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FROM UNILATERAL NEGLECT TO THE BRAIN BASIS OF CONSCIOUSNESS

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ABSTRACT

According to the dominant focus model, the differential activation of the thalamocortical network is a sufficient condition for the diversity of states of consciousness to occur, and coherent patterns of interactive forebrain activation peaks are sufficient to generate specific conscious figures against ground. These minimal assumptions are consonant with the known properties of unilateral neglect. It becomes unnecessary to suppose that consciousness is an independent entity, occupies a dedicated location in the brain, is contingent on a minimal level of neural complexity, plays a causal role in enabling perception or action, or evolved because it plays any such role.

Key words: unilateral neglect, consciousness, attentional gradient, dominant focus, forebrain activation

John Marshall, honored in this Special Issue, has contributed greatly to the field of unilateral neglect. He has concluded that "studies of consciousness have brought better understanding of the unconscious" (period!) (Marshall, 2000). Referring to neglect phenomenology, I show the obverse; that one can arrive at a working notion about consciousness in the brain without resorting to exotic postulates. I use familiar and established facts about unilateral neglect as illustrations. I select these facts not because they suffice for an understanding of neglect, a complex area of on-going investigation, but only for their relevance to the brain basis of consciousness.

Unilateral neglect patients may (a) fail to notice contralesional objects and events, (b) fail to search or orient contralesionally either automatically, or deliberately, (c) fail to initiate action in the contralesional direction, and (d) disown left-sided body parts, that they also fail to attend to or use. The probability of each of these neglect behaviors depends on whether objects or events compete for attention on the ipsilesional side.

How can patients who are unaware of one side of objects and scenes, not know that they are missing anything, make no effort to explore in the neglected direction, and subjectively feel that nothing untoward has happened to them? What sort of thing must consciousness be, that it can be circumscribed in such a fashion, ebbing and flowing as external stimulation shifts laterally across the perceptual field? Or that it can be coaxed from regional oblivion by simple lateralized activating maneuvers such as vestibular stimulation, and recede to its former state when the stimulation ceases?

Since Shallice (1972) ushered in the modern era of neuropsychological inquiry into the brain basis of consciousness, diverse conjectures have been offered about where in the brain "it" is located, and how it functions: *left angular gyrus, prefrontal cortex* and *intrathalamic nuclei* are representative attempts at anatomical localization. Other suggestions are more abstract: an *operating system*, a *"global workspace"*, overviewed by a "self" (Baars, 1997, endorsed by Dehaene and Naccache, 2001) or simply "that part most deeply recessed from the outside world that is furthest from input and output" (Sherrington, 1933, p. 26). I propose that such "centered" views of the organization of consciousness circuitry are inconsistent with how consciousness ebbs and flows in patients with neglect (other difficulties with the centered type of model are discussed elsewhere: Kinsbourne, 1988, 1997; Dennett and Kinsbourne, 1992). Instead, I refer to a model for consciousness that was inspired by the neuropsychology of unilateral neglect, show that it is compatible with neglect phenomenology, and then apply it to mental operations that are typically believed to be due to "consciousness". The model is an "uncentered" field construct, which makes minimal assumptions. It tries to clarify to what brains states we are referring when we call them conscious. Specifically, it contradicts the powerful intuition that when one does something consciously, it is one's consciousness that is doing it. The model proposes an ever-changing "dominant focus' of thalamocortical activation as the neural basis of conscious experience. The term is adapted from Rusinov (1973), who used it in a Pavlovian context. Kinsbourne (1988, 1997) further delineates this model.

MECHANISM OF NEGLECT

Neglect has multiple components, that implicate diverse areas of neocortex. These components, with

their differing impact on cognition, are characterized by an imbalance in the distribution of attention at the level of behavior, and an activation imbalance at the neural network level. Attending (and automatic orienting) are laterally biased, with ipsilesional hyperattention and contralesional inattention. Opponent processing with negative feedback may be the mechanism that is destabilized in unilateral neglect (Kinsbourne, 1970, 1977, 1993) and has been modeled accordingly (Hilgetag et al., 1999). Specifically, lateral attending is steered by a difference-minimizing feedback system. The directional orientation of its vector resultant is determined by the relative activation of the two opponent processors. An imbalance skews the attentional set point sideward: the greater the imbalance, the more the center of attention shifts toward the ipsilesional periphery; in the extreme, the attentional gradient continues to rise to the right-most extreme of the viewed or imaged panorama or display, the contralesional processor being unopposed and totally disinhibited.

