be incorporated, and then construct a more specific model, extending feature integration theory (Triesman, 1988) to give the general representation more teeth.

5.   THE CENTRAL REPRESENTATION

I start from my discussion in the previous section to build a neural representation containing the information that is needed for consciousness to arise. In more detail, evidence from neglect studies, single cell activations in anaesthetised and awake animals, and brain imaging on healthy subjects was presented above to implicate the lateral parietal lobes (LPL) as playing an important role in controlling attention and awareness. Both attributes can occur in a range of possible frames of reference: neglect can be observed tied to an object or to a trunk-centred frame of reference or a variety of other reference frames (Milner, 1997). This diversity implies that the LPL is composed of a set of modules, each carrying information from the environment, as well as modulation by possible body input. Thus the LPL is eminently suited to carry what I term the "Central Representation", defined as follows:

> The central representation is the combined set of multimodal activations involved
> in fusing sensory activity, body positions, salience and intentionality for
> future planning; it involves an attentive competitive process between the
> various modules it contains to single one out to be conscious and be used for
> report to other working memory sites for further planning or action.

Several other important features of the central representation (CR) need discussion, in relation to the criteria of Sec. 3:

1)   The CR must have access to sensory input, such as in vision, coded at a
     high level. Thus, the CR must have good access to temporal lobe repre-

sentations to use the categorisation built there to guide action.

2) The CR also must have access to the bodily input that is needed to guide actions in terms of the intentionality coded for various sorts of actions: of the limbs, eyes, head or fingers, which are being discovered as coded in the superior parietal lobe (Kalaska et al., 1997). This intentionality must be furnished with the parameters of the objects on which the actions must be taken; thus, cerebellar and vestibular input also must be accessible to the central representation, as it is in the parietal lobes.

3) Salience of the inputs in the sensory field is an important attribute for the guidance of actions. This quality arises from limbic input that is already activated to provide saliencies of inputs from the orbitofrontal cortex by way of the cingulate and is compounded by activations in the retro-splenial (posterior cingulate) gyrus, encoded as parts of episodic memory (Izquierda et al., 1997; Mesulam, 1985, 1998). Such connections have been especially emphasised by Mesulam (1985), who wrote, in discussing the important limbic connections to the parietal lobe involved in neglect, that:

> However, the cingulate and retrosplenial projections are much more selective and may be related to more complex and learned aspects of motivation

Both this aspect and those noted under points (1) and (2) above support the lateral parietal lobe (LPL) as the site for the CR because the inferior parietal lobe has good connections to the temporal lobe, as well as to the lateral parietal lobe to body inputs.

1) Several modules are involved in the CR in the LPL; the total activity must undergo an overall competition, possibly aided by thalamo-nucleus reticularis processing. A simulation of such a model has been given earlier (Taylor & Alavi, 1995). The existence of such competition is supported by attentional deficits observed in subjects with pulvinar lesions (Posner et al., 1987).

2) Siting the emergence of awareness in the LPL, as the product of the attentive competition ongoing there, is supported by a simulation of the data of Libet and colleagues (1964). The simulation involved the creation of sensory experience (that of a gentle touch on the back of the patient's hand) by direct stimulation of the cortex in patients undergoing an operation for dyskinesia and related movement problems. In the

simulation (Taylor, 1996a), I used a simplified model of the cortico-thalamo-nucleus reticularis circuit that led to the observed dependence of the delay of awareness on the strength of the threshold current for experiencing the touch on the back of the patient's hand.

3) I suggested a similar competition (Taylor, 1996b) as occurring to explain the experimental results of subliminal effects on lexical decision response imes obtained by (Marcel, 1980). The experiment involved measurement of the reaction times of subjects to deciding if the first or third of three letter strings were words or not. Subliminal exposure to priming words occurred with the second letter string under one condition, with the presentation of polysemous words such as 'palm', on which the lexical decision had to be made to the third word. The prior exposure caused the decision to be speeded up or delayed in characteristic ways, according to the semantic relations of the three words to each other. The simulation was able to explain the results by means of a competition that is assumed to occur on the phonological store, aided and abetted by activations from a semantic memory store.

4) Various simulations of attention (Mozer & Sitton [1998] and references therein) have led to considerable success in explaining numerous psychophysical aspects (serial search times and pop-out, and so on). These explanations are supported by the identification of the competitive module as being in the parietal lobe, following the observations of (Corbetta et al., 1998; Nobre et al., 1997).

