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Consciousness without a cerebral cortex:
a challenge for neuroscience and medicine

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SHORT ABSTRACT (117 words)

A broad range of diverse evidence regarding the functional organization of the vertebrate brain is reviewed for its bearing on the neural organization of consciousness. It is proposed that the vertebrate brain plan implements a functional design exploiting the interdependence of target selection, action selection and motivation to optimize integration for action in real time, and that an upper brain stem system organized for conscious function is an inherent part of this design. This perspective helps us understand the purposive, goal-directed behavior exhibited by mammals after experimental decortication, as well as evidence that children born without a cortex are conscious, and suggests that an adequate account of conscious functioning cannot be based on the cerebral cortex alone.

LONG ABSTRACT (252 words)

A broad range of evidence regarding the functional organization of the vertebrate brain – spanning from comparative neurology over experimental psychology and neurophysiology to clinical data – is reviewed for its bearing on conceptions of the neural organization of consciousness. A novel principle relating target selection, action selection and motivation to one another as a means to optimize integration for action in real time is introduced. With its help the principal macrosystems of the vertebrate brain plan can be seen to form a centralized functional design in which an upper brain stem system organized for conscious function plays a key role. This system forms the prototypical core around which an expanding forebrain could serve as a medium for the elaboration of conscious contents, culminating in the cerebral cortex of mammals. The highly conserved upper brainstem system, which extends from the roof of the midbrain to the basal diencephalon, integrates the massively parallel and distributed information capacity of the cerebral hemispheres into the limited-capacity, sequential mode of operation required for coherent behavior. This perspective sheds light on the division of labor among the three principal cortical territories implicated in attentional and conscious functions, and helps us understand the purposive, goal-directed behavior exhibited by mammals after experimental decortication, as well as evidence that children born without a cortex are conscious. Taken together these circumstances suggest that brainstem mechanisms play an integral part in constituting the conscious state, and that an adequate account of neural mechanisms of conscious function cannot be confined to the thalamocortical complex alone.

KEYWORDS:

Action selection, anencephaly, central decision making, consciousness, control architectures, hydranencephaly, macrosystems, motivation, target selection, zona incerta.

Consciousness without a cerebral cortex: a challenge for neuroscience and medicine.

1. Introduction

The four semi-independent pacemakers of the non-cephalized nervous system of the cubomedusa equip this predatory jellyfish with flexible directional locomotor responsiveness to asymmetric sensory inputs (Satterlie & Nolen, 2001). There is no reason to assume that the environmental guidance thus supplied by its radially arranged nerve net involves or gives rise to experience of any kind. Our own environmental orientation, on the other hand, commonly takes place in a state of wakefulness we call conscious, which typically involves seeing, hearing, feeling or other kinds of experience. Somewhere between medusa and human there is a transition to conscious function, and the nature of the capacity it bestows has exercised psychology, neuroscience and cognitive studies virtually since their inceptions (James 1890; Adrian et al. 1954; Mandler 1975; Baars 1988).

There is no compelling reason to think that nervous systems more complex than those of the medusa, and capable of performing more sophisticated functions, should not also perform in a perpetual night of unconsciousness. The fact that not all of them do so suggests that consciousness has some role or function to fill in the neural economy of brains thus endowed (Searle 1992). In exploring what this might involve, the exclusive concern throughout what follows will be with consciousness in its most basic and general sense, that is, as the state or condition presupposed by any experience whatsoever. Given recent proliferation of terminology surrounding the concept of consciousness (see Morin 2006 for a useful analysis and integration), the following additional remarks should help place this usage in context.

As employed here, the attribution of consciousness is not predicated upon any particular level or degree of complexity of the processes or contents that constitute the conscious state, but only upon whatever arrangement of those processes or contents makes experience itself possible. To the extent that any percept, simple or sophisticated, is experienced, it is conscious, and similarly for any feeling, even if vague, or any impulse to action, however inchoate. This agrees well with the type of dictionary definition that renders consciousness as “the state or activity that is characterized by sensation, emotion, volition, or thought” (Webster’s Third New International Dictionary, unabridged edition, 1961). In this basic sense, then, consciousness may be regarded most simply as the “medium” of any and all possible experience.

With regard to the way in which this medium might be implemented neurally, the present treatment is committed to an architectonic rather than a quantitative (or “graded”) view. That is, as here conceived, a conscious mode of functioning is dependent upon quite specific neural arrangements creating interfaces of particular kinds between specific domains of neural function, rather than a result of a general increase in informational capacity or complexity achieved by expansion of a structural substrate which below a certain size does not support consciousness. Thus, what disqualifies the medusa nerve net in this regard is *not* its simplicity, but its lack of specific structural arrangements required to support conscious function. Given an arrangement capable of supporting consciousness, its contents may differ widely in complexity or sophistication. The range of possibilities in this regard is felicitously captured by the “scale of sentience” of Indian tradition (Bagchi, 1975), as follows:

“This”

“This is so”

“I am affected by this which is so”

“So this is I who am affected by this which is so”

Each “stage” in this scale, from mere experienced sensation to self-consciousness, falls within the compass of consciousness as here defined, and presupposes it. Accordingly, to see, to hear, to feel or otherwise to experience something is to be conscious, irrespective of whether in addition one is aware that one is seeing, hearing, etc., as cogently argued by Dretske (1993; see also Searle 1992; Merker 1997). Such additional awareness, in reflective consciousness or self-consciousness, is one of many contents of consciousness available to creatures with sophisticated cognitive capacities. However, as noted by Morin (2006), even in their case it is present only intermittently, in a kind of time-sharing with more immediate, unreflective experience. To dwell in the latter is not to fall unconscious, but to be unselfconsciously conscious. Reflective awareness is thus more akin to a luxury of consciousness on the part of certain big-

brained species, and not its defining property.

The exploration of the constitution of the conscious state to be pursued here will yield a conception of its functional role revolving around integration for action. As such its functional utility will turn out to be independent of the level of sophistication at which the contents it integrates are defined. This opens the possibility that the evolution of its essential mechanisms did not have to await advanced stages of cortical development, but took place independently of it. As we shall see, certain fundamental features of vertebrate brain organization suggest that key mechanisms of consciousness are implemented in the midbrain and basal diencephalon, while the telencephalon serves as a medium for the increasingly sophisticated elaboration of conscious contents.

With some notable exceptions (e.g. Scheibel & Scheibel 1977; Panksepp 1982; Thompson 1993; Bogen 1995; Watt 2000; Parvizi & Damasio 2001), brainstem mechanisms have not figured prominently in the upsurge of interest in the nature and organization of consciousness that was ushered in with cognitivism in psychology and neuroscience (Mandler 1975; Miller 1986; Baars 1988). Few cognitivists or neuroscientists would today object to the assertion that “cortex is the organ of consciousness”.¹ This is, in a sense, a return to an older view of the supremacy of the cerebral cortex from which a fundamental discovery of the late 1940s had stimulated a partial retreat. In keeping with the sense that the cerebral cortex is the organ of higher functions it had been widely assumed that the regulation of its two primary states – sleep and wakefulness – was a cortical function as well (see, e.g., the critical discussion of this stance in Gamper 1926, pp. 68-78). Then, in the late 1940s, Moruzzi and Magoun (1949) discovered that local stimulation of circumscribed cell groups in the pons and midbrain of experimental animals exerts a global activating influence on the cerebral cortex as well as on behavioral state, and that experimental lesions in these brainstem sites are capable of rendering animals somnolent and even comatose (Magoun 1954; cf. Parvizi & Damasio 2003). This came as a shock to the corticocentric perspective, and stimulated an avalanche of research on brainstem regulation of sleep and wakefulness and its relationship to the conscious state (summarized in symposium volumes edited by Adrian et al. 1954; Jasper et al. 1958; and Eccles 1966).

These efforts proved to be so successful that the once daring proposal that the brainstem regulates cortical state is unproblematic today. The same cannot be said of an allied, largely neglected, but even more radical proposal that emerged from the same pioneering wave of consciousness studies. Some of the principals in these developments – notably the neurosurgeon Wilder Penfield and his colleague Herbert Jasper – went on to re-examine the routine assumption that another “higher function”, closely allied to that of sleep and wakefulness, namely consciousness, is an exclusively cortical affair (Penfield and Jasper, 1954). On the basis of a set of clinical and physiological observations centered on the epilepsies these authors proposed that *the highest integrative functions of the brain are not completed at the cortical level, but in an upper brainstem system of central convergence supplying the key mechanism of consciousness* (Penfield, 1952). Since their proposal is the natural point of departure for the present one, which elaborates and updates it in the light of subsequent developments, a brief review of its history follows.

2. Clinical beginnings

Penfield and Jasper left the anatomical definition of the upper brainstem system they invoked somewhat vague, but it was suggested to include the midbrain reticular formation and its extension into what was then known as the “nonspecific” thalamus (a nuclear grouping encompassing the midline, intralaminar and reticular thalamic nuclei). They regarded this anatomically subcortical system to be functionally supra-cortical in the sense of occupying a superordinate position relative to the cerebral cortex in functional or control terms (Penfield & Jasper 1954, pp. 28, 77; see further Sections 3 and 4, below). They called it the “centrencephalic system”, and assigned it a crucial role in the organization of conscious and volitional functions (ibid., p. 473). Figure 1 is based on a figure illustrating A. Fessard’s lucid account of the conceptual setting for these ideas, included in the first of the symposium volumes cited above (Fessard 1954).

