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THE NEUROANATOMY OF CONSCIOUSNESS AND THE ZOMBIE-WITHIN

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Abstract:

In Chapter 3 of their book, Milner & Goodale (1995) concede that, since the ventral and dorsal streams as defined by Ungerleider & Mishkin (1982) bifurcate "downstream" of the striate cortex (V1), neither stream can account for the visual functions which survive lesions of V1 ("blindsight"). However, on their Figure 3.1 (p. 68) they show another pathway which I call the 'Sub-Cortical (S-C) to dorsal pathway' (SUPERIOR COLLICULUS, PULVINAR, POSTERIOR PARIETAL CORTEX) which bifurcates from the ventral pathway (LATERAL GENICULATE NUCLEUS, V1-V5, INFERO-TEMPORAL CORTEX) at the retina. Not only does the S-C to dorsal pathway explain blindsight. It also coincides exactly with Michael Posner's (Posner & Petersen 1990; Posner and Dehaene 1994) "posterior attention system". This allows us to identify the superior colliculus and pulvinar with that part of the "zombie-within" (Place 1997) which involuntarily attracts the focus of conscious attention to any input which it identifies as problematic and the posterior parietal cortex as the structure which, in addition to its role in the feedback control of voluntary movement, maintains voluntary control over the focus of conscious attention (in the ventral stream in the case of vision) until a satisfactory categorization of the input is achieved. This, when combined with the known functions of the ventral pathway, allows us, in the case of vision, to identify actual anatomically defined structures corresponding to most of the functionally defined modules envisaged in 'Consciousness and the zombie-within' (Place 1997) up to the point where conscious experience gives way to categorization.

1. Consciousness and its Functions

In the paper (Place, 1997) which I presented at last year's inaugural conference at Claremont, I described two parallel, but complementary and continuously interacting input-to-output transformation systems in the brain which I referred to respectively as 'consciousness' and 'the unconscious automatic pilot' or 'zombie-within'. On this hypothesis, *consciousness* has four sequentially ordered functions:

- (1) to *categorize* on the basis of what Broadbent (1971) calls the "evidence" and which I equate with conscious experience any input that is identified by the zombie-within as *problematic*, in that it is either *unexpected* or *motivationally significant*, i.e., significant relative to the individual's current or perennial motivational concerns,
- (2) to *react emotionally* to inputs which have been identified as problematic, both before ("physical" pleasure/pain) and after they have been categorized ("mental" pleasure/pain), thereby ensuring that the subsequent processes of response-selection and response-execution are brought into an adaptive relation to the individual's current and perennial motivational concerns,
- (3) to *select a response* appropriate both to the presence of a thing of that kind and to the individual's motivational concerns with respect to it, and
- (4) to initiate and monitor the *execution* of the response selected.

Although much of what goes on within consciousness in this sense is unconscious in so far as human subjects cannot give a running commentary on what is happening, as they can in the case of their conscious experiences, the crucial central role that conscious experience plays in the processing of problematic inputs justifies, I maintain, both the extension of the term consciousness to cover the whole system whereby such inputs are processed, and the identification of that process with the activity of the whole of the cerebral cortex in mammals. In order to provide the "evidence" on which the

subsequent functions of categorization, emotional reaction, response-selection and response-execution, are based consciousness must have available to it a much detailed and a much more comprehensively analysed body of input information than is required by the zombie. This is provided by the various sensory projection areas in the cerebral cortex and the adjacent “association areas” (V1-V5 in the case of vision). Moreover, because of the large number of alternatives that need to be assessed in making sense of and adapting to novel and otherwise problematic inputs, consciousness *qua* problematic input processor has to be what Broadbent (1958) calls a “limited capacity channel” (LCC) access to which is controlled by the process of *selective attention*. Recent research by Hal Pashler (1991; 1997) has shown that there is not just one LCC, as Broadbent thought, dealing with the categorization of inputs, but at least two others, one dealing with response-selection and another dealing with response-execution.¹

2. The Unconscious ‘Automatic Pilot’ or ‘Zombie-within’

The functions of the *unconscious automatic pilot* or *zombie-within* are

- (1) to continuously *scan* the total current input so as to alert consciousness to any input it identifies as *problematic*,
- (2) to *protect consciousness from overload* either by ignoring those non-problematic inputs which require no response or by responding appropriately, but automatically and *without categorization*, to those for which there already exists a well practised skill or other ‘instinctive’ response pattern.