In conclusion, I site the CR in the LPL as the confluence of information on salience, episodic memory, high level coding of inputs, and information on body state. I claim that the content and extended temporal dynamics of activation of the CR, in parallel with synchronised feature-level activations in numerous other connected areas, that leads to consciousness of a given input or of a thought in the brain.

6. A MODEL OF THE EMERGENCE OF AWARENESS

The above discussion only lays out the bare bones of the central representation. To give it teeth, I will now put together a framework from

which to understand some of the dynamic processes that are involved in the emergence of awareness of an input. I will again consider here only visual inputs, although no reason exists in principle for why the framework does not also apply to other sensory modalities. I will start by considering how to modify the framework of the feature integration theory (Triesman, 1988) to include the unique role of the central representation. Feature integration is used here because it forms a useful model incorporating a considerable amount of psychophysical data on vision. Feature integration is used here as a plug-in model for the attentional component of the system.

The original model of feature integration assumed that an input was initially encoded on a set of feature maps (for separate colour, texture, motion, and so on) and its spatial position on a master 'spatial' map. An 'object file', acting as a temporary object representation, was also set up by the input on a separate module. This object file uses spatio-temporal coding, as well as other attributes (such as the name) of an object to give it identity. Attention drawn to a particular position on the master spatial map causes correlated activations at the same positions on the feature maps and integrates them together to bind with the activation in the object file.

I will extend the above model in terms of a modified version of the feature integration theory presented in Henderson (1994), which includes the manner in which information about objects is stored across saccades; it reduces the object files to having solely space-time co-ordinates. This theory agrees with the conclusions of Pashler (1998) on attentional selection: "selection by any criterion seems to be ultimately mediated by location selection."

Further information on semantic categories and object models are in quite separate modules in the ventral pathway. Henderson's modification was based on numerous psychophysical experiments to assess the level of storage of visual inputs, both across saccades and across short delays. The experiments that supported the extension of the feature integration theory used pairs of objects (letters, together with shape distractors), which were either shown at a central visual position within a single eye fixation, viewed across a saccade movement, or viewed at different retinal and spatial locations over time. Information about the objects was observed in subjects to be maintained over time both by episodic object representations (the 'object files') and by long-

term memory representations (the 'object models'). Neither representation was found to code specifically for sensory information, and as Henderson wrote, "Object files can be thought of as episodic object tokens that are individuated by spatio-temporal coordinates." Thus the master map of space and the object files are identified in the extended version (Henderson, 1994) of the feature integration theory.

The use I make here of this model is as follows. First, the spatial nature of the object files labels supports their being placed in the LPL as part of the central representation; involvement of parietal lobe in the process of feature integration had already been suggested in Triesman et al., (1990). Second, and more important, the placement of the spatial object files in the CR leads to the proposal that visual awareness arises in the object files map itself, which is through a competition taking place on the CR (Taylor, 1999). Third, the sensory components of the object files encoded in earlier visual processing stages are made accessible to awareness, we propose, through feedback coupling to the LPL.

The extension is given in Fig. 2, which contains amendments to Fig. 7 of Henderson (1994) in terms of identifying the object-files module with the central representation and the concomitant competition being carried out there. At the same time we have introduced salience and episodic memory inputs from the limbic system, following the comments of Mesulam (1985) mentioned earlier, and also an input from the superior parietal lobe to include possible intentionalities available to be made on the input. In terms of the original feature integration theory of (Triesman, 1988), this approach corresponds to siting the attentional control identically in the object file itself, and identifying them with the master map of locations. This map is placed in the LPL, but outside the superior parietal lobe, and thus is in either the medial or the inferior parietal lobes (denoted by I/MPL in Fig. 2), which in humans still consist of a considerable amount of cortex, although in non-human primates, this is reduced, and the homologue to the inferior parietal lobes (BA 39/40) may not exist (Milner, 1997). Thus, Fig. 2, has more relevance to the human than to the primate case.