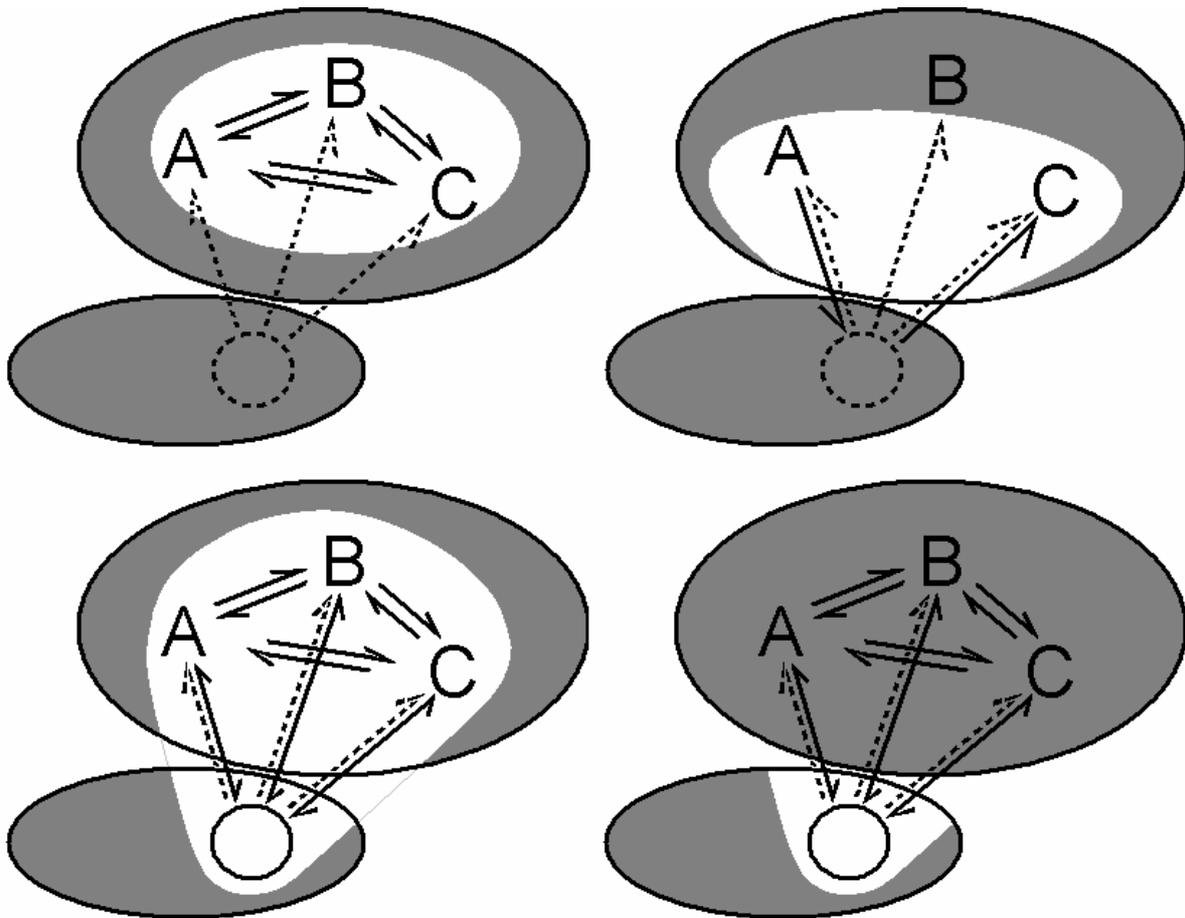


Figure 1: Four principal alternatives regarding interactions between cortex and brainstem in the constitution of the conscious state. Cortex (large oval) and brainstem (small oval) in highly schematic side (sagittal) view. Small circle: “centrencephalic system”. In each alternative, normal waking cortical function is assumed to require “enabling” activation originating in the brain stem, marked by three dashed arrows radiating from brainstem to cortex. **Upper left:** the “corticocentric” alternative, in which integration through cortico-cortical connections alone is sufficient to constitute the conscious state. **Upper right:** Cortical integration via a subcortical relay, such as might occur via the dorsal thalamus. Only one such relay is depicted for the sake of clarity. The scheme is still corticocentric, since integration is cortical, albeit dependent upon extracortical relays for its implementation. **Lower left:** Centrencephalic hypothesis, based on diagram IV in Fessard (1954). Here an essential functional component of consciousness is supplied by brainstem mechanisms interacting with the cortex. **Lower right:** Primary consciousness implemented in the brainstem alone, as in cases of cortical removal or damage discussed in Sections 4.4 and 5 of the text.

The Penfield and Jasper proposal emerged from extensive experience derived from an innovation in neurosurgical practice: they routinely removed sizeable sectors of cortex in conscious patients for the control of intractable epilepsy (Penfield & Jasper 1954). By performing the surgery under local anesthesia only, the authors ensured that their patients remained conscious, cooperative, and capable of self-report throughout the operation. This allowed the neurosurgeons to electrically stimulate the exposed cortex while communicating with the patient, in order to locate functionally critical areas to be spared when removing epileptogenic tissue. They then proceeded to remove cortical tissue while continuing to communicate with the patient. They were impressed by the fact that the removal of sizeable sectors of cortex such as those diagrammed in the composite of Fig. 2 never interrupted the patient’s continuity of consciousness even while the tissue was being surgically removed.

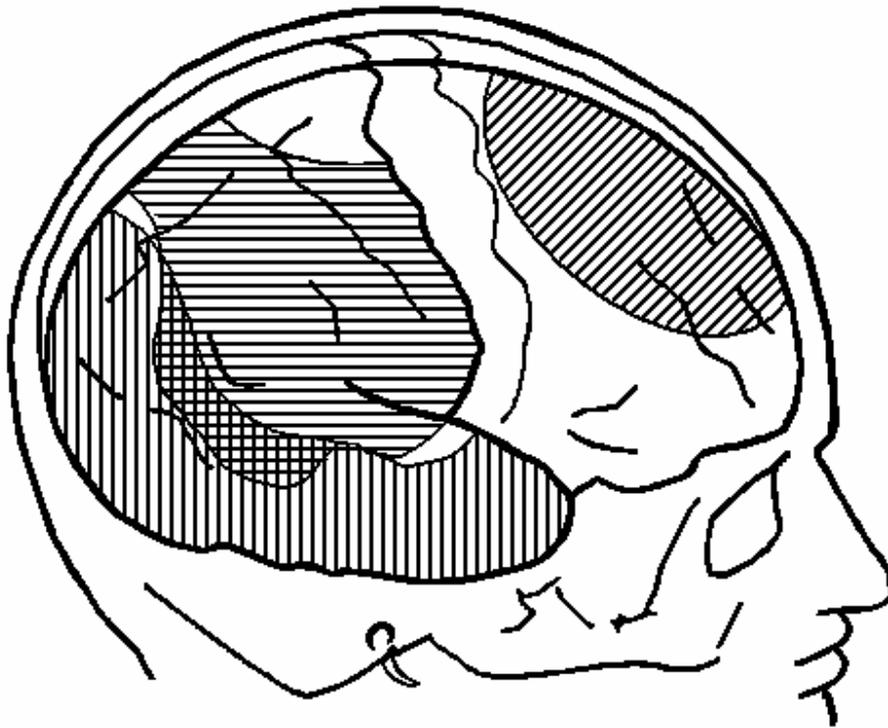


Figure 2. Large cortical excisions performed under local anesthesia by W. Penfield for the control of intractable epilepsy in three patients, entered on a single diagram. The patients remained conscious and communicative throughout the operation. All removals extended to the midline. The two posterior cases were right-sided, while the frontal removal was left-sided, and has been mirror-imaged. In no case was the removal of cortical tissue accompanied by a loss of consciousness. Redrawn after figures VI-2, XIII-2, and XVIII-7 of Penfield & Jasper (1954).

The authors note that a cortical removal even as radical as hemispherectomy does not deprive a patient of consciousness, but rather of certain forms of information, discriminative capacities, or abilities, but not of consciousness itself (Penfield & Jasper 1954, p. 477; Devlin et al. 2003). That does not mean that no cortical insult is capable of compromising consciousness: in adult humans massive bilateral cortical damage will typically issue in a so called persistent vegetative state (Jennett 2002). This by itself does not, however, allow us to make an equation between cortical function and consciousness, since such damage inevitably disrupts numerous brainstem mechanisms normally in receipt of cortical input, as discussed further in subsequent sections (see Shewmon 2004 for the conceptual and empirical complexities of the vegetative state). What impressed Penfield and Jasper was the extent to which the cerebral cortex could be subjected to acute insult without producing so much as an interruption in the continuity of consciousness. Their opinion in this regard bears some weight, since their *magnum opus* of 1954 – *Epilepsy and the functional anatomy of the human brain* – summarizes and evaluates experience with 750 such operations.

When the exposed cortex was stimulated electrically to assess functional localization, stimulation parameters were adjusted so as to avoid triggering epileptic seizures in the patient. From time to time seizures were nevertheless triggered inadvertently. Over the large number of operations performed, every variety of seizure was thus produced by cortical stimulation, except one: Penfield and Jasper never saw the complete electrographic pattern that accompanies absence epilepsy induced by electrical stimulation of any part of the cerebral cortex (Penfield & Jasper 1954, p. 480). This pattern of 3 per second trains of

“spike and wave” discharges evolves synchronously in the two hemispheres, down to a coincidence in the two hemispheres of the very first abnormal spike detectable in the electroencephalogram (Gibbs et al. 1936, 1937; Penfield & Jasper 1954, p. 483, Fig. XII-3, p. 624, Fig. XV-26, etc.).

Seizures of this type bear directly on our topic because of their conspicuous association with disturbances of consciousness (ibid., pp. 24, 28). In fact, they are often *initiated* by a lapse of consciousness (ibid., p. 477), and in pure form they “consist almost solely of a lapse of consciousness” (Penfield & Jasper 1954, p. 480). Without a preceding “aura” or other warning, and in the midst of normal activities, the patient assumes a vacant expression (“blank stare”) and becomes unresponsive. Ongoing activities may continue in the form of automatisms (as complex as automatic speech, implying organized cortical activity), or they may arrest for the duration of the often brief seizure episode. At the end of such a seizure, which may last no more than a few seconds, the patient, who typically remains upright throughout, sometimes actively moving, resumes conscious activities where they were interrupted, has amnesia for what transpired during the episode, and may have no knowledge that the episode took place except indirectly, by means of evidence for the lapse of time available to the discursive, post-seizure, intellect.

Penfield and Jasper recognized in these seizures “a unique opportunity to study the neuronal substratum of consciousness” (ibid., p. 480; cf. Blumenfeld & Taylor 2003). The coincident bilateral onset and cessation of these seizures suggested to the authors an origin in a centrally placed upper brainstem site of paroxysmal induction (Penfield & Jasper 1954, pp. 27, 473, 477, 482, 622-633). Though in their experience the pattern was not triggered by cortical stimulation, it could be evoked experimentally in the cat by stimulation of the midline thalamus (Jasper & Droogleever-Fortuyn 1947). Modern methods have added both detail and qualifications to the Penfield and Jasper account (see review by Meeren et al. 2005), yet upper brainstem involvement in absence epilepsy has stood the test of time, and is still being actively pursued both clinically and through research employing animal models (Stefan & Snead 1997; Danober et al. 1998; Derensart et al. 2001; McCormick & Contreras 2001; Blumenfeld & Taylor 2003; Strafstrom 2006). We shall return to this matter in Section 4.5.3 below.

Penfield and Jasper stressed that the postulated centrencephalic system is *symmetrically related to both cerebral hemispheres* (in the sense of radial rather than bilateral symmetry: Penfield & Jasper 1954, p. 43, and figures on p. 145 and 173). They denied that this system “functions by itself alone, independent of the cortex” and suggested instead that it “functions normally only by means of employment of various cortical areas” (Penfield & Jasper 1954, pp. 473-474). They conceived of it as a convergently innervated upper brainstem system serving to coordinate and integrate the functional economy of the forebrain as a whole, intimately involved in conscious and volitional functions as well as in the laying down of memories across the lifespan (Penfield & Jasper 1954, pp. 140-145; 282).