These functions of the zombie-within are performed entirely unconsciously and, I assume, are mediated entirely by structures in the midbrain. Like its namesake in popular mythology, the zombie-within is a creature of habit, routine and unquestioning conformity to the instructions it receives from consciousness. Anything out of the ordinary is immediately passed on for processing by consciousness. The one respect in which it differs from the traditional picture of its mythical namesake is in its capacity to learn from experience, limited though that is to the progressive shaping of minor variations in behaviour by their immediate consequences. The detailed analysis of sensory input made available to consciousness by the sensory projection and association areas of the cortex is not available to and is not needed by the zombie. Nevertheless, many of the reactions it controls are highly adaptive and have the appearance of having been intelligently thought out. This is due partly to the fact that they were “thought out” in consciousness before they became habitual, and partly to the automatic shaping of behaviour by its consequences after conscious intervention has ceased.

3. The Layout of Consciousness and the Zombie-within

The multiple functions identified within both consciousness and the zombie-within imply a multiplicity of modules within both systems. Figure 1, which I was only able to show in its manuscript form last year shows the arrangement of these modules as I currently construe it. As you will see, it shows the output from the sense organs splitting into two streams, *consciousness* on the left, the *zombie* on the right. The zombie is shown as consisting of four functionally defined modules:

- (1) the *PROBLEMATIC INPUT DETECTOR (PID)* which separates inputs into problematic and non-problematic on the basis of relatively coarse criteria of unexpected/expected and motivationally significant/insignificant, and transmits the former *via*

¹ There is reason to think that in the human brain there are two more limited capacity channels, one which selects the name assigned to the concept or category in question by the natural language spoken by the individual concerned and another which constructs a syntactically articulated sentence appropriate to the ‘thought’ which emerges from a further stage in the categorization process.