We add that the further prefrontal and sensory area contributions to the model of Fig.2, beyond the feature integration theory (Triesman, 1988; Henderson, 1994) incorporate aspects from the early- and late-stage models

of the emergence of consciousness (Pollen, 1999; Crick & Koch, 1998). The various additional modules in Fig.2, beyond the central one of the CR, give the extra contents of consciousness. Thus, the process of the development of awareness of an object according to the above model occurs through the following stages:

1) early visual coding leads to activations of feature representations in V4, MT, and similar early visual areas in both the ventral (temporal lobe) and the dorsal (posterior parietal lobe) streams;

2) a set of possible intentions for motor actions on the objects of the visual scene is set up in the superior parietal lobe;

3) emotional salience and earlier relevant episodic memories associated with the inputs are activated in the limbic system, especially the cingulate and retrosplenial gyrus, by inputs being fed subcortically to the amygdala and hippocampus and so activating the limbic system preconsciously;
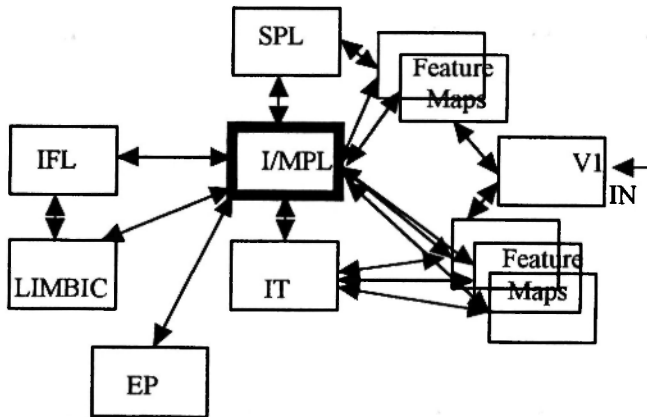

Fig. 2: The updated version of the feature integration theory including the central representation and other supporting modules. SPL=superior parietal lobe, as siting of intentionality; I/MPL-inferior and middle lateral parietal lobe, as siting of attentional controller and the NCC; IFL= inferior frontal lobe; IT= inferior temporal lobe siting of object models; EP = episodic memory components.

3) object models are also activated at a preconscious level in the temporal lobe on the basis of previously encoded categories;

4) attentional focus and awareness of the object at the centre of the fovea arises by the process of winning the competition between the various activations (object files) still present on I/MPL in the central representation, and those just created by new visual inputs that have just arrived. The object file activities consist of representations that are encoded in a spatial form, as is basic to the feature integration theory (Triesman, 1988; Henderson, 1994). The object file activities, together with features coded in earlier cortices, are bound to the spatial object file activity either by synchronisation or by attention or by both (Luck & Beach, 1998), as part of the competitive processing.

I conclude that the central representation is spatial, but previously mentioned evidence indicates that the visual component is not retinotopic. The various component modules of the central representation are thus expected to have a spatial encoding of sensory inputs, modulated by body inputs in the manner discussed earlier. Thus a set of spatial maps is in the central representation for various sensory inputs. I show in Fig.3, in schematic form, the resulting set of spatial maps for vision, audition and somatosensation.
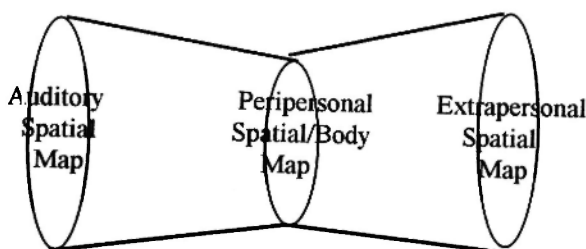

Fig. 3: The set of spatial maps as part of the central representation. The peripersonal map involves kinetic/visual neurons; that of extra-personal space is of the usual visual field in trunk-oriented co-ordinates. Finally the auditory spatial map is correlated with the extrapersonal map.

The intersection regions correspond to the representation of peripersonal space (that around the body). Very few distinct modules may be present in the central representation: it may even consist of only one such overall, with all the spatial maps fusing into a continuous one, or being several such maps but in register (as for the relation between the extra-personal visual map and the auditory one). Such a restricted number of modules will enable the attentional competition to be run more swiftly and efficiently.