3. Bringing the centrencephalic proposal up to date.

A valuable review of the centrencephalic proposal in light of developments up till the end of the 1980s is provided by Thompson (1993, published posthumously). He calls attention to the relevance of the clinical literature on so called “subcortical dementia” to the centrencephalic theory, and further suggests that animal evidence for a subcortical “general learning system” may supply some of the anatomical detail left unspecified by Penfield and Jasper. This “general learning system” is defined by neural structures which when damaged produce deficits in *each* member of a set of highly diverse learning tests for rats. As identified through a long-term research program conducted by Thompson and colleagues, it consists of the basal ganglia, including the *substantia nigra* and ventral tegmental area, ventrolateral thalamus, superior colliculus, median raphe and pontine reticular formation. The functional significance of key members of this constellation (which has access to sensory information independently of the cortex) will be considered in some detail in Section 4, below, for which the following preliminary considerations will set the stage.

The central claim of the Penfield and Jasper hypothesis is a claim regarding systems-level organization of neural functions. The idea that a system can be “anatomically subcortical but functionally supra-cortical” is a statement about brain macrosystems and how they relate and interact with one another. It is most easily

approached from the side of the “final common path” of all brain output as far as actual behavior is concerned, namely brainstem and spinal motoneuron pools. Not only are these clusters of final output cells invariably innervated by multiple sources of afference (Kuypers & Martin 1982; Nudo & Masterton 1988; Ugolini 1995; Graf et al. 2002), but individual motoneurons receive synaptic input from diverse sources utilizing different transmitters (Holstege 1991; Wentzel et al. 1995). These sources include spinal and brainstem pattern generators (Grillner 2003), various territories of the brain stem reticular formation (Jordan 1998), and a multitude of both direct and indirect brainstem and forebrain afferents, among which the indirect ones often are relayed via the reticular formation (Zahm 2006).

Thus the fact that the motor cortex maintains direct connections with brainstem and spinal motoneurons by no means implies that it ever is in sole command of behavior. At every level of its descending innervation of motoneuron pools it is but one of many inputs determining final outcomes. Moreover, the motor cortex accounts for but a fraction of descending cortical output, and is responsible for only select forms of distal behavior (Lawrence & Kuypers 1968; Kuypers 1982, 1987; Lang & Schieber 2003). In such a setting the idea that the output of a subcortical structure might over-ride a cortical one and in this sense could exercise supra-cortical control over behavior is hardly controversial. When an act of deliberate effort (say driven by prefrontal executive systems) is successful in overriding or inhibiting a given behavioral tendency, the cortex is in command of behavior, temporarily exercising determining control over its course. The fact that such effort does not always succeed (say in the face of sufficient magnitudes of fear, hunger or pain) means that the frontal executive can be overridden by more primitive mechanisms. When a subcortical source prevails in such competitive interactions, an anatomically subcortical system has exercised supra-cortical functional control over behavior.

It is necessary, in other words, to distinguish “higher” in the sense of cognitive sophistication from “higher” in control terms. In this light the Penfield and Jasper proposal amounts to a claim that certain upper brainstem systems in receipt of convergent cortical projections occupy a superordinate position in the latter sense. As we shall see in detail in subsequent sections, the diverse hemispheric as well as brainstem input to these structures equips them for the kind of superordinate decision making crucial for the global sequencing and control of behavior (Prescott et al. 1999). It is also within processes dedicated to “integration for action” that we shall find a well-defined functional role for a particular mode of neural organization that qualifies as conscious, in good agreement with the Penfield and Jasper proposal. To set the stage for a treatment of that more demanding topic in Sections 4 and 5, two lines of evidence regarding brainstem function that bear on their proposal will be briefly reviewed.

3.1 The Sprague effect

Complete removal of the posterior visual areas of one hemisphere in the cat (parietal areas included) renders the animal profoundly and permanently unresponsive to visual stimuli in the half of space opposite the cortical removal (Sprague 1966; Sherman 1974; Wallace et al. 1989). The animal appears blind in a manner resembling the cortical blindness that follows radical damage to the geniculostriate system in humans. Yet inflicting *additional* damage on such a severely impaired animal at the midbrain level *restores* the animal’s ability to orient to and to localize stimuli in the formerly blind field (Sprague 1966; Sherman 1977; Wallace et al. 1989). This is accomplished by removing the contralateral superior colliculus or by an intervention as small as a knife-cut that severs fibers running in the central portion of the collicular commissure. That is, adding a small amount of damage in the brainstem to the cortical damage “cures” what appeared to be a behavioral effect of massive cortical damage. The restored visual capacity is limited essentially to the ability to orient to and approach the location of moving visual stimuli in space (Wallace et al. 1989). Visual *pattern* discrimination capacity does not recover after the midbrain intervention (Loop & Sherman 1977), though the midbrain mechanism can be shown to play a role even in such tasks (Sprague 1991).

The Sprague effect is a consequence of secondary effects generated at the brainstem level by the unilateral cortical removal (Hikosaka & Wurtz 1989; Hovda & Villablanca 1990; Jiang et al. 2003). The damage not only deprives the ipsilateral superior colliculus of its normal and profuse cortical input (Palmer et al. 1972; Sprague 1975; Berson & McIlwain 1983; Harting et al. 1992), but unbalances collicular

function via indirect projection pathways. Chief of these is the powerful inhibitory projection from the *substantia nigra* to the colliculus, which crosses the midline in a narrow central portion of the collicular commissure (Wallace et al. 1990; McHaffie et al. 1993; Sprague 1996; for additional possibilities, see Durmer & Rosenquist 2001). The “restorative” interventions partially correct this imbalance, allowing the collicular mechanism to resume at least part of its normal functional contribution to behavior, with partial restoration of vision as a result.

The point is underscored by the analogous circumstances pertaining to the neglect of one half of space that follows more limited inactivation of the cortex (by reversible cooling) at the junction of occipital, parietal and temporal lobes in one hemisphere of the cat. This neglect too lifts upon inactivation (by reversible cooling) of the superior colliculus opposite to the cortical inactivation (Lomber & Payne 1996). Analogous restorative effects of midbrain damage on neglect caused by frontal cortical damage have been observed in a human patient (Weddell 2004). Though the unawareness featured in cases of unilateral neglect in humans is far from a simple entity (see review by Mesulam 1999), it bears on our topic by being perhaps the closest approximation to an impairment that includes specific effects on consciousness produced by localized cortical damage (Driver & Vuilleumier 2001; Rees 2001; see also Jiang et al. 2003).

The Sprague effect demonstrates that hidden in the hemianopia or neglect caused by cortical damage lies a deficit on the part of a brainstem visual mechanism disabled as a secondary effect of the cortical removal. This means that a functional deficit following damage limited to the cortex cannot as a matter of course be taken to reflect an exclusively cortical contribution to functional capacity, since the deficit may reflect “remote” effects on brainstem systems as well. As Sprague originally expressed it: “The hemianopia that follows unilateral removal of the cortex that mediates visual behavior cannot be explained simply in classical terms of interruption of the visual radiations that serve cortical function. Explanation of the deficit requires a broader point of view, namely, that visual attention and perception are mediated at both forebrain and midbrain levels, which interact in their control of visually guided behavior.” (Sprague 1966, p. 1547). That conclusion agrees well with the Penfield and Jasper perspective reviewed in the foregoing, and it tells us that without cognizance of potential subcortical contributions to a deficit caused by cortical damage, the scope of functions attributed to the cortex will be counterfactually inflated.

3.2 Target selection in the midbrain

Though superficially inconspicuous, the superior colliculus in the roof (“tectum”) of the midbrain exhibits considerable structural and functional complexity. Long known to play a role in “visual grasping” or “foveation” (Hess et al. 1946; Schiller & Koerner 1971), further study has revealed unexpected sophistication in its functional organization (Sparks 1999; Krauzlis et al. 2004; Keller et al. 2005; May 2005). It is the only site in the brain in which the spatial senses are topographically superposed in laminar fashion within a common, premotor, framework for multi-effector control of orienting (Merker 1980). Its functional role appears to center on convergent integration of diverse sources of information bearing on spatially triggered replacement of one behavioral target by another, and evidence is accumulating for a collicular role in target selection (Wurtz & Mohler 1974; Schlag-Rey et al. 1992; Glimcher & Sparks 1992; Basso & Wurtz 1998; Horowitz & Newsome 1999; Basso & Wurtz 2002; McPeck & Keller 2004; Krauzlis et al. 2004; Carello & Krauzlis 2004; Cavanaugh & Wurtz 2004; see also Grobstein 1988, pp. 44-45). Such a role has direct implications for the topic of superordinate control functions.

A collicular role in target selection is unlikely to be a passive reflection of decisions taken in other structures. It is not fully accounted for by the powerful input it receives from the *substantia nigra* (Basso & Wurtz 2002), and the diversity of collicular afferents precludes any one of them from exercising sole control over collicular function. These afferents include a wide range of brainstem (Edwards et al. 1979; Edwards 1980) and visual as well as nonvisual cortical sources (Kawamura & Konno 1979; Sherman et al. 1979; Harting et al. 1992; Harting et al. 1997; Collins et al. 2005). Cortical afferents are monosynaptic, originating in layer V pyramidal cells, placing the colliculus as close to the cortex as two cortical layers are to one another. In the cat they include some 17 visual areas (Harting et al. 1992), and in primates contributions from both the dorsal (parietal cortex) and the ventral (temporal cortex) “streams” of the visual

system (Fries 1984; Webster et al. 1993, Steele & Weller 1993). Any sensory modality used in phasic orienting behavior appears to receive obligatory representation in the colliculus. Besides the major spatial senses of vision, audition and somesthesia they include pain (Wang & Redgrave 1997) and exotic ones such as infrared (Hartline et al. 1978), electroreceptive (Bastian 1982), magnetic (Nemec et al. 2001), and echolocation systems (Valentine & Moss 1997), depending on species.

In the colliculus these diverse convergent inputs are arranged in topographically organized sheets layered one upon the other through the depths of the colliculus (Harting et al. 1992; May 2005). Intrinsic collicular circuitry distributes excitatory as well as inhibitory collicular activity within and across layers and across major collicular subdivisions (Mize et al. 1994; Behan & Kime 1996; Lee et al. 1997; Meredith & Ramoa 1998; Binns 1999; Özen et al. 2000; Zhu & Lo 2000; Doubell et al. 2003; Bell et al. 2003; Meredith & King 2004). There is thus no dearth of complex intrinsic collicular circuitry – only beginning to be systematically charted – for collicular decision-making based upon its diverse sources of afference.

The collicular role in target selection is accordingly likely to be causal (Carello & Krauzlis 2004; McPeck & Keller 2004; see also Findlay & Walker 1999; Yarrow et al. 2004; and Section 4.2, below). This would place the colliculus at the functional apex rather than bottom of control processes in its domain. The selection of a target for behavior is the brain's final output in that regard. It is the pivotal event for which all other processes are but a preparation, summing them up in the actual decision to settle on one target for action rather than another (McFarland & Sibly 1975; Dean & Redgrave 1984; Allport 1987; Tyrrell 1993; Brooks 1994; Isa & Kobayashi 2004).