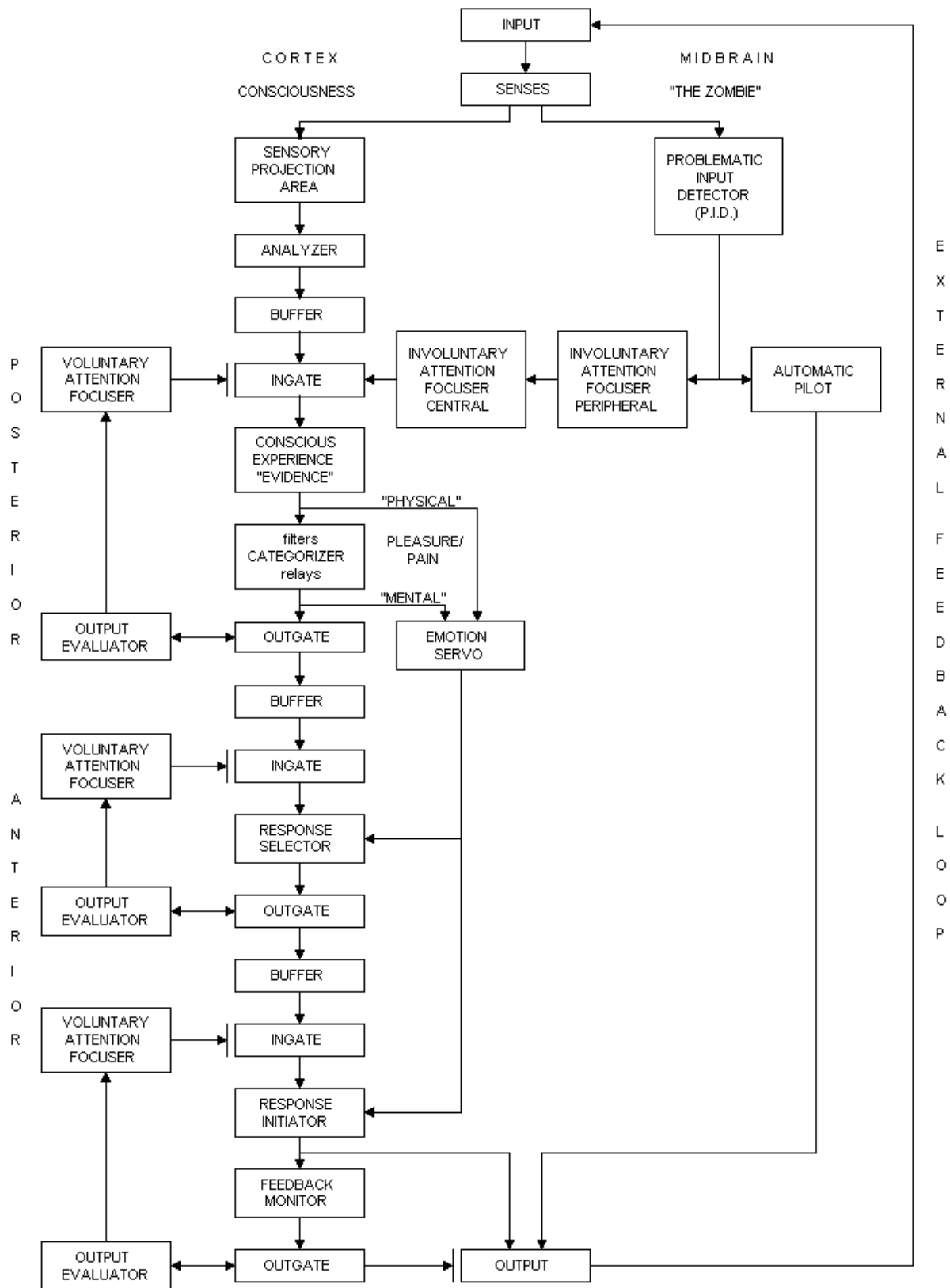


Figure 1: Consciousness and the Zombie-within - Suggested Layout of Modules

- (2) the *INVOLUNTARY ATTENTION-FOCUSER (PERIPHERAL)* which mobilises and directs movements of the head eyes and body so as to bring the *source* of the problematic input within the range of all relevant sense organs, and
- (3) the *INVOLUNTARY ATTENTION-FOCUSER (CENTRAL)* which attracts the focus of *conscious experience* to that part of the sensorium where the problematic input is located, while either ignoring or routing non-problematic inputs to output *via*
- (4) the *AUTOMATIC PILOT*.

Consciousness consists of the *SENSORY PROJECTION AREA* and *ANALYZER* which between them assemble the "evidence" on the basis of which categorization of the input will be based, three sequentially ordered limited capacity channels (LCCs), concerned respectively with *input-categorization (perception)* (consisting of *CONSCIOUS EXPERIENCE/"EVIDENCE"* and the *CATEGORIZER*), *RESPONSE-SELECTION* and *response-execution* (consisting of the *RESPONSE INITIATOR* and *FEEDBACK CONTROL*). In order to protect it from overloading, Broadbent's model requires that each of these LCCs be provided with a system of subordinate modules, including

- (a) an *INGATE* which controls access to the LCC,
- (b) a *BUFFER* or short term memory store in which inputs waiting to obtain access to the LCC are held until the ingate clears,
- (c) a *VOLUNTARY ATTENTION-FOCUSER* which maintains the focus of attention on the task in hand until it is satisfactorily completed, and
- (d) an *OUTPUT EVALUATOR* which checks the candidate outputs of the LCC and allows the attention-focuser to open the ingate to a new input once the previous information processing task has been satisfactorily completed, while at the same time opening
- (e) an *OUTGATE* which allows the approved output schema to proceed either directly to the initiation of a response or into the buffer of the next LCC in line.

Lying outside this system of three limited capacity channels, but interacting with it, is the *EMOTION SERVO*. The *emotion servo* is brought into play by the action of the input-categorization LCC. This activation occurs both before categorization in response to "raw" uninterpreted conscious experience, as in the case of "physical" pleasure and pain, and after categorization, as in the case of "mental" pleasure and pain. Its function is to provide motivation both for response-selection and for response-execution.

4. Locating these Modules within the Brain - The Ventral and Dorsal Pathways

I was first alerted to the possibility of mapping the modules laid out on Figure 1 with specific anatomically defined structures within the brain by seeing Figure 2 which is reproduced from Milner and Goodale's (1995) book *The Visual Brain in Action* (Figure 3.1, p. 68) when it was shown by Mel Goodale in the course of his talk at Claremont last year. As most of you know, recent neuropsychological research on visual agnosias of which Milner and Goodale's book is the culmination has drawn attention to the functional significance of an anatomically identified bifurcation within the brain between two "streams", the *ventral* stream and the *dorsal* stream. As originally defined by Ungerleider and Mishkin (1982) and as illustrated on Figure 2, these two streams bifurcate downstream of the striate or primary visual cortex (V1). The ventral stream travels *via* the extra-striate visual areas (V2-V5) to the *infero-temporal cortex*. The dorsal stream travels upwards to "terminate" in the *posterior parietal cortex*. In other words, the bifurcation between the two streams lies entirely within the cerebral cortex.