7. THE THREE-STAGE MODEL

So far, the discussion has not led to any reflexive characteristic of consciousness, with no intimations of self. I noted in Sec. 3 that the facility G of introspection has no clear neural mechanism, so that such a lacuna is to be expected. I have several times had to duck the issue of self and self consciousness, always leaving that 'until a later section'. That point has now been reached, and the buck stops here. To proceed, I will turn to the three-stage model of (Taylor, 1999; Taylor et al., 1998). This model was based on the further decomposition of mental states into separate nonconscious, phenomenally conscious, and introspective/thinking conscious components. The second of these I denoted in (Taylor, 1999) as 'passive' consciousness, the third as 'active' consciousness. The nonconscious part involves preprocessing activity in various modalities, and activation of object and automatic action-based responses. By the passive component of consciousness is meant that which is involved with buffer/slave working memory activity, sited in posterior parietal cortex; this activity decays away over a second or so unless actively refreshed by the so-called executive component (Baddeley, 1986). By the active component of consciousness, I meant the thinking, imagining, self-realising part. The frontal lobes are predominantly the neural substrate of the active component of consciousness, and achieve control of attention, rehearsal of buffered posterior working memory activity, as well as transformations of other neural activities to desired forms (such as in rotating of mentally held images) (Carpenter et al., 1999). The nature of the three stage model is shown in Fig.4.
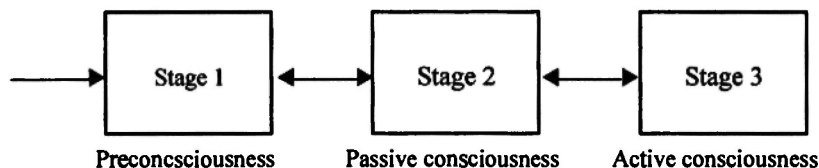
Fig. 4:   The three stage model of awareness. Stage 1 involves preprocessing and automatic neural activity, phenomenal consciousness occurs of stage 2 activity, while there is active (thinking, introspective) awareness of stage 3 activity.

I hoped, by such a division of consciousness, to get a handle on the self and introspection. To see whether that approach is justified, the two strong claims that I made in the previous paragraph about this division of consciousness have to be probed. These claims were:

1)   the validity of the three-stage model of mental processing: mental states divide into three sorts: nonconscious, passively conscious, and actively conscious;

2)   the siting of these three components are effectively in three different, but overlapping, networks of modules in the cortex supporting nonconscious, passive, and active consciousness respectively.

The purpose of the next part of this section is to analyse and criticise the second of these two claims; the first will be discussed in Sec. 8. For the moment, active and passive consciousness are taken to mean, respectively, informally phenomenal/sensory and thinking/introspective consciousness. In the former, no sense of self-involvement occurs; in the latter, self is known and experienced as such by the conscious subject.

To begin, let me consider the partition of cortical sites supporting the relevant activities associated with passive and active consciousness. Where are these sites located, and in particular are they different? I will justify the differentiation of the NCC into one part involved with passive and one with active consciousness: as a first approximation, I will posit that the active/ passive subdivision of consciousness corresponds to the anterior/posterior division of the cortex. I will later expand that concept to concentrate more precisely on the NCC in the LPL. It will be there that difference must occur between sitings of these two forms of consciousness and that the crucial component of the NCC involved with introspection will be discovered.

I justify the claim that the anterior/posterior division of the NCC is related to the active/passive decomposition of consciousness by marshalling the available evidence. This relation arises by looking at the different activations across the brain that are brought about by tasks of increasing complexity. Such increased task complexity I identify with an increase in the 'active' conscious component of mental processing. As load increases in working memory tasks, such as by increasing the length of time for holding information, or of its complexity, the frontal system becomes activated and even has an inhibitory effect on posterior sites. The evidence for this phenomenon is now impressive.

Several different paradigms have been used to study frontal function. One example is the n-back test for working memory, in which a subject must report any symbol that occurred n times ago in a repeatedly updated sequence of such images (updated every 10 seconds) visible to them (Cohen et al., 1997; Braver et al., 1997). The dependence of activation on the length of time that a subject must hold putative targets in working memory is dramatic, with a sudden increase as n increases to two, especially in a number of prefrontal regions (BA8/6, 46/9, 44, 44/6, insula, 6), with associated increase posteriorly in the supramarginal gyrus (BA40). A corresponding decrease in activation also occurs in several auditory and visual posterior regions, as well as in several mainly midline prefrontal regions.

This division of labour between front and back of the cortex into short-term perception and long-term duration was replicated by a further study of the 2-back paradigm (Awh et al., 1996). The authors concluded that

> The specific brain regions activated by storage and rehearsal are consistent
> with clinical and neuroimaging evidence implicating posterior parietal regions
> in storage and anterior speech mechanisms in rehearsal.

in other words, dissociation in front versus back, with experience being separated into active (rehearsal) versus passive (storage).