The functional prediction from the loss of such a structure is not the absence of target acquisition, but its impoverishment. Not only is the brain redundantly organized in this regard (Schiller et al. 1979; Tehovnik et al. 1994; Schall 1997; Lomber et al. 2001), but the loss of a superordinate function in a layered control architecture does not disable the system as a whole (Brooks 1986, 1989; Prescott et al. 1999), just as a well organized army need not cease functioning on the loss of its commander. A macaque with experimental collicular lesions is not incapable of moving its eyes onto targets, but exhibits a reduced variety of eye and orienting movements and is indistractable, a common finding in other species as well (Denny-Brown 1962; Schneider 1967; Casagrande & Diamond 1974; Goodale & Murison 1975; Albano & Wurtz 1978; Schiller et al. 1979; Merker 1980; Mort et al. 1980; Schiller & Lee 1994). This may reflect a compromised *scope* and *sophistication* of target selection, and the role of the intact colliculus would accordingly instantiate the Penfield and Jasper conception of a *highest integrative function* which while *anatomically subcortical* is *functionally supra-cortical*.

4. Integration for action

As noted in Section 3 above, in drawing the contrast between “higher” in cognitive terms and “higher” in control terms, competition for control over behavior ends only at the stage of the “final common path” of motoneurons. It is along that approach, among upper brainstem mechanisms of “integration for action”, that we shall identify a prototype organization for conscious function. The issue takes us to the very origin of the vertebrate brain plan, which is not only cephalized, but centralized. Not all animals rely on centralized neural organization to control behavior, even when possessed of a brain. A number of invertebrate forms, including insects, concentrate considerable neural resources to segmental ganglia. Their brain is in a sense no more than the anterior-most of these ganglia, in receipt of the output of the specialized receptors of the head. It does not necessarily exercise a command function in the sense of central control of behavior (see Altman & Kien 1989).

The decentralized neural control of an insect such as the ant allows its body to survive without its brain. Moreover, if given adequate somatic stimulation in this condition, it will perform many of the complex behaviors in its repertoire with apparent competence, though naturally without relation to the distal environment (Snodgrass, 1935). A vertebrate, on the other hand, does not survive for more than seconds after the loss of its brain, since in vertebrates even vital functions are under central brain control. The difference with respect to insects is underscored by the contrasting disposition of motor neurons. In insects they are concentrated to segmental ganglia but are rare in the brain (Snodgrass 1935), while in

vertebrates they populate the brain in sets of distinctively organized motor nuclei. Motor control in vertebrates has “moved up,” as it were, to that end of the neuraxis which leads in locomotion and is in receipt of the output of the chief exteroceptors (cf. Grillner et al. 1997).

The basic organizational features of the vertebrate brain are highly conserved across taxa despite unequal development of one or another of its senses or subdivisions (Nieuwenhuis et al. 1998). All vertebrates, that is, have “in outline” the same brain plan, assembled from primitive beginnings in chordate ancestry (Northcutt 1996b; Butler & Hodos 1996; Holland & Holland 1999). The prominent role of large, image-forming eyes and their central connections in this development came to exert a profound effect on the manner in which the vertebrate brain plan was centralized, with implications for our understanding of the way in which “higher” in cognitive terms relates to “higher” in control terms. That development involves the integrative machinery straddling the so called synencephalon, or junction between midbrain and diencephalon, to which we now turn.

4.1 The synencephalic bottleneck and how the vertebrate brain came to be centralized around it.

There was a time in pre-vertebrate ancestry when the midbrain and diencephalon alone, or rather the first rostral differentiations of the neural tube that can be homologized with the vertebrate midbrain and diencephalon (Holland et al. 1994; Lacalli 1996, 2001; Wicht 1996; Holland & Holland 1999, 2001), constituted the functionally highest and also anatomically most rostral subdivision of the neuraxis. It housed the neural circuitry connecting a primitive, unpaired “frontal eye” and other rostral sensory equipment (Lacalli 1996) with premotor cells in cephalochordate filter feeders (represented today by *Amphioxus*, the lancelet). As far as is known they lacked a sense of smell, and they were without a telencephalon altogether (Holland et al. 1994; Butler 2000).

Though our brain nomenclature historically groups the diencephalon together with the telencephalon to make up the forebrain, there is nothing fundamental about such a grouping, as the above phylogenetic circumstances show. Rather, for what follows it will be convenient to retain the primitive grouping of midbrain and diencephalon together under the label mesodiencephalon or “optic brain”. In all vertebrates these two segments of the neuraxis, along with the transitional “synencephalon” (pretectum) wedged between them, house the primary terminations of the optic tract (cf. Butler 2000). The latter covers their external surfaces in the form of a ribbon of fibers running obliquely from the optic chiasm beneath the hypothalamus across the diencephalon and mesencephalon up to the latter’s roof (“tectum”). Along the way it innervates structures as different as hypothalamus, ventral thalamus, dorsal thalamus, pretectum, accessory optic nuclei and superior colliculus (tectum). The same territory also houses some of the major *integrative structures of broad functional scope common to all vertebrates* (cf. Fig. 3).

The principal poles of this integrative machinery are the hypothalamus forming the floor of the diencephalon on the one hand, and the superior colliculus forming the roof of the midbrain on the other. The former is an intricate nuclear aggregate critical for the mutual regulation and integration of a vertebrate’s entire repertoire of goal-directed, motivated behavior covering exploratory, foraging, ingestive, defensive, aggressive, sexual, social, and parental modes of behavior (Swanson 2000), to name the principal ones. The other pole, colliculus/tectum, serves the intermodal integration of the spatial senses by which vertebrates relate to their surroundings via coordinated orienting movements of eyes, head and body, as already summarized in Section 3.2 above. Between these two is wedged additional integrative machinery in the form of midbrain reticular formation, ventral thalamus, periaqueductal gray, the ventral tegmental/*substantia nigra* pivot of the striatal system, as well as “locomotor centers” and basic mechanisms serving navigation, to some of which we shall return in subsequent sections.

This concentration of conserved integrative machinery to the mesodiencephalon, I suggest, reflects the costs and benefits of evolving image-forming eyes in the ancestors of vertebrates (cf. Northcutt 1996a). Full use of the potential powers of visual guidance meant evolving solutions to an intricate set of sensori-motor problems. The confounding of sensory information by the sensory consequences of movement (re-afference: von Holst & Mittelstaedt 1950) is particularly problematic for image-forming eyes, requiring their stabilization with respect to the world during movement. This is done by vestibular counter-rotation

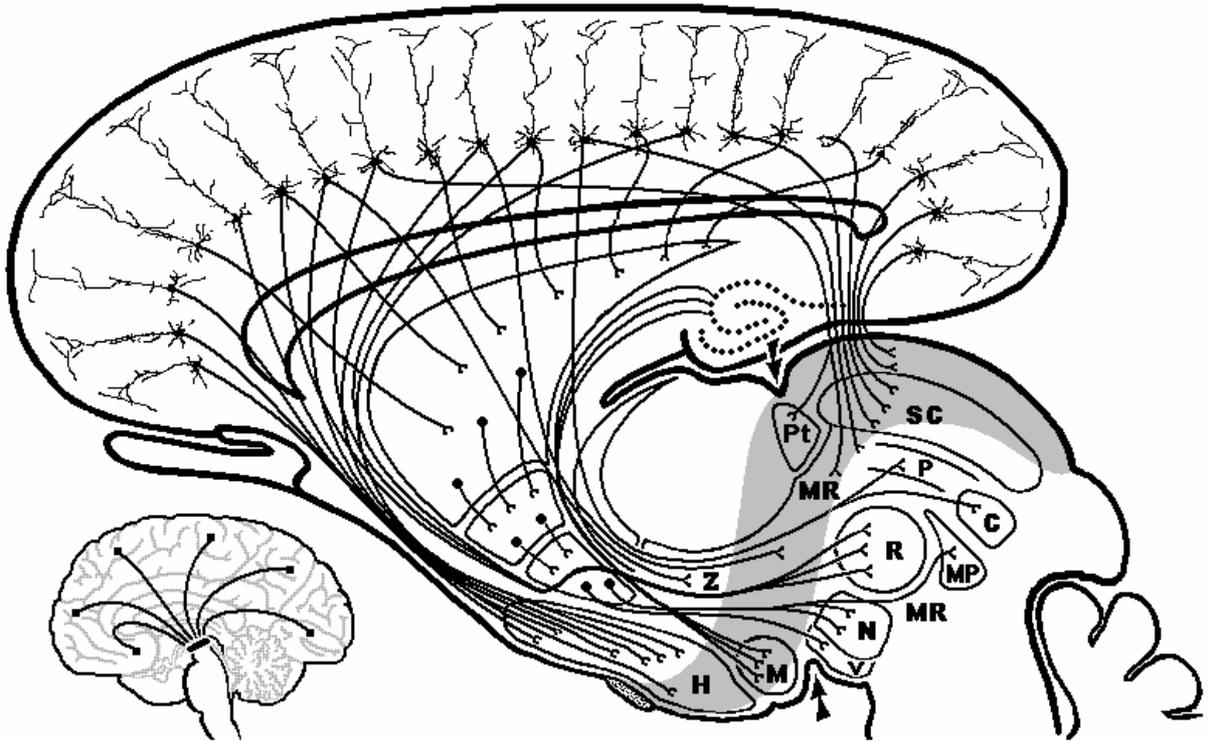
punctuated by quick resets of the eyes, which concentrates blurring-time to the brief reset episodes. Thus *vision alone among all the senses features independent spatial mobility of the receptor array itself*, and a full-fledged oculomotor system was evolved by the immediate ancestors of true vertebrates (Fritsch et al. 1990; Wicht 1996, p. 253; Braun 1996, p. 272). The reflex circuitry connecting vestibular and oculomotor nuclei, centered on the medial longitudinal fasciculus, is also among the most conservative and basic features of the brainstem in all vertebrates (Windle & Baxter 1936; Carpenter 1991).

Yet with eyes free to turn in their orbits there is no longer a fixed relation between retinal location and spatial direction relative to body or head, nor to the localizing function of any sensory modality which (in whole or in part) bears a fixed relation to the head. Hence the need for intermodal integration, for which the sensory integrating mechanism of colliculus/tectum – present in the roof of the midbrain of even jawless vertebrates – provides the basic, early and conserved solution (Iwahori et al. 1999; Zompa & Dubuc 1996). But once these basic problems of vision were solved, a bonus was within reach: mobile eyes present a highly efficient means for sampling the environment, provided their control can be linked to motivational mechanisms ensuring their appropriate deployment in accordance with shifting needs.

It appears, in other words, that as the vertebrate brain plan took shape in pre-vertebrate ancestry under pressure of the evolution of mobile, image-forming eyes a central association between optic control circuitry and major neural mechanism for the integration of behavior/action were forged in segments of the neuraxis covered and innervated by the optic tract (cf. Fig 3). At the time when this optic orienting machinery and associated integrative mechanisms evolved, the forebrain was still dominated by olfaction (Wicht & Northcutt 1992; Braun 1996; Northcutt & Wicht 1997). The sense of smell added no fundamentally new control requirements comparable to those of vision, and olfaction accordingly could be integrated with the mesodiencephalic control system by caudally directed fiber projections. These simply happen to arrive at the “optic brain” from an anterior direction, whereas other sensory afferents reach it from a caudal direction (somatosensory, octavolateral – i.e. vestibular/auditory/lateral line/electrosensory, etc.), or directly “from the side” through the optic tract (cf. Butler 2000).