Studies of the behaviour of patients with lesions restricted to one or other of these two streams show that lesions of the ventral stream result, depending on the site and extent of the lesion, in a variety of functional disorders involving the loss or disturbance of visual conscious experience associated with a loss or disturbance of the ability to recognise objects and the situations in which they occur, conditions

such as *prosopagnosia* (loss of the ability to recognise faces) and *simultanagnosia* (loss of the ability to recognise the relations between multiple objects in a visually presented scene). Lesions of the dorsal stream result in disturbances of the visual control of voluntary movement.

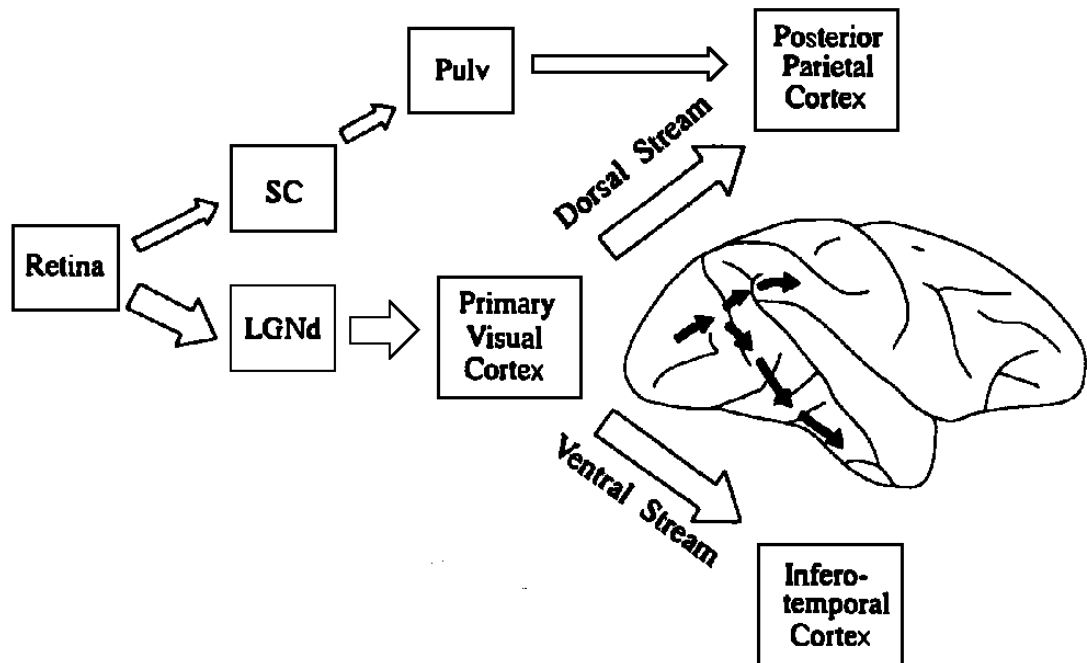


Figure 2: The Ventral and Dorsal Streams (After Milner & Goodale, 1995, Figure 3.1, p. 68)

As Milner and Goodale (*op.cit.*, p. 67) concede, since the two streams bifurcate downstream of the striate cortex (V1), they cannot be invoked to explain the phenomena of 'blindsight', i.e., the visual functions that survive lesions of V1. What is needed to explain *that* is a pathway leading from the retina which by-passes V1 and leads to the posterior parietal cortex where the characteristic movements of reaching for an unseen object are generated and controlled. Just such a pathway is shown in the upper part of Figure 2. I call this pathway the "*Sub-Cortical (S-C) to Dorsal² pathway*". For although it is shown for convenience on Figure 2 above both the dorsal *and* ventral streams properly so-called, in fact, until it reaches its "destination" in the posterior parietal cortex, it is composed of structures (the *superior colliculus* and *pulvinar*) which lie *below* the cortex in the midbrain and thus below both dorsal *and* ventral streams.

As is apparent from Figure 2, identifying the S-C to Dorsal pathway gives us a second pair of visual pathways with the same "destinations" as the dorsal and ventral streams (the posterior parietal and infero-temporal cortices respectively), but bifurcating *at the retina* rather than downstream of the primary visual cortex (V1). Balancing the S-C to Dorsal pathway is what we may call the "*ventral pathway*" (to distinguish it from the ventral stream which forms part of it) consisting of the *lateral geniculate nucleus*, the *primary visual cortex* (V1), the *ventral stream* (V2-V5) and the *infero-temporal cortex*. The two pathways so-defined differ in two respects:

- Whereas, apart from the lateral geniculate nucleus, all the structures composing the ventral pathway are in the cortex, all the structures composing the S-C to Dorsal pathway, apart from its final "destination", the posterior parietal cortex, are sub-cortical.