Another paradigm with similar results is that of location versus face matching over several seconds (Haxby et al., 1994). This model has shown that the prefrontal cortex has domain specificity for working memory organisation, with more dorsal sites involved in spatial representations and more ventral involved with object representations. In brain-imaging results, posterior sites were found to be negatively correlated with increased rCBF

over increasing delay periods, as compared with the frontal sites with an increase of rCBF signal. The conclusion from this and related studies (Haxby et al., 1995) was (Ungerleider et al., 1998), "Thus, prefrontal regions likely play a more important role in the maintenance of a representation during working memory."

The front/back division of NCC is supported by the recent discovery of two separate networks that are involved in the motion after-effect (MAE) mentioned in Sec. 2: a posterior one, involving early visual areas and MT, and an anterior one, which appears to be involved at different times and to be performing quite different parts of the total task (Schmitz et al., 1998a, 1998b). The time series for the group-averaged signal from MT and one from BA40 are shown in Fig. 5.

The difference between the two signals is clear: the signal for MT follows the periods of motion, with a slightly longer period of BOLD signal after the motion-down period, so demonstrating the motion-after-effect signal (of about 9 seconds, agreeing with the psychophysically determined signal that is determined outside the scanner). The signal from BA40 is quite different, arising only strictly in the MAE period after the motion-down period. This differentiation between brain regions is supported by analysis of the correlation matrix between the various active areas, which breaks down into two separate submatrices when correlations less than 0.4 are dropped, as shown in Fig.1.

The decomposition of Fig.1 is in agreement with the differences between the shapes of the time series seen in Fig.5; the two regions have very different temporal response during the total experiment. The decomposition is consistent with the results interpreting the posterior network (comprising extra-striate cortex, including MT) as passively pre-processing the signals, and the anterior net as actively checking for the MAE effect, as well as supporting its experience.

The anterior/posterior NCC and active/passive functional division is also supported by the existence of very different temporal features of single cells in frontal as compared with posterior sites (Fuster, 1995; Goldman-Rakic, 1996). The frontal cells are able to continue relevant activity over many seconds, as part of a monkey performing a delayed task.

It is relevant to consider other parts of the neural architecture of the brain to determine how a given region can support the function of consciousness
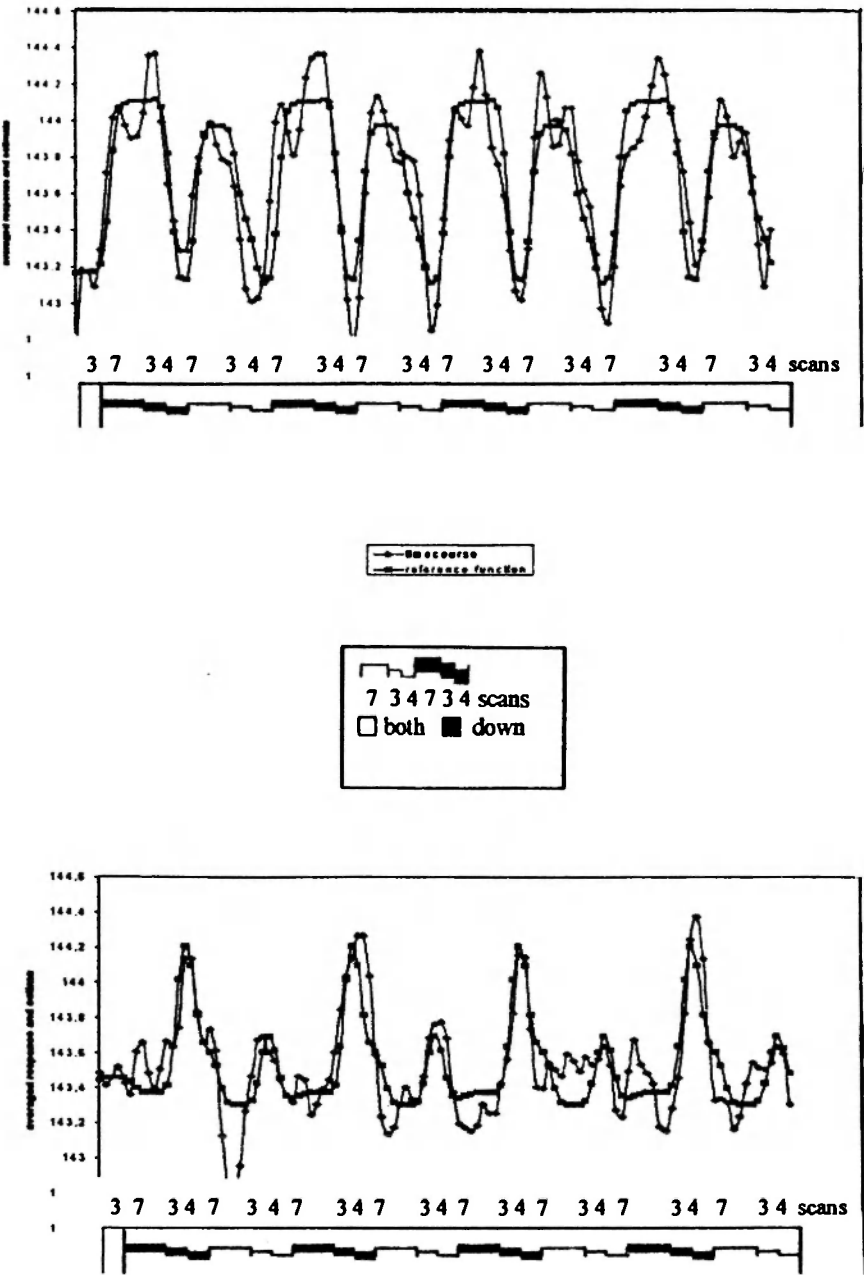
Fig. 5:   Time series of MAE from group study for MT and BA40.