Minimal Model for Consciousness

No one knows how consciousness is instantiated in the brain. A working hypothesis should strive for the greatest possible generality, based on the least number of assumptions. Like other theorists, I assume that consciousness is, or pertains to, a physical brain state. At the risk of seeming counterintuitive, the field model that follows dispenses with most additional current assumptions.

The dominant focus model proposes that consciousness is inherent in certain differentiated brain states, and inseparable from them. It is neither an agent nor an epiphenomenon. Consciousness is an attribute of network activity and has no independent existence. Consciousness has no causal powers over and above the causal powers of the corresponding neural activity. Therefore whatever one (i.e., the brain) does consciously or intentionally is done by the underlying mental/neural operations rather than by being conscious per se.

In this integrative field theory (Kinsbourne, 1988), the peaks of activation of the cortical manifold designate the location of cell assemblies that represent what is being experienced. Those activated representations that are momentarily stable are candidates for constituting the focus of awareness, as are rival representations of a similar nature. The activation can be stimulus driven, enhanced by novelty or by attention, endogenously imaged or generated by vector completion on account of its close contextual fit (Kinsbourne, 1997). The successful candidate of the moment is termed the dominant focus or configuration. When attention is focal, the activation landscape would exhibit more contrast between peaks and troughs than if attention is diffused. The dominant configuration includes implicit or explicit preparation for action [c.f., Shallice's (1978) dominant action system construct]. The conscious experience arises as a perceptual figure against its background, that is, as a dominant focus against the rest of the forebrain activation manifold. Both the dominant focus and the background are necessary. Thus the whole cortical field or network contributes to generating the experience. Each attribute of a percept is marked for location, and the attributes are "bound" into integrated representations through a physiological process that depends on the fact of shared locations. Possible physiological mechanisms have been much discussed (e.g., Singer, 1993, Llinas et al., 1998; Varela et al., 2001).

The following intuitively attractive assumptions are *not* made:

(1) *Something beyond mere activation of the corresponding cell assemblies renders their representational contents conscious.*

An example is the proposition that an above-threshold level of complexity is required for consciousness (Tononi and Edelman, 1998). Though differentiated, the activation configuration need not be complex, only neither flat, nor rhythmically hypersynchronized as in a generalized seizure.

(2) *Certain brain areas are specialized for generating conscious experience.*

The model discards the widespread assumption that consciousness is so special, that it has to rely on a dedicated conscious awareness module, system, process or type of neuron.

(3) *One has to use one's consciousness to perform certain mental operations.*

The evidence shows that one only becomes conscious of what neural processes have achieved at the end point of their processing sequences, too late to have caused the outcome consciously (Velmans, 1991). We are not conscious of the sequential information processing, but only of its finished product (Lashley, 1956). In the special case in which the processing is hesitant or impeded by focal brain damage, representations that are intermediate in the processing sequence, and normally are too evanescent to become conscious linger into awareness.

(4) *Voluntary actions have to be consciously intended before the neural programming can begin.*

Actions are underway in the brain before the individual forms the corresponding intention (Libet et al., 1983; Wegner, 2002). Jackendoff (1987) expresses a similar point by referring to conscious representations as intermediate; the cognitive work was already dome when they were selected preconsciously (Halligan and Oakley, 2000). Since awareness comes after the action, not before, it

cannot launch or serve as the agent of certain computations, as in working memory (see also Pockett, 2004; Hassin et al., 2005). Nor can it be that one has to consciously intend before one can execute certain ('voluntary') actions. Rather, it is in the nature of certain mental operations that their outcomes become conscious, by virtue of the amplitude, duration, novelty and/or contextual fit of the representations that are involved. For instance, unawareness of hemiplegia is not due to the patient's inability to monitor the limb's movements *consciously*. It is due to his/her inability to activate the representations that when activated are subjectively experienced as the intention to move the affected limb. Had he/she been able to activate these representations, then they would have become conscious of their intention – not the other way round. More generally, particular processes, such as working memory or novelty monitoring, are not due to the assistance of "consciousness". Rather, when they are activated and under way, the individual becomes conscious of them.

(5) *So unique a phenomenon as consciousness must have evolved because it serves an important adaptive function.*

No one knows whether consciousness is unique to humans, or even to the vertebrate phylum. Nor does the mere fact that people are conscious justify the assumption that being conscious was selected for adaptive cause. It is more parsimonious to suppose that selection pressures were exerted on the neuronal machinery that generates behavior, and that generates the retrospective awareness of its products alongside.