² "Dorsal" here only in the sense that, like the dorsal stream properly so-called, it "terminates" in the posterior parietal cortex.

- Unlike the ventral pathway all of whose component structures apart from its "destination", the infero-temporal cortex, are concerned only with the processing of *visual* information, all the structures composing the S-C to Dorsal pathway without exception process information from all sensory modalities.

In addition to the function which it shares with the intra-cortical dorsal stream of mediating the visual control of voluntary movement, Michael Posner (Posner & Petersen, 1990; Posner & Dehaene, 1994) has shown that the S-C to Dorsal pathway also has an important role in the control of selective attention, constituting, as it does, Posner's (Posner & Dehaene, *op.cit.*, p. 76) "posterior attention system (posterior parietal cortex, pulvinar and superior colliculus)". This concatenation of evidence allows us, in the case of the visual modality, to identify the bifurcation between consciousness and the zombie-within as shown on Figure 1 with the bifurcation at the retina between a *ventral* pathway consisting of the *lateral geniculate nucleus*, the *primary visual* or *striate cortex* (V1), the *extra-striate visual areas* (V2-V5) and the *infero-temporal cortex* corresponding to the upstream portion of what I am calling "consciousness", and the *S-C to Dorsal pathway* consisting of the *superior colliculus*, *pulvinar* and, more doubtfully in view of its cortical location, the *posterior parietal cortex* corresponding to the zombie. These relationships are shown Figure 3 in similar format to that of the upper part of Figure 1 with the ventral pathway on the left and the S-C to Dorsal pathway on the right.