assigned to it. An important difference occurs between the frontal cortex, with its supporting basal ganglia and thalamus giving closed loops of recurrent activity (Alexander et al., 1986), and the relative absence of such neural architecture in the posterior cortex. This difference is known to be at the root of motor effects in Parkinson's disease, as well as related to the frontal lobe deficits mentioned earlier. Such a difference can help in understanding the division of labour of the cortex into areas able to be 'active' in holding and refreshing neural activity and those only passively keeping it going by suitable but limited recurrence (either cortically or sub-cortically based). This division is precisely that of working memory into 'slave' systems and the central executive of Baddeley (1986), supported by the brain imaging evidence (the n-back, MAE, and delayed matching experiments) reported earlier.

Finally, an fMRI study has been made that is supportive of the front/back decomposition (Laureys et al., 1998). This study concerned a patient in a transient vegetative state, brought about by carbon monoxide poisoning. The patient was found by PET imaging during the vegetative state (as compared with after full recovery to consciousness) to have reduced activity, especially in the left and right inferior and superior parietal lobules, as well as in the superior and middle frontal gyri.

Nevertheless, my identification of the division of the NCC into anterior and posterior cortical sites, with the correlated subdivision of consciousness into a phenomenal or passive form and an introspective or active form, is correct but may not be the only way to gain understanding of the internal nature of consciousness. Indeed such an anterior/posterior subdivision of the NCC is apparently contrary to the siting of consciousness itself in the parietal lobes, as deduced from experimental data in Sec. 3 and developed into the central representation in Sees. 5 and 6. How can there be any active consciousness if is not sited in the CR in the lateral parietal lobes? My purpose in the remainder of this section is to reconcile this framework with the three-stage model.

The brain imaging experiments, which I mentioned above to support the anterior/posterior division of cortex along the active/passive divisions of consciousness, are correct only if parietal cortical involvement is included in both parts. This limitation was already noted in quotes from the n-back experiments and is clear also in the MAE results and in the face matching

results. Finally, a quote from the vegetative state analysis (Laureys et al., 1998) explicitly notes the differential involvement of parietal along with frontal cortex between the vegetative and aware states. The conclusion of the study was that there is a "...critical role for polymodal associative cortices, especially in the posterior cerebral cortex" for consciousness. Thus, certain components of the parietal lobes are involved in active consciousness. Further evidence for this involvement is available from other recent brain imaging experiments, to which I now turn.

One such experiment required the subjects to respond to a go/no-go paradigm (Konishi et al., 1999). Whilst lying in the bore of a 1.5 Tessla Siemens magnet in an fMRI test, the subjects viewed a fixation cross on which would appear a green or a red square for 0.5 seconds; they were to respond to the green square by pressing a response button, to the red square with no such press. An event-related method could be used to separate those brain regions active during inhibition of the go response in the no-go situation from the positive responses in the go case. The subjects were asked to put themselves into a set corresponding to responding to the go trials as rapidly as possible, thereby increasing the inhibition needed to stop this response in the no-go trials. The most active sites during the no-go responses were in the right inferior frontal sulcus, almost identically situated to that observed during set change in the Wisconsin Card Sorting test (Konishi et al., 1998). This result supports the anterior/posterior and active/passive cortical divisions of the NCC. More relevant to the present discussion is the significant activation of the left supramarginal gyrus in the parietal lobe observed during the go condition (Konishi et al., 1999). This activation can be related to the central representation in terms of the likely strategy being used by the subjects striving to respond as rapidly as possible: they constantly monitor for a green square and respond when it appears; anything else is ignored. But this strategy implies that the subjects only become aware they are experiencing the input for the go response. In other words, only the go signal reaches active (introspective) consciousness, and this signal is correlated with activation of the left inferior parietal lobe.