Indeed, however much the telencephalon subsequently expanded, even to the point of burying the mesodiencephalon under a mushrooming mammalian neocortex, no other arrangement was ever needed, and that for the most fundamental of reasons. No efferent nerve has its motor nucleus situated above the level of the midbrain. This means that the very narrow cross-section of the brainstem at the junction between midbrain and diencephalon (synencephalon, marked by arrows in the main part of Fig. 3 and by a black bar in the inset) carries the total extent of information by which the forebrain is ever able to generate, control or influence behavior of any kind. If, therefore, integration is for action, as proposed here for the mesodiencephalic control system, information-theory poses no obstacle to having an expansive neocortex make its contribution in this regard by convergent projections onto the highly conserved and pre-existing machinery of the midbrain and basal diencephalon, which therefore could retain its old integrative functions (see Fig. 3). Indeed, a bottleneck of this kind is exactly what is needed in order to convert the massively parallel and distributed information capacity of the cerebral hemispheres into a limited-capacity, sequential mode of operation featured in action selection for coherent behavior (McFarland & Sibly 1975; Allport 1987; Tyrrell 1993; Baars 1993; Cabanac 1996; Cowan 2001; Mandler 2002, chapt. 2).

Figure 3. Schematic saggittal diagram depicting cortical convergence (in part via the basal ganglia) onto key structures in the region of the “synencephalic bottleneck” (marked by thick arrows in the main figure and by a black bar in the inset). Abbreviations: **C**, nucleus cuneiformis; **H**, hypothalamus (preoptic area included); **M**, mammillary bodies; **MP**, “mesopontine state control nuclei” (locus coeruleus, pedunculo-pontine and laterodorsal tegmental nuclei, and dorsal raphé); **MR**, midbrain reticular formation; **N**, substantia nigra; **P**, periaqueductal gray matter; **Pt**, pretectum; **R**, red nucleus; **SC**, superior colliculus; **V**, ventral tegmental area; **Z**, zona incerta. The dual axon seen issuing from some of the pyramidal cells of cortical layer 5 is an illustrative convenience only. Shaded region marks the surface course of the optic tract.



That is, one need not know anything more about the vertebrate brain than the fact that its most rostral motoneurons are located *below* the synencephalic bottleneck to know that the total informational content of the forebrain must undergo massive reduction in the course of its real-time translation into behavior. In the setting of such obligatory “data reduction” in a stretch of the neuraxis hosting major systems for the global regulation of behavior, a so far unrecognized optimizing principle lies hidden in the mutual dependency that links the motivational, the sensory and the action selection requirements of the brain’s control tasks. They form a “selection triangle”, whose principle is introduced here for the first time. The efficient neural implementation of this principle may harbor the secret of conscious function itself.

4.2 The “selection triangle”: a proposed key to conscious function

Elementary necessities of animal existence such as food, shelter or mates are not typically found in the same place at any given time, and they each require different and often incompatible behaviors. An animal’s activities accordingly unfold under constraint of multiple goals or motives derived from the evolved and acquired needs it must fill through the sequence of its diverse actions over time (Tinbergen 1951; Baerends 1976). The tasks set by these goals compete for an animal’s behavioral resources, and since the actions by which they are implemented are always confined to the present (where they typically are executed one at a time), their scheduling (action selection) features perpetual trade-offs in the time and effort that is allocated to them (McFarland & Sibly 1975). The ethological insight that animal behavior rests upon a foundation of diverse goal functions entailing sometimes incompatible tasks or behaviors requiring sequencing/selection entered the so called behavior-based approach to robotics under the name “action selection” (McFarland & Houston, 1981; Brooks 1986; Maes 1990; Tyrell 1993; Blumberg 1994; Prescott et al. 1999; see also Meyer & Wilson 1991).

The needs reflected in the time budget of an animal’s task allocations are, however, only one side of the equation of efficient decision making. The fulfillment of needs is contingent on available *opportunities*. These are scattered in the world as ever-shifting targets of approach and avoidance among lively and often unpredictable contingencies within which they must be detected, located, and identified, often

among multiple competing alternatives, all in real time. Interposed between the needs and their fulfillment through action on the world is the body with its appendages and other resources for getting about in the world and manipulating its objects. In concrete terms an action is a time series of bodily locations and conformations. These are what connect needs with opportunities. In so doing they themselves become a factor in singling out a given opportunity (target) for action (target selection). This is so because determining which one of several available potential targets is the best current choice for action will often depend not on current needs alone, but additionally on the disposition of the body relative to those targets (in terms of its posture and position, movement trajectory, energy reserves, etc., cf. Körding & Wolpert 2006).

In principle each of the decision domains just invoked – action selection, target selection, and motivational ranking – may be defined in its own terms, without regard to the others. They may even make their contributions to behavior independently of one another (Brooks 1986; Altman & Kien 1989). But from the inherent functional relationship just sketched, i.e. the fact that in terms of optimal performance *target selection is not independent of action selection, and neither of these is independent of motivational state* (reflecting changing needs), it follows that savings are achievable by exploiting that triangular dependency. It is not possible to reap the benefits of those savings short of finding some way of interfacing the three state spaces – each multidimensional in its own right – within some common coordinate space (decision framework) upon that their separate momentary states interact and constrain one another. This extends to such a tripartite interaction the principle already derived for the efficient management of motivational trade-offs, namely that different motives be convertible through a motivational “common currency” and that all relevant motivational variables be subject to convergence among themselves at some point (McFarland & Sibly 1975; see also Cabanac 1992, and further below).

The principle of a centralized brain system dedicated to this decision domain follows from this, though not the particulars of the three-way interface that must form its center-piece. Evolving such an interface is far from a trivial problem, all the more so since its decisions must be made in real time. The brain, of course, has no direct access to either the target states of the world or the action states of the body that must be compared and matched in the light of motivational priorities. It is saddled with an inverse problem on both sensory and motor sides of its operations (Kawato et al. 1993; Gallistel 1999). The indirect reflections of relevant parameters to which it does have access come to it, moreover, in diverse data formats. The differences between the spatial senses among themselves in this regard are mild compared to those between any one of these senses and the various musculoskeletal articulations and configurations they serve to control. How then to compare the former with the latter? Add to this the already mentioned circumstance that every movement confounds the sensory information needed to guide behavior, and that the needs to be taken into account differ not only in urgency but in kind, and the size of the design problem begins to emerge in outline.

To exploit the savings hidden in the functional interdependence between target selection, action selection and motivation, this confounded complexity must be radically recast, to allow the three domains to interact directly in real time for the determination of “what to do next”. It is the principal claim of the present target article that the vertebrate brain incorporates a solution to this decision problem, that it takes the general form of a neural *analog reality simulation* of the problem space of the tri-partite interaction, and that the way this simulation is structured constitutes a conscious mode of function. It equips its bearers with veridical experience of an external world and their own tangible body maneuvering within it under the influence of feelings reflecting momentary needs, i.e. what we normally call reality.² To this end it features an analog (spatial) mobile “body” (action domain) embedded within a movement-stabilized analog (spatial) “world” (target domain) *via* a shared spatial coordinate system, subject to bias from motivational variables, and supplying a premotor output for the control of the full species-specific orienting reflex. The crucial separation of body and world on which this arrangement hinges has recently been worked out in formal terms by David Philipona and colleagues (Philipona et al. 2003, 2004).

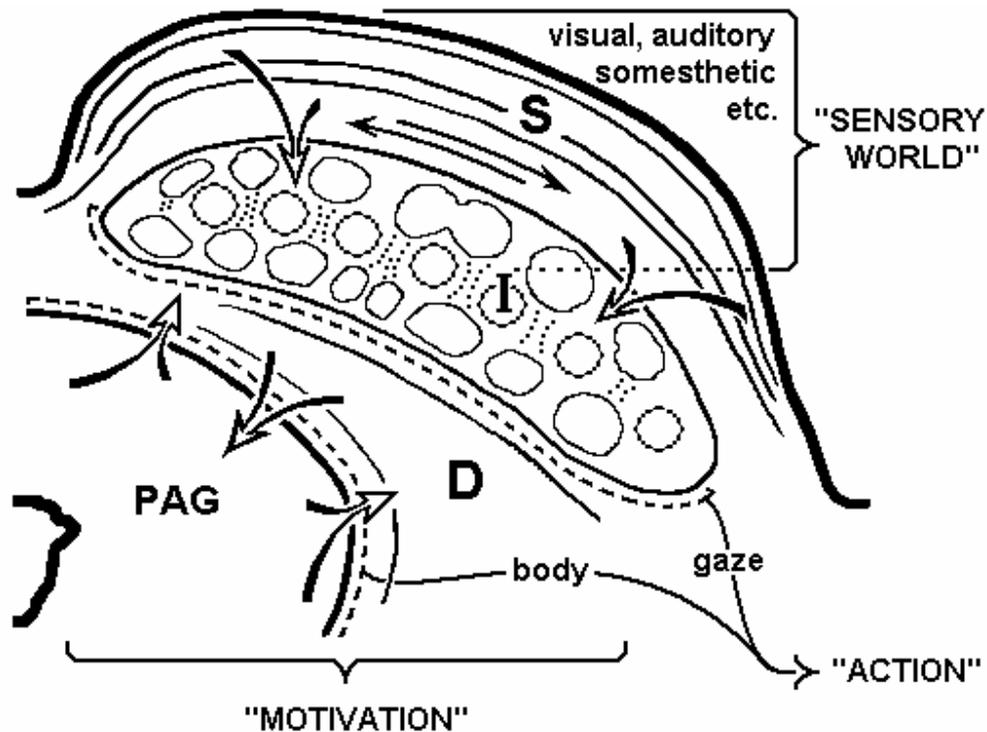
We have already seen in Sections 3.2 and 4.1 that the roof of the midbrain of vertebrates houses a sophisticated laminar superposition of the spatial senses in a pre-motor framework for orienting. It appears to contain the essential signals for bringing these senses into registry (Jay & Sparks 1987; Van Opstal et al. 1995; Groh & Sparks 1996; Populin & Yin 1998; Krauzlis 2001; Zella et al. 2001) and for stabilizing the

world relative to the body. Such stabilization is likely to utilize not only vestibular information (Bisti et al. 1972; Horowitz et al. 2005), but cerebellar “decorrelation” as well (Dean et al. 2002, 2004; cf. Hirai et al. 1982; May et al. 1990; Niemi-Junkola & Westby 2000; Guillaume & Pélisson 2001). The layered spatial maps in the roof of the midbrain would, in other words, represent the vertebrate brain’s first bid for an analog simulation of a distal “world” (Scheibel & Scheibel 1977). We also saw that the other pole of the “optic brain”, the hypothalamus, houses the basic circuitry for regulating and integrating motivational states related to goal-directed behaviors. Its output is brought to bear on the intermediate and deep layers of the superior colliculus not only by direct projections (Beitz 1982; Rieck et al. 1986), but indirectly, via massive and organized projections from hypothalamic nuclei to different sectors of the periaqueductal gray substance (see refs. 36, 37, 39, 222 & 256 in Swanson 2000; Goto et al. 2005).