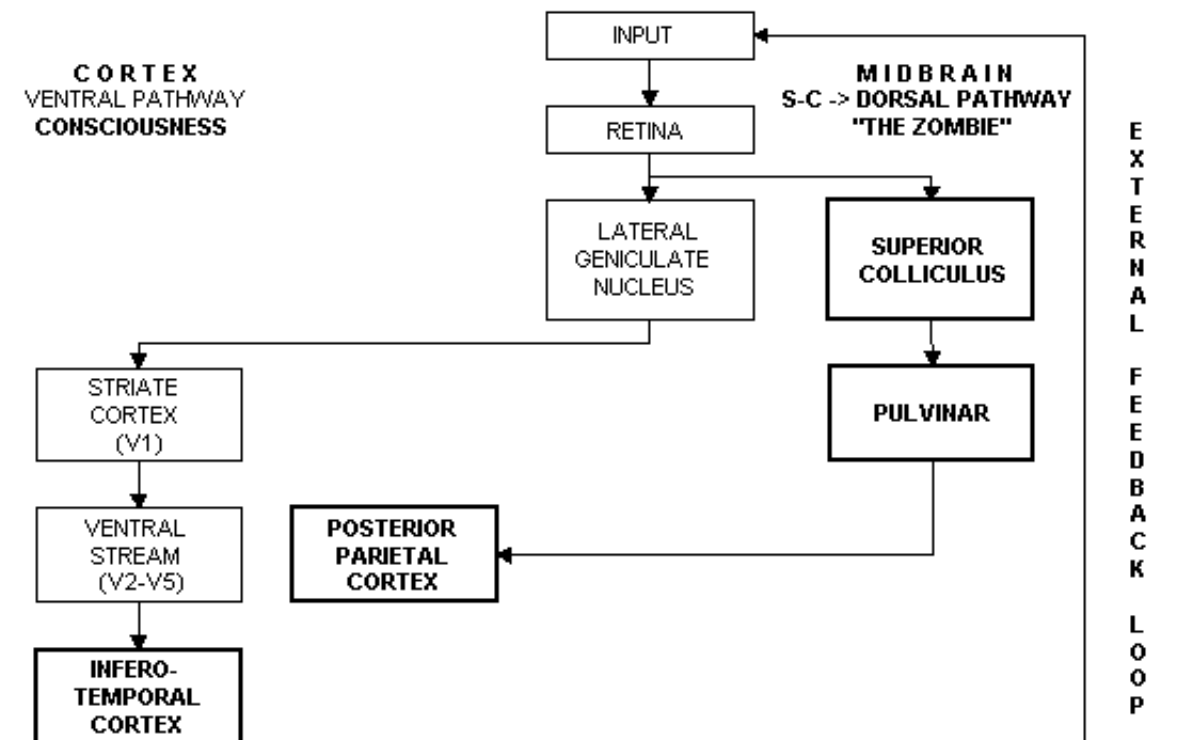


Figure 3: The Dorsal and Ventral Pathways - Multimodal Modules in Bold

5. Provisional Anatomical Conclusions

Assuming that this analysis is approximately correct, we are in a position to make some tentative identifications of the modules shown on Figure 1 with some of the actual structures that have been identified anatomically within the brain as laid out on Figures 2 and 3. These tentative identifications are set out on Figure 4 which is a re-working of Figure 1 with the names of the neural structures substituted for the functional descriptions of the modules with which they have been provisionally identified in the preceding discussion in the special case of vision. Thus, in place of the SENSES we have the RETINA. In place of the SENSORY PROJECTION AREA we have the STRIATE CORTEX.

In place of the ANALYZER we have V2-V5. In place of the PROBLEMATIC INPUT DETECTOR (PID) we have the MIDBRAIN RETICULAR FORMATION.³ In place of the AUTOMATIC PILOT we have the CEREBELLUM. In place of the INVOLUNTARY ATTENTION FOCUSER - PERIPHERAL we have the SUPERIOR COLLICULUS.⁴ In place of the INVOLUNTARY ATTENTION FOCUSER - CENTRAL we have the PULVINAR.⁵ In place of the VOLUNTARY ATTENTION FOCUSER we have the POSTERIOR PARIETAL CORTEX. Finally, in place of CONSCIOUS EXPERIENCE "EVIDENCE" we have the INFERO-TEMPORAL CORTEX.⁶

You will notice that Figure 4 omits the connection between the PULVINAR and the POSTERIOR PARIETAL CORTEX shown on Figures 2 and 3 and which is needed to explain the visual control of reaching for objects and obstacle avoidance when the relevant parts of V1 have been destroyed ("blindsight"). This has been done in order not to obscure the functionally much more important connection between the PULVINAR and the INGATE controlling access to the INFERO-TEMPORAL CORTEX *alias* CONSCIOUS EXPERIENCE. Further "downstream" the only identification to have emerged at all clearly from the preceding discussion is that between the FEEDBACK MONITOR and the DORSAL STREAM.⁷ However, two other identifications have been included on the basis of what has been known for a long time, that between RESPONSE INITIATION and the PYRAMIDAL TRACT and between the EMOTION-SERVO and the HYPOTHALAMUS. Likewise the recent work on "numb-sense" mentioned above will doubtless soon make possible the identification of the somaesthetic counterparts of the purely visual structures shown on Figure 4. It may be that similar identifications can already be suggested for other sensory modalities. If not, future research will doubtless allow us to fill these gaps too.

³ As shown by Morazzi & Magoun (1949).

⁴ I was first alerted to the role of the superior colliculus in coordinating, at a pre-conscious level, the position and sensitivity of the different sense organs in relation to particular locations in environmental space by a seminar given in Oxford under the auspices of the McDonnell-Pew Centre for Cognitive Neuroscience by Professor Barry Stein of Wake Forest University in 1994 (Stein and Meredith 1995) More recently, my attention was drawn by Antti Revonsuo to evidence summarised by Rafal and Robertson (1995) of the role of the superior colliculus in controlling the reflexive orientating response whose absence on the affected side of the body is characteristic of the phenomenon of unilateral neglect.

⁵ A study by Vanni, Revonsuo and Hari (1997) provides evidence suggesting that the pulvinar is involved in modulating activity in the ventral stream (V2-V5), where object recognition or, as I would think, the preparation of the "evidence" for it occurs and that the effect of such modulation is to "select the next target for ventral processing". If this may be interpreted to mean that the pulvinar controls which parts of the total visual input are currently subject to "ventral processing" and hence in the focus of conscious attention, it supports the suggestion that the function of this structure is to regulate the involuntary attraction of the focus of conscious attention to problematic inputs by processes which are themselves necessarily pre-conscious, i.e., part of what I am calling the "zombie-within".