Another result supporting the involvement of the parietal lobes in active consciousness has stemmed from a study of binocular rivalry (Lumer and Rees, 1999). Subjects were scanned in an fMRI experiment during the

binocular presentation to the separate eyes of a grating and a face. The change of activity during the alternation of the visual percept that they were experiencing was detected by correlating the activity between various regions. In particular, a network of areas was discerned, involving extra-striate areas, as well as others lying outside the classically defined visual regions. The subjects noted of these regions,

> ...they were located bilaterally in the superior and inferior parietal cortex (with a right hemisphere dominance) and in the right superior frontal cortex, middle frontal gyrus, inferior frontal gyrus, and insula.

Here again the parietal lobes are involved with the experience of a shift of percept from one to the other of the pair of binocularily presented images.

The data in Taylor et al. (1998), and on which Fig.4 was based, also support the involvement of posterior sites in the creation of active consciousness. The paradigm involved subjects listening to an auditory stream of syllables pa/ta/da/... while lying in the bore of a 1.5 T magnet. They heard the syllables under three different levels of attention:

1) inattention, when they had to perform another distracting task (detect the fusion frequency of flickering light observed through goggles);

2) passive listening, when they had no task to perform; and

3) directed attention, requiring them to count the number of times they heard the syllable 'ta'.

Further regions were activated successively under the three different conditions. The new regions brought on stream under condition (3), compared with (2), involved both anterior and posterior sites: bilateral inferior frontal gyrus, as well as the superior temporal gyrus and adjacent parietal lobe. Again an intermingling of anterior and posterior modules supports the third stage experience.

I conclude that active consciousness requires a network involving both posterior and anterior sites: the central representation is involved in both the passive and the active components of consciousness. Active consciousness involves the frontal components more preponderantly than does its passive companion. Both divisions involve parietal sites, which must next be further subdivided to support the division of consciousness into its separate active and passive components. Nevertheless, the functional nature of this subdvision needs to be analysed. I turn to that next.

8.   THE INNER CONTENT OF CONSCIOUSNESS

The problem of the subjective nature of conscious experience, the answer to the question "what is it like to be a bat?" of Nagel (1974), has not yet begun to be addressed. At the same time, the attempted division of consciousness into a passive and active component needs a different slant. The problem of the detailed enumeration of the components of consciousness is very hard. But relating the active/passive division to one based on higher order thoughts is possible (Rosenthal, 1986). This approach separates mental states into nonconscious ones, those which involve thoughts about the nonconscious states, thereby making them conscious, and higher order thoughts still about the second-order thoughts. Thus there is proposed the sequence

$$MS_1 \leftrightarrow HOT_2 \leftrightarrow HOT_3$$

where MS_1 denotes a general mental (nonconscious) state; HOT_2 a second-order thought about that state; and HOT_3 a third order thought that one is thinking about the second-order thought. The two-sided arrow indicates communication in both directions, although the detailed nature of this communication and the definition of mental states or thoughts, is not specified in much detail. There can also be even higher-order thoughts still about the next lower-order thoughts. It is proposed (Rosenthal, 1986),

> that it is natural to identify a mental state's being conscious with one's having a roughly contemporaneous thought that one is in that mental state.

Moreover

> ...that second-order thought would itself be a conscious thought only if one also had a third-order thought that one had the second order thought.