Consciousness is often described as the ultimate challenge to cognitive neuroscience, but it may not be. The assumptions listed above may credit it with unwarranted complexity, if not mystery. How far can one get with a more modest, stripped-down theory of consciousness? In neglect, consciousness comes and goes with minimal provocation. I resort to the phenomenology of unilateral neglect in order to show how just a few assumptions might suffice to generate a heuristic working hypothesis about how consciousness is instantiated in the brain. I list eight manifestations of neglect to support the view that consciousness is uncentered, and that its moment-to-moment contents reflect the distribution of activation across the whole cerebral manifold (Kinsbourne, 1988, 1997). For clarity of exposition I will refer to neglect in its most frequent manifestation, as neglect of the left side of space and/or person, due to a right-sided brain lesion.

1. Attention diminishes in a gradient from right to left in various frames of reference, notably the perceptual field.

Patients orient to the right more than to the left, and in severe cases, to the right extreme of an object stimulus, and the right-most stimulus in an array. They discover items with diminishing probability the more they are to the left of other items. This suggests a right-to-left gradient of diminishing activation. Disconnection of information flow to a consciousness module would not be expected to result in such a flexible and variable bias. It is not likely that information from the right and the left of a stimulus object would flow along different pathways to the central location, such that one is cut off, and not the other. Also, the slope of a patient's attentional gradient continually changes, suggesting a dynamic rather than a hardwired neural infrastructure of connections.

2. The patient does not orient toward and explore the external space of which he is unaware, and does not orient toward or explore his neglected body part.

A centered "viewer" would observe the absence of input as a blank patch on the screens of the Cartesian theater (Dennett and Kinsbourne, 1992). The viewer would then be expected to launch a compensatory attempt to pick up information from the affected region (like a patient with hemianopia rotates his head toward the contralesional side). Instead, in neglect the arena of consciousness itself has shrunk on one side; the patient who neglects a part of space or of his body does not experience the fact that he is neglecting it. Inattention to left sided events itself shrinks the field of awareness. A central decision mechanism has no additional explanatory value. According to a field-activation model, to be aware that one is not gathering information about a particular body part or spatial area, one must be able to represent it internally. It is not that one has to be conscious of it to represent it; instead, one has to be able to represent the body part to become conscious of it. If one cannot, then experientially it does not exist, and nothing motivates a leftward search. The extrapersonal or personal percept cannot even be represented as once having existed.

3. The patients are oblivious of, and indifferent to, what might happen on the neglected side of space and of the body.

When questioned about their failures to detect and act on one side, they are defensive. This reinforces the view that in neglect neural territories that are specialized to represent the ignored territories are underactivated, and that underactivation is a sufficient condition for their contents to vanish from the experienced field. Therefore it must not be that consciousness is implemented by a structure afar after information is shuttled to it. Rather, nothing need be transmitted anywhere. The activated cell assembly contributes its representational contents to awareness. Since different cell assemblies can be injured, different patterns of neglect exist (Vallar, 1998). This shows that different cortical fields participate when consciousness is intact, each contributing what it is specialized uniquely to represent. When they are activated, then their subjective attributes enter consciousness.

4. Different visual reference frames are represented in different bilateral brain areas, unilateral damage to which can cause neglect with reference to specific frames (Rizzolatti and Camarda, 1987). Many patients with neglect exhibit highly selective deficits, for instance neglect only for person, or only extrapersonal (Vallar, 1998).

The gradient pattern of deficit in neglect may point to a general design characteristic of the mechanism by which mirror image locations reconcile their opposing tendencies in the mammalian nervous system (Kinsbourne, 1974). When unilaterally impaired, opponent mechanisms at multiple levels of the neuraxis in many mammals would be apt to exhibit the behavioral consequences of imbalance.

5. The imbalance between the hemispheres can be corrected.

If neglect is due to a right-to-left gradient of diminished activation of neuronal assemblies that have representational content, then the vanished contents should be recoverable if one were to correct the activation imbalance. This could be accomplished by increasing the activation of the right hemisphere, or by decreasing the activation of the left hemisphere (Kinsbourne, 1974). Successful maneuvers of both kinds have been reported (Vallar et al., 1997; Rosetti and Rode, 2002). In a much-replicated finding, Silberpfennig (1941) irrigated the contralesional ear with lukewarm water and restored the full sweep of lateral visual and bodily awareness. After the irrigation and its effect on consciousness have worn off, the patient does not remember this sudden lifting of the restriction on her perceptual world. Since Cappa et al. (1986), this finding has been much replicated. Vestibular irrigation activates the contralateral hemisphere (Schiff and Pulver, 1999). Hilgetag et al. (2001) applied repetitive transcranial magnetic stimulation (TMS) to the cerebral hemispheres of normal subjects. They elicited a shift of attention, such that ipsilateral targets were better detected than before, and vice versa. Olivieri et al. (1999) reduced directional neglect by applying TMS to the intact hemisphere. These results support the view that a balance of activation between the hemispheres controls the gradient of lateral attention. The patient becomes aware because the activation imbalance is corrected, not the other way round. The hypothesized imbalance of activation between hemispheres has been demonstrated directly in patients with extinction when bilaterally stimulated, by fMRI (Driver et al., 2001).