⁶ Although there is much evidence supporting the idea that activity in the infero-temporal cortex provides the "evidence" in Broadbent's (1971) sense on which the categorization of problematic *visual* inputs is based, what is missing is convincing evidence that information from other sensory modalities is integrated with the visual "evidence" within this structure, as would be required if the unity of conscious experience which is demanded by functional considerations, as much as by the evidence of phenomenology, is to be explained by its concentration within an anatomically defined structure. There is some evidence (Gibson and Maunsell 1997), drawn to my attention by my attention by Antti Revonsuo, that there are cells in IT which respond to cross-modal associations between visual and auditory stimuli in a delayed match-to-sample memory task. But similar evidence in the case of the somaesthetic, olfactory and gustatory modalities appears to be missing. Moreover, as we have already seen, there is reason to think that the integration of the visual and somaesthetic feedback "evidence" which forms an integral part of the conscious control of voluntary movement, even when there is no conscious experience of the target towards which that movement is directed, takes place within the posterior parietal cortex. On the other hand, the fact that lesions of IT are associated with selective impairment of "semantic memory" may perhaps be explained on the hypothesis that such lesions disrupt the "evidence" on which the categorization of problematic sensory inputs in all sensory modalities are based. An alternative explanation might be that the boundary between conscious-experience/"evidence" and the categorization that is selected on the basis of it is located *within* rather than downstream of IT.

⁷ Needless to say, this identification is shorthand for a complex set of relations. These involve a movement *schema* supplied by the categorizer and selected by the response-selection system against which the feedback from the movement as it develops (passing from V1 along the *dorsal stream* to the posterior parietal cortex in the case of the visual feedback, arising within the parietal cortex itself in the case of the kinaesthetic) is compared. Any discrepancy between the feedback and the pre-selected schema triggers a correction.