The periaqueductal gray is a midbrain territory intimately related to the deeper collicular layers. It surrounds the cerebral aqueduct, and plays a critical role in the expression of a variety of emotion-related behaviors such as defensive, aggressive, sexual, vocal and pain-related ones (Fernandez de Molina & Hunsperger 1962; Adams 1979; Panksepp 1982, 1998; Jurgens 1994; Behbehani 1995; Holstege et al. 1996; Lonstein et al. 1998; Mouton 1999; Watt 2000; Kittleberger et al. 2006). Its longitudinal columns are functionally organized in terms of high-level tasks, goals, strategies, or contexts, such as “inescapable versus escapable pain” (Keay & Bandler 2002). It achieves particular prominence in mammals, and stimulating it electrically in conscious humans evokes powerful emotional reactions (Nashold et al. 1969; Heath 1975; Iacono & Nashold 1982). Functionally the periaqueductal gray is continuous and reciprocally interconnected with the immediately overlying deep layers of the superior colliculus (Sprague et al. 1961; Grofova et al. 1978; Cadusseau & Roger 1985; Harting et al. 1992, fig. 27; Wiberg 1992; Gordon et al. 2002; Bittencourt et al. 2005). Here, then, in the intermediate and deep collicular connections with hypothalamus and periaqueductal gray, lies a connective interface between the brain’s basic motivational systems and the orienting machinery of the collicular analog “world”.

The third member of the selection triangle enters this system through the prominent projections from the substantia nigra to the intermediate collicular layers (Mana & Chevalier 2001; Jiang et al. 2003; see also Sections 3.1 and 3.2). Here the final distillate of basal ganglia action-related information is interdigitated with the lattice-work of histochemically defined compartments that organize the input-output relations of the intermediate colliculus (Graybiel 1978; Illing & Graybiel 1986; Illing 1992; Harting et al. 1997). It appears, in other words, that the territory extending from the dorsal surface of the midbrain to the aqueduct houses the connectivity needed to implement a three-way interface of the kind outlined in the foregoing, and it is hereby proposed to do so. The elements of this scheme are sketched in Fig. 4.

Figure 4. The three principal domains of “world” (target selection), “body” (action selection), and “motivation” (needs) that must interact to optimize decision processes in real time, portrayed in their proposed “primary” implementation in the roof of the midbrain. The extension of its logic into the forebrain, and the cerebral cortex of mammals in particular, can be conceived in terms of this primary system “writ large”, as follows (cf. Fig. 6 in particular): A dorsolateral to ventromedial path from the surface of the colliculus to the midbrain aqueduct corresponds to a posterior to frontal to medial path in the cortex. In the reverse direction, and in functional terms, it reads “motivation”, “action” and “world”. **S**, **I** and **D**: superficial, intermediate and deep layers of the superior colliculus, respectively. **PAG**: the periaqueductal gray matter surrounding the midbrain cerebral aqueduct. Bidirectional arrow aligned with the collicular lamina stand for compensatory coordinate transformations. Drawing based in part on Harting et al. 1997.



Such a conception fits seamlessly with the proposed role of the superior colliculus in target selection outlined in section 3.2 above. As noted there, the selection of a target for action is the final event in the brain's real-time decision-making regarding "what to do next". The significance of gaze control, moreover, goes far beyond the matter of moving eyes-and-head in space: the gaze plays an organizing role in a wide range of behaviors by "leading" many forms of action, as has been shown in exquisite detail for manual reaching and manipulation (Johansson et al. 2001; see also Werner et al. 1997; Stuphorn et al. 2000; Schneider & Deubel 2002; Courjon et al 2004; Jackson et al. 2005). Nor is the output of the tecto-periaqueductal system limited to the species-specific orienting reflex: it includes escape behavior (Sprague et al. 1961; Merker 1980; Dean et al. 1989) as well as a number of innate postural schematisms associated with behaviors under periaqueductal control (Holstege et al. 1996; Lonstein et al. 1998).

In its primitive beginnings, the "world" of the proposed neural reality simulator presumably amounted to no more than a two-dimensional screen-like map of spatial directions on which potential targets might appear as mere loci of motion in an otherwise featureless noise field, defined more by their displacement than by any object features (see Stoerig & Barth 2001, for a plausible simulation). Advances on this primitive arrangement apparently proceeded by adding to it more sophisticated information from a rostral direction. Thus the ability of a frog to side-step stationary barriers during prey-catching is dependent upon input to the tectum from the region of the caudal thalamus and pretectum, just anterior to the tectum (Ewert 1968; Ingle 1973b). With the elaboration of the telencephalon, culminating in the neocortex of mammals, the arrangement was expanded further (see Section 4.5), into a fully articulated, panoramic three-dimensional world composed of shaped solid objects: the world of our familiar phenomenal experience.

4.3 Inhabiting a neural simulation

Whether primitive or advanced the fundamental simplifying device of the proposed simulation space is to associate the origin of its shared body-world coordinate system for orienting with the head representation of its analog body. This does *not* mean that the coordinate system itself is head centered (i.e. moves with the head). At brainstem levels it appears, rather, to be oculocentric (Moschovakis & Highstein 1994;

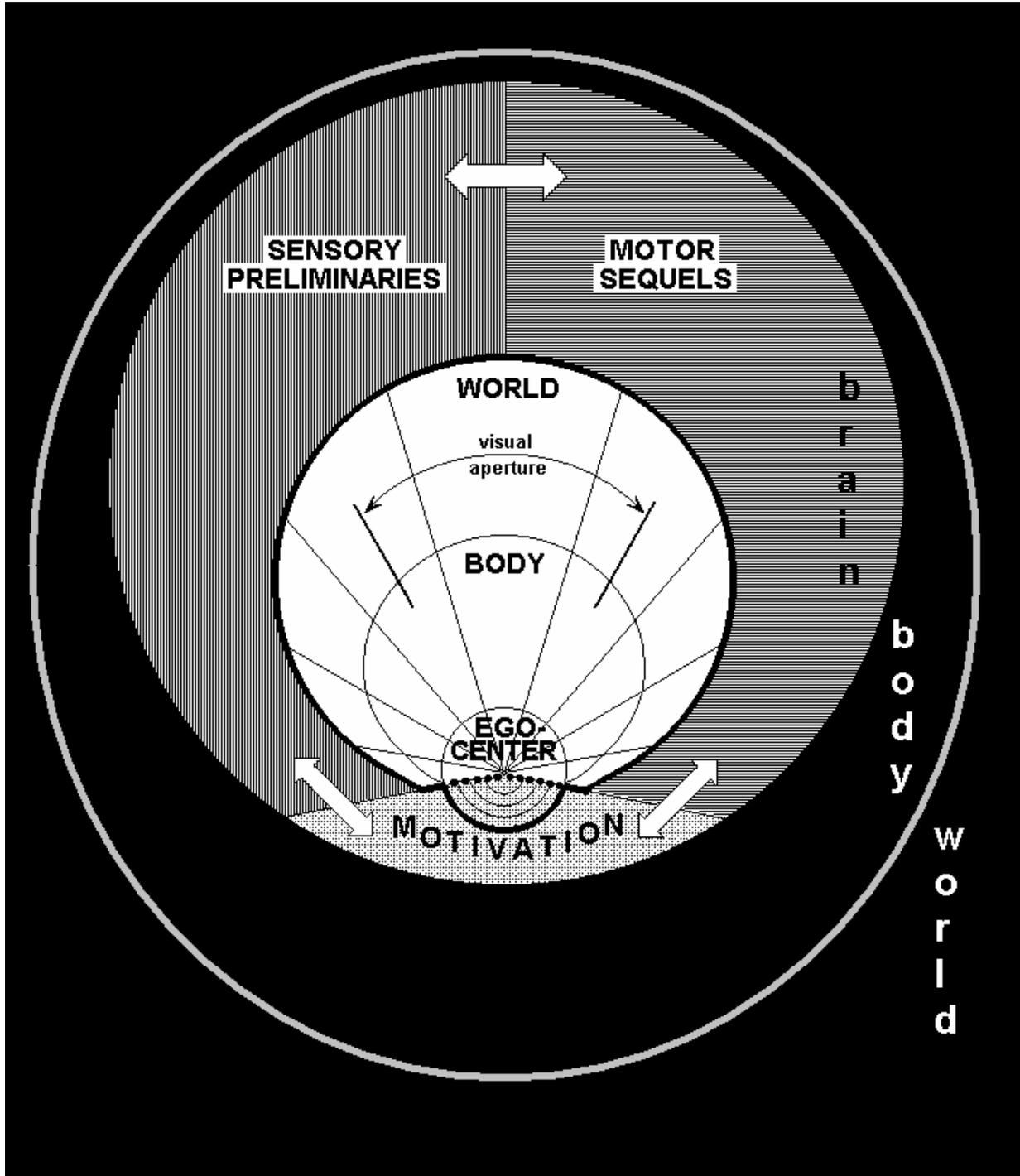
Moschovakis 1996; Klier et al. 2001). It means only that the coordinate system origin is lodged in the head representation of the simulated analog *visual* body, say in close proximity to its analog eye region. With such a location, a number of sensory-sensory mismatches and the contamination of sensory information by movement caused by the largely rotary displacements of eyes and head involved in perpetual orienting movements can be remedied – to a first approximation – by spherical coordinate transformations. This economy of control helps explain the fact that at the brainstem level not only eye movements but also head movements, despite their very different musculo-skeletal demands, utilize a common intermediate control system organized in separate horizontal and vertical, i.e. spherical, coordinates (Grobstein 1989; Masino & Grobstein 1989; Masino & Knudsen 1990; Masino 1992). In humans, covert orienting of attention as well as the visuomotor map for reaching (Vetter et al. 1999; Gawryszewski et al. 2005) appear to be framed in spherical coordinates.³

There is reason to believe that the implicit “ego-center” origin of this coordinate space is the position we ourselves occupy when we are conscious, and that the analog body and analog world of that space is what we experience as and call our tangible, concrete body and the external world (cf. footnote 2). This would explain the irreducible asymmetry adhering to the relation between perceiving subject and apprehended objects defining the conscious state: the ego-center places the conscious subject in an inherently “perspectival”, viewpoint-based, relation to the contents of sensory consciousness. It is from there objects are apprehended, objects do not apprehend the subject (cf. Merker 1997). By the same token, the one necessary constituent of consciousness that can never be an object of consciousness is that very vantage point itself, namely the origin of the coordinate system of the simulation space. It cannot be an object of consciousness any more than an eye can see itself (Schopenhauer 1819, vol. 2, p. 491; see Baars 1988, pp. 327ff for this and other “contextual” aspects of consciousness).