These findings indicate that awareness, including awareness of absence, requires the ability to represent the relevant perceptual field. In the intact state, one cannot represent the previous abnormal brain state, and thereby re-experience it and appreciate the contrast between states, and vice versa.

6. Response factors modulate the degree of hemispheric bias.

Using the left rather than the right hand for line bisection increases the leftward bias in normative pseudoneglect. Schiff and Lamon (1989) have induced similar hemispheric biases in normal subjects by holding the left face or hand clenched. A patient with neglect may be aware of stimuli when he uses the left hand to respond, but not when he uses the right hand (Bisiach, personal communication). Using the left hand appears to activate the right hemisphere.

7. When touched on a neglected body part, patients sometimes refer the touch to the mirror image (homotopic) body location (allochiria).

So stimulus-induced activation may bring the stimulus into consciousness, but not suffice to integrate it with an underactivated location on the representation of the body surface.

8. The patient is as unaware that he has ceased to form intentions to move toward the left, as he is unaware that he no longer moves in that direction.

This is because he can no longer represent the leftward intention, and therefore cannot become aware that it is not happening. In order to intend (consciously) one has to be able to activate the corresponding representations.

These eight ways in which patients exhibit neglect indicate that what one is conscious of comes and goes as a function of the fluctuating activation levels of the representing neuronal assemblies. The contrast between being conscious and being unconscious is not qualitative, but a matter of degree and easy transition. To render its representational content a viable candidate for inclusion in the conscious field, a neuronal assembly has to attain and hold a critical level of activation for a critical period of time (Kinsbourne, 1997). If so, then it will compete with other comparably qualified cell assemblies for inclusion in the dominant focus, the overall configuration of which determines what is experienced at any given moment.

The Uses of Consciousness

What is consciousness good for? Dehaene and Naccache (2001, p. 9) suggest the following (in italics):

1) *"The ability to maintain representations in an active state for a durable period of time in the absence of stimulation seems to require consciousness"*.

A representation maintained over time becomes conscious by virtue of its duration. Consciousness does not maintain a representation, but results from a representation being maintained.

2) *"Three classes of computations that seem to require consciousness"*:

a) *"Durable and explicit information maintenance"*

These are representations that meet the activation and duration conditions for consciousness, which occurs when they meet these conditions, that is, when they are already fully formed.

b) *"Novel conditions of operation"*

Representations that are amplified due to their novelty are relatively long lasting, because the brain has no immediately available tactic for processing them further.

c) *"Intentional behavior"*

Intention occurs not before but after the decision has been made preconsciously.

Similar to Dehaene and Naccache (2001), Baars (1997) nominates mental operations that are computationally inefficient, error-prone, and wide-ranging in their associations, involved in problem solving. Such processes would involve relatively long-lasting representations that would linger into consciousness, having already been initiated preconsciously.

Intuitively, consciousness appears to be necessary for mental operations, such as decision making under circumstances of uncertainty or conflict, working memory, and problem solving. But consciousness is not necessary for them. Rather, they necessarily become conscious. As Halligan and Oakley (2000) pointed out, "The contents – of conscious experience do not go on to do anything more, nor do they directly influence any other processing". Those mental operations become conscious which require that specific representations remain present for a relatively long time while the brain manipulates and matches them. They have to remain highly activated to resist interference, while the brain uses them for reference in its computing. The contrasting, fluent and fleeting states of mind, intermediary between the origin and the completion of the percept, or action plan or navigation, succeed one another too quickly for any one of them to become conscious. Each has been supplanted by the next before there was time to entrain in the dominant focus. Only the finished product, the fully-fledged percept, or intention, end of the line for the processing of the moment, survives into awareness. If a lesion derails a fluent processing sequence by slowing or blocking a stage transition, then an intermediate representation will linger into awareness.

Epilogue

What then *is* consciousness? (Believers think this is the 'hard question'). In his brief commentary on what he disapprovingly refers to as "the mystery of consciousness", Marshall (2000) endorses Lewes' (1893) dismissive remark "Consciousness – designates an ultimate fact, which cannot therefore be made more intelligible than it is already". I concur. It is something about the brain in action that cannot be further "reduced", that is, better understood. Since it is not in the nature of consciousness to have any effect on anything, there is in practice no problem of consciousness *per se*. It is therefore not surprising that, in Marshall's (2000) words, "No one knows what the problem of consciousness is".

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