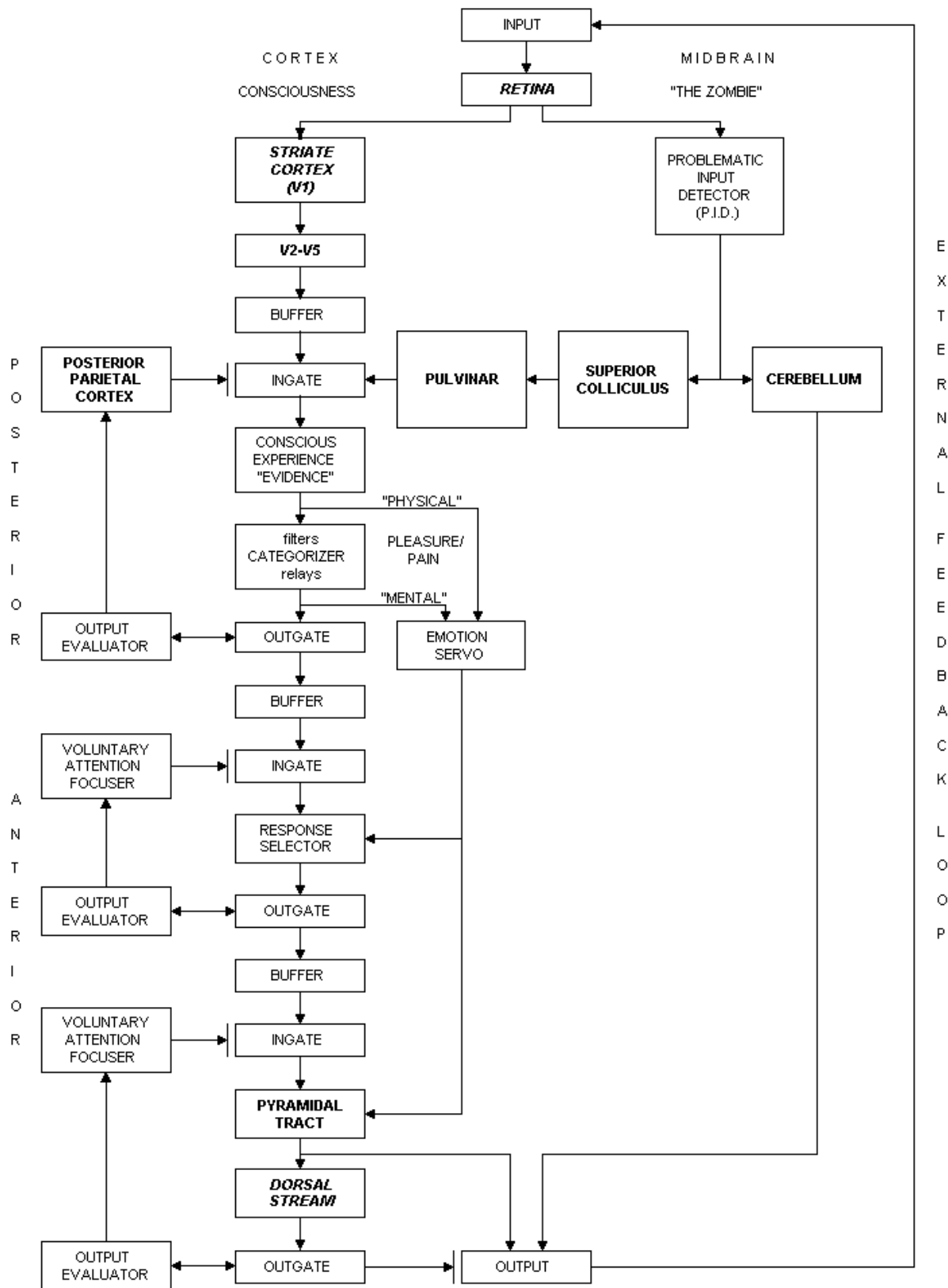


Figure 4: Consciousness and the Zombie-within – Identifications in Bold

But there, for the present, I shall let the matter rest. I hope I have said enough to persuade you that we are now in a position to answer the question which has remained unanswered since my (Place, 1956) paper ‘Is consciousness a brain process?’, namely, ‘If consciousness *is* a brain process, which of the various processes in the brain that we now identify neuroanatomically is it?’ It turns out in the light of what has been said above that that question is too simplistic. But complicated though it is, I hope I have persuaded you that the rudiments of an answer are within our grasp.

References

- Broadbent, D.E. (1958) *Perception and communication*. Pergamon.
- Broadbent, D.E. (1971) *Decision and stress*. Academic Press.
- Gibson, J.R. and Maunsell, H.R. (1997) Sensory modality specificity of neural activity related to memory in visual cortex. *Journal of Neurophysiology*, 78 (3): 1263-1275.
- Milner, A. D. and Goodale, M. A. (1995) *The Visual Brain in Action*. Oxford: Oxford University Press.
- Moruzzi, G. and Magoun, H. W. (1949) Brain stem reticular formation and activation of the EEG. *Electroencephalography and Clinical Neurophysiology*. 1: 455-473.
- Pashler, H. E. (1991) Shifting visual attention and selecting motor responses: distinct attentional mechanisms. *Journal of Experimental Psychology: Human Perception and Performance* 17: 1023-1040.
- Pashler, H. E. (1997) *The Psychology of Attention*. Cambridge, MA: MIT Press.
- Pellionisz, A. and Llinás, R. (1979) Brain modeling by tensor network theory and computer simulation. The cerebellum: distributed processor for predictive coordination. *Neuroscience*, 4: 323-348.
- Place, U.T. (1956) Is consciousness a brain process? *British Journal of Psychology* 47: 44-50.
- Place, U.T. (1997) Consciousness and the Zombie-within. Paper presented at the Inaugural Conference of the Association for the Scientific Study of Consciousness, Claremont, CA, June 15th 1997.
- Posner, M.I. and Dehaene, S. (1994) Attentional networks. *Trends in Neuroscience* 17: 75-79.
- Posner, M.I. and Petersen, S.E. (1990) The attention system of the human brain. *Annual Review of Neuroscience* 13: 25-42.
- Raichle, M.E., Fiez, J.A., Videen, T.O., MacLeod, A.-M.K., Pardo, J.V., Fox, P.T. & Petersen, S.E. (1994) Practice-related changes in human functional anatomy during non-motor learning. *Cerebral Cortex* 4: 8-26.
- Rafal, R. and Robertson, L. (1995) The neurology of visual attention. In M.S. Gazzaniga (ed.) *The Cognitive Neurosciences*. Cambridge, MA: MIT Press, ch. 40, pp. 625-648.
- Stein, B.E. and Meredith, M.A. (1993) *The Merging of the Senses*. Cambridge, MA: MIT Press.
- Ungerleider, L. G. and Mishkin, M. (1982) Two cortical visual systems. In D. J. Ingle, M. A. Goodale, and R. J. W. Mansfield (eds.) *Analysis of Visual Behavior*. Cambridge, MA: M.I.T. Press.
- Vanni, S., Revonsuo, A. and Hari, R. (1997) Modulation of the parieto-occipital alpha-rhythm during object-detection. *Journal of Neuroscience*, 17 (18): 7141-7147.