Should these reasons appear somewhat abstract and rarefied, there is a far more concrete indication to the same effect: our very body bears a tell-tale sign allowing us to recognize it as the product of a neural simulation. Vision differs topologically from somesthesia and audition by its limited angular subtense, particularly in animals with frontally directed eyes. The other two senses can be mapped *in toto* onto a spherical coordinate system for orienting, while vision is only partially thus mapped. This is not in itself a problem, but becomes one given that vision can be directed not only to the external world but to the body itself. This necessitates some kind of junction or transition between the distal visual world and the proximal visual body, and there a problem does arise.

Though as we have seen the ego-center is present in consciousness by implication only, its location can be determined empirically (Hering 1879; Roelofs 1959; Howard & Templeton 1966; Cox 1999; Neelon et al. 2004). It is single, and located behind the bridge of the nose inside our head. From there we *appear* to confront the visible world directly through an empty and single cyclopean aperture in the front of our head (Hering 1879; Julesz 1971). Yet that is obviously a mere appearance, since if we were literally and actually located inside our heads we ought to see not the world but the anatomical tissues inside the front of our skulls when looking. The cyclopean aperture is a convenient neural fiction through which the distal visual world is “inserted” through a missing part of the proximal visual body, which is “without head” as it were or, more precisely, missing its upper face region (see Harding 1961). Somesthesia by contrast maintains unbroken continuity across this region. The empty opening through which we gaze out at the world betrays the simulated nature of the body and world that are given to us in consciousness. The essentials of the arrangement are depicted in highly schematic form in Fig. 5.

Figure 5. Highly schematic depiction of the nested relation between ego-center, neural body and neural world constituting the analog neural simulation (“reality space”) proposed as a solution to the tri-partite selection problem described in the text. Black depicts the physical universe, one part of which is the physical body (black oval), both of which are necessarily outside of consciousness. One part of the physical body is the physical brain (circle; shaded and unshaded). The heavy black line separating the reality space from other functional domains within the brain indicates the exclusion of those domains from consciousness (unshaded). Arrows mark interfaces across which neural information may pass without entering consciousness. The designation ego-center is a sensorimotor construct unrelated to the concept of self-consciousness. See text for further details.



The simulated nature of our body and world is further supported by a number of phenomena that alert us to the synthetic nature of what we typically take to be physical reality itself, i.e. phenomena such as inattention blindness, change blindness and allied effects (Rensink et al. 1997; Simon & Chabris 1999; O'Reagan et al. 2000; Rensink 2002). Such "deletions from consciousness" can be countered by appropriately placed microstimulation of the superior colliculus (Cavanaugh & Wurtz 2004). These various indications all support the conclusion that what we confront in sensory consciousness is indeed a

simulated (synthetic) world and body.

As central residents of that simulation we are subject to ever shifting moods, feelings, urges, emotions and impulses. These, then, would be those aspects of the brain's motivational dynamics that reach consciousness (cf. Panksepp 1982, 1998; Cabanac 1992). The reason they do so, according to the present proposal, is their relevance to the tripartite determination of what to do next, as outlined in the foregoing. A striking illustration of this principle is afforded by respiratory control (Merker 2005). It is automatic and unconscious as long as partial pressures of blood gases stay within normal bounds, yet intrudes most forcefully on consciousness in the form of an acute sense of panic when they go out of bounds. Extreme blood gas values are an indication that urgent action on the environment – such as removing an airway obstruction or getting out of a carbon dioxide filled pit – may be imperative. That is what suddenly makes action selection and target selection relevant to respiratory control, which accordingly “enters consciousness” in the form of a powerful feeling of suffocation.

This example further illustrates the lack of any necessary connection between cognitive sophistication and the reason for something to enter consciousness. Even quite elementary functions may benefit from the efficiency provided by the triangular action-target-motivation interface of consciousness. It serves optimal decision-making in real time, on the broad front of its tripartite information base, concisely packaged in its multivariate simulation space. Such a utility is particularly valuable when a moment's hesitation may make a big difference in outcome, as in the suffocation example (but also in, say, agonistic encounters), quite apart from anything to do with advanced cognition. The evolution of such a utility could accordingly proceed independently of cognitive capacity, to crown the optic brain with its tectal machinery at the very outset of the vertebrate lineage, at a time when the telencephalon was still largely devoted to olfaction.

In its peculiar nesting of a body inside a world around an ego-center in a shared coordinate space subject to motivational bias, this interface possesses the essential attributes of phenomenal consciousness. As implemented in the midbrain and diencephalon, the arrangement is proposed to have served as the innate core and prototype on which all further elaboration of conscious contents was subsequently built. Centered on the colliculus extending into periaqueductal gray, it will be further defined in Section 4.5 below. A felicitous term for the functional state supported by the basic (mesodiencephalic) prototype arrangement would accordingly be “primary consciousness” (Hodgson 1878; Petty 1998; Trevarthen & Reddy in press).

4.4 Coherent, motivated behavior under sensory guidance in the absence of the cerebral cortex

The superordinate functional position attributed to mesodiencephalic mechanisms in previous sections is supported by a number of empirical findings that receive a unified interpretation in its light. When the behavioral effects of local brain stimulation are systematically surveyed by means of depth electrodes it is common to find that the most coherent, integrated and natural-looking (whole, or “molar”) behavioral reactions – be they orienting, exploration, or a variety of appetitive, consummatory, and defensive behaviors – are evoked by stimulation of diencephalic and midbrain sites, while stimulation at more rostral or caudal levels tends to evoke more fragmentary or incomplete behaviors (Bard 1928; Hess & Brugger 1943; Kaada 1951; Hess 1954; Hunsperger 1956; Fernandez de Molina & Hunsperger 1962; Hunsperger 1963; Hunsperger & Bucher 1967; Schaefer & Schneider 1968; Orlovsky & Shik 1976; Adams 1979; Carrive et al. 1989; Schuller & Radtke-Schuller 1990; Bandler & Keay 1996; Brandao et al. 1999; Holstege & Georgiadis 2004).

All of the behaviors just mentioned are also exhibited by experimental animals after their cerebral cortex is removed surgically, either in adulthood or neonatally. Best studied in this regard are rodents (Woods 1964; Wishaw 1990). After recovery, decorticate rats show no gross abnormalities in behavior that would allow a casual observer to identify them as impaired in an ordinary captive housing situation, though an experienced observer would be able to do so on the basis of cues in posture, movement and appearance (Wishaw 1990, on which what follows relies, supplemented by additional sources as indicated). They stand, rear, climb, hang from bars and sleep with normal postures (Vanderwolf et al. 1978). They groom, play (Pellis et al. 1992; Panksepp et al. 1994), swim, eat, and defend themselves (Vanderwolf et al. 1978)

in ways that differ in some details from those of intact animals, but not in outline. Either sex is capable of mating successfully when paired with normal cage mates (Carter et al. 1982; Whishaw & Kolb 1985), though some behavioral components of normal mating are missing and some are abnormally executed. Neonatally decorticated rats as adults show the essentials of maternal behavior which, though deficient in some respects, allows them to raise pups to maturity. Some, but not all, aspects of skilled movements survive decortication (Whishaw and Kolb 1988), and decorticate rats perform as readily as controls on a number of learning tests (Oakley 1983). Much of what is observed in rats (including mating and maternal behavior) is also true of cats with cortical removal in infancy: they move purposefully, orient themselves to their surroundings by vision and touch (as do the rodents), and are capable of solving a visual discrimination task in a T-maze (Bjurstén et al. 1976; see also Bard & Rioch 1937).

The fact that coherent and well-organized molar behaviors are elicited by local stimulation in the mesodiencephalic region of intact animals and that coherent motivated behavior under environmental guidance is displayed spontaneously by animals lacking a cerebral cortex means that the neural mechanisms required to motivate, orchestrate and provide spatial guidance for these behaviors are present in the parts of the brain that remain after decortication. Some aspects of these behaviors are dependent upon basal ganglia and basal forebrain functions remaining after the loss of their principal (cortical) source of afference (Whishaw 1990, p. 246), while the basic competences of decorticate animals reflect the capacity of upper brainstem mechanisms to sustain the global patterning, emotional valence, and spatial guidance of the postures and movements of orienting, defense, aggression, play, and other appetitive and consummatory behaviors (Adams 1979; Sakuma & Pfaff 1979; Panksepp 1982; Masino 1992; Swanson 2000; Holstege & Georgiadis 2004; Maskos et al. 2005). The particulars of the dependence of these behaviors on key structures located in the mesodiencephalic region has been repeatedly reviewed (Swanson 1987, 2000; ten Donkelaar 1988; Houk 1991; Padel 1993; Jürgens 1994; Behbehani 1995; Haber & Fudge 1997; Panksepp 1998; Winn 1998; Mouton 1999; Prescott et al. 1999; Watt 2000; Horvitz 2000; Bassett & Taube 2001; Groenewegen 2003; Watt and Pincus 2004; Zahm 2006).

It is into the premotor circuitry of these ancient and highly conserved upper brainstem mechanism that a wide range of systems place their bids for “where to look” and “what to do”, irrespective of the level of sophistication of any one of these “bidding” systems. Each of them has independent access to effectors, and their upper brainstem interactions are not infrequently mediated by collaterals of such projections. The cerebral cortex is one prominent input to this system through the direct and indirect fiber projections emphasized in the foregoing and sketched in Fig. 3 (see also Swanson 2000; Zahm 2006). This relationship is, however, not a one-way affair. In fact, the manner in which the telencephalon is interfaced and integrated with the mesodiencephalic control system adds further definition to the central role of upper brainstem mechanisms in conscious functions.

4.5 Including the forebrain

Three cortical regions figure repeatedly and prominently in studies of cerebral mechanisms related to attention, neglect and consciousness, namely the posterior parietal cortex, the prefrontal cortex and a medial territory centered on the cingulate gyrus (Posner & Petersen 1990; Lynch et al. 1994; Corbetta 1998; Mesulam 1999; Rees & Lavie 2001; Clower et al. 2001; Baars et al. 2003, fig. 1; Han et al. 2003; Blumenfeld & Taylor 2003). A special connective and functional relationship exists between these three cortical territories and the mesodiencephalic system outlined in the foregoing. It is most easily approached by considering their mutual interface in the nuclei of the dorsal thalamus. The latter can be divided into first-order (largely sensory relay) and higher-order (“association”) thalamic nuclei (Sherman & Guillery 2001), and it is with the latter, higher-order nuclei, that the mesodiencephalic system maintains an intimate and complex relationship.

The two major higher-order nuclei of mammals are the mediodorsal nucleus, whose cortical projections define the prefrontal cortex, and the pulvinar complex related to a set of posterior cortical areas, including extrastriate visual areas such as those of the posterior parietal cortex. Though proposed to serve as thalamic relays for cortico-cortical interactions (Sherman & Guillery 2001), these nuclei are not devoid of

extra-telencephalic input, and both receive prominent input from the superior colliculus (Benevento & Fallon 1975; Harting et al. 1980; Lyon et al. 2005). Afferents to the pulvinar originate largely from the superficial collicular layers, while those destined for the mediodorsal nucleus are predominantly of intermediate layer origin. The latter projection targets a zone at the lateral edge of the mediodorsal nucleus related to the frontal eye fields (see Sommer & Wurtz 2004), the cortical territory most directly implicated in unilateral neglect of frontal origin (see Mesulam 1999, and references therein).