Thus, the consciousness of the mental state arises from having the second-order thought about it. Introspective consciousness itself comes from a third-order thought about the second-order one. This division has close similarity to the division of consciousness into active and passive that I gave above and developed in (Taylor, 1999). This division is also related to the division of consciousness into 'phenomenal' and 'access' in (Block, 1995), which, however, has been strongly criticised by Rosenthal (1991) and will not be

considered here further from lack of space. The HOT division appears to be different to the passive/active one I gave above, being a respective separation into solely non-introspective and introspective components of consciousness; these components correspond to second-order and to third-order thoughts respectively. On the other hand some active conscious experiences, such as hard thinking about an intellectually demanding problem, may possess a only low level of introspection, so would correspond to a second-order thought according to this division of consciousness. Yet, the presence or absence of introspective features in experience is basic to answering the "how it is like to be" question and gets to the nub of the inner experience most crucially. I will use this phenomenal/introspective division as more basic for the purposes of this section: to explore the inner content of consciousness, the 'what it is like to be' features. Thus introspective thoughts are to be considered as a special case of active consciousness; the sitings of neural activations for the latter are relevant but will now be restricted to tasks involving a strong introspective component.

I will identify provisionally the concepts of 'mental states' and 'thoughts' in terms of specific cortical activity; I propose the following tentative identities (modulo many caveats):

(Id1) MS ≡ Nonconscious activity up to category/higher-order feature level
(Id2) HOT ≡ working memory activity

Identity Id1 is relatively acceptable because the mental state MS has been assumed to be nonconscious. The identification Id2 is also acceptable as identifying a 'thought' as based on report. The results of brain imaging on working memory tasks given above indicate that the working memory sites observed also include frontal sites, such as Broca's area, that are known to be involved in subvocal speech.

My identifications Id1 and Id2 lead to the following problem: at least two different sites of activation must be in the central representation associated with the two levels of thought, those at second order and those at third order. Thus, to justify the separation of consciousness into two forms, nonintrospective and introspective, following the higher-order thought approach, subdividing the central representation into two parts is necessary. One part would create nonintrospective consciousness, and the other the introspective variety. The first part would involve working-memory activities,

based directly on sensory input (or that from frontal cortex), that are involved in the CR discussed earlier in Sees. 4 and 5. This approach would lead to phenomenal consciousness or thoughts at conscious level. The second part would consist of a further working-memory site solely dedicated to attentional processing on inputs from the first working-memory system, together with inputs from frontal sites containing information on the self (mainly in mesial frontal cortex, observed through deficits), though still with attendant lower level bound posterior activity.

Such a subdivision is tentatively supported by the brain imaging results reported above. Thus, inferior parietal lobe sites are activated in the go/no-go paradigm, the binocular rivalry and the motion after-effect experiments. All involve subjects introspecting their experience for report (in the case of binocular rivalry, only the shift from one concept to another, without report, should be enough to cause introspection). On the other hand, there are the other parts of the parietal lobes, the superior parietal lobes and the intraparietal sulcus, whose destruction can cause loss of awareness, such as in extinction, and which are activated in more general working memory and attentional processing tasks. Thus, preliminary evidence suggests the required separation of function in the central representation; much more needs to be done, however.

9. SUMMARY

In summary, the LPL is the essential site in the brain for consciousness. I emphasised the crucial feature of the central representation, based there, in comparison with the feature-integration theories (Triesman, 1988; Henderson, 1994): *the object file module has been fused with both the master map of spatial locations and the attentional module.* Awareness of an input arises by its representation on the object file (attentional map/central representation) winning the competition there. This effect leads in general to identification of initial awareness of an input with its 'token', as a specific object, not its 'type' or category. The identification of the type of an input will be expected to take longer, as there has to be conjoint activation of the object model module with the central representation, and then resulting activation of the relevant

working memory, such as the phonological store for verbal report. Similar object-specific coupling to the sensory feature maps must also be enhanced. The differences in the speeds of processing to awareness for the different codes for vision mentioned earlier (Moutoussis & Zeki, 1997) may involve different access times to different codes.

A second conclusion, allowing for further analysis of the central representation, is that it must split into two components. One involves lower (second)-order thoughts, corresponding to the initial buffer working-memory activities creating phenomenal consciousness of the related nonconscious representations (to which they are bound and which give the content of consciousness). A second component of the central representation is activated when introspection occurs and is very likely sited in the inferior parietal lobes; this component will be expected to have frontal activity bound to it to give the self content associated with past experiences. It is through this component that exploring the answer to the 'how it is like to be' question is possible.

The final conclusion of the approach presented here is that awareness occurs in each sensory modality in a spatial manner. Specific features (colour, shape, etc) or categories of input are not part of direct awareness, but are involved in response to the category names of perception. These activities are suitably bound to the winning working memory activations, thereby guiding consciousness in its further processing. At the base of it, however, consciousness is purely spatial and temporal.

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