The cingulate gyrus, finally, is related to the mesodiencephalic system by its projections to the intermediate and deep layers of the colliculus (Sherman et al. 1979; Harting et al. 1992), the periaqueductal gray matter (An et al. 1998; Floyd et al. 2000), and by a conspicuously heavy projection to the *zona incerta* (Mitrofanis & Mikuletic 1999, Figs. 6, 7). This latter structure is a mammalian derivative of the ventral thalamus of comparative terminology mentioned in section 4.1, and has emerged from obscurity only recently (see review by Mitrofanis, 2005). It sends topographically organized inhibitory projection to the superior colliculus, and reaches up into the thalamus above it to selectively innervate its higher-order nuclei bilaterally, likewise with powerful GABAergic inhibition (Power et al. 1999; Barthó et al. 2002; Trageser & Keller 2004; Lavallée et al. 2005).

Collicular input to the higher-order nuclei is excitatory, while their incertal input is inhibitory. This implies dynamic competition between colliculus and *zona incerta* for influence over the two principal thalamic dependencies of the prefrontal and the posterior parietal cortex. In this competition the inhibitory incertal element stands under cingulate cortex influence and is also in a position to inhibit the colliculus directly and with topographic specificity (Ficalora & Mize 1989; Kim et al. 1992; Ma 1996; May et al. 1997). These circumstances cannot but profoundly affect the functional dynamics of the three cortical territories with which we are concerned. The principal pathways relating them to the mesodiencephalic control system and the higher-order thalamic nuclei are depicted schematically in Fig. 6.

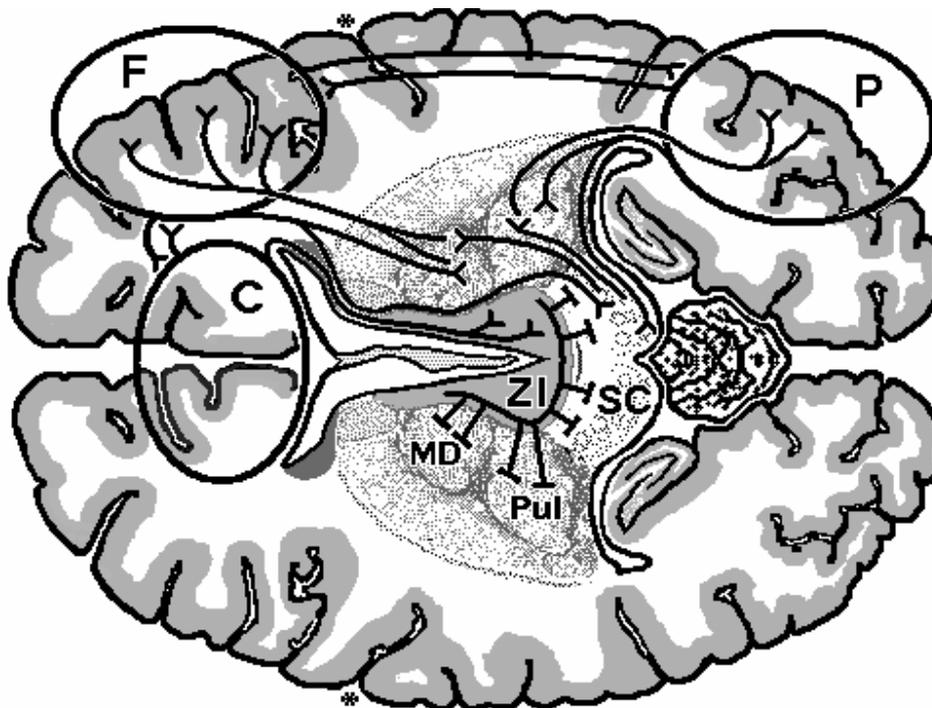


Figure 6. Composite diagram illustrating the interface between the mesodiencephalic system and the thalamocortical complex. Principal pathways by which the superior colliculus and the *zona incerta* relate to one another as well as to the dorsal thalamus and the cerebral cortex are indicated in black heavy lines. Excitatory connections end in a “Y”, inhibitory connections in a “T”. Abbreviations: **P**: parietal; **F**: frontal; **C**: cingulate cortex; **SC**: superior colliculus; **ZI**: zona incerta; **Pul**: pulvinar complex; **MD**: mediodorsal nucleus of the thalamus. The central sulcus is marked by an asterisk. See text for further detail.

Supplying a key node in the relations depicted in Fig. 6, the *zona incerta* is monosynaptically (and often reciprocally and bilaterally) connected with on the order of 50 separate structures along the entire length of the neuraxis from spinal cord to olfactory bulb (author's own conservative inventory of the literature, not counting connections with individual cortical areas separately). Internally, the *zona incerta* features ubiquitous mutual connectivity in a setting of cytoarchitectonic and cytological heterogeneity in which GABAergic cells are prominent (Benson et al. 1991, 1992; Nicolelis et al. 1992; see Power & Mitrofanis 1999, 2001; and Bartho et al. 2002, p. 1002 for connective details). A combination of reciprocal external connectivity with ubiquitous internal mutual inhibition is the theoretically optimal solution for implementing global competitive interaction among structures separated by long distances (see McFarland 1965; Snaith and Holland 1990; and Prescott et al. 1999, p. 27-29 for background). The *zona incerta* accordingly may implement such a scheme, and is hereby proposed to do so, as schematically illustrated in Fig. 7.

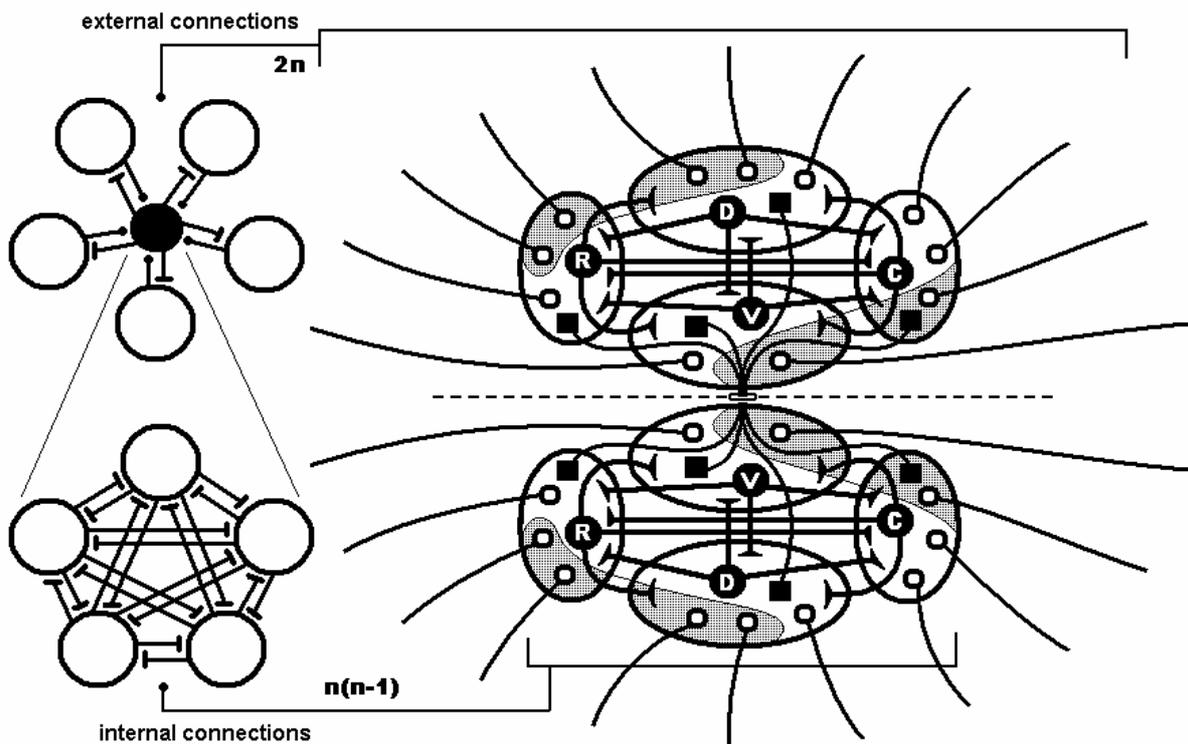


Figure 7. Schematic diagram of *zona incerta* connectivity to the rest of the brain and of its subdivisions to one another, depicted bilaterally to emphasize the prominent commissural, “midline-straddling”, nature of incertal connectivity. Ovals represent the principal incertal subnuclei, shown physically separated for graphical clarity. Labels R, D, V and C mark the rostral, dorsal, ventral and caudal subnuclei, respectively, and connections among them. Filled squares indicate that each subnucleus projects to all subnuclei on the opposite side. Open circles stand for incertal connections with the rest of the brain (typically reciprocal in nature). Shaded regions stand symbolically for the fact that functionally defined subregions of the *zona incerta* (sensory modalities, motor, limbic, etc.) often cut across its nuclear subdivisions. Inserts *on the left* summarize the two connective schemes that appear to be combined in the *zona incerta*. Long-distance (external) connections, for which wiring-efficiency is at a premium, connect n entities to a central hub (the *zona incerta* itself) by $2n$ (i.e. reciprocal) connections (expandable to new targets at the low cost of 2). Internal connectivity within the *zona incerta* (wiring efficiency *not* at a premium), by contrast, appears to follow the $n(n-1)$ connective principle (lower diagram, expanding the filled central circle of the upper diagram). The scheme as a whole idealizes evidence supplied by the pioneering studies of Mitrofanis and colleagues (references in the text), and awaits refinement in the light of further detailed studies.

The *zona incerta* – or the ventral thalamus of non-mammals – thus supplies the integrative machinery of the optic brain with a connective hub that seems designed to conduct mutually inhibitory trials of strength

among a truly diverse set of afferents. They include, but are not limited to, visual, auditory, somatosensory, vestibular (Horowitz et al. 2005), cerebellar, striatal, collicular, motor, and limbic ones. The outcome of the competition – i.e. a neural decision – is conveyed to the intermediate and deep layers of the superior colliculus by a topographically organized inhibitory projection, as already mentioned. The collicular return projection to the *zona incerta* – like that of many incertal afferents – is non-topographic, implying greater specificity of incertal influence over the colliculus than the reverse. At the same time incertal inhibitory output ascends into the association nuclei of the dorsal thalamus, establishing the *zona incerta* as a connective bridge straddling the mesodiencephalic and the thalamocortical systems.

Coupled with the scope of its connectivity along the neuraxis, this nodal position of the *zona incerta* lends it a potentially strategic role as an arbiter of moment to moment decision making “in the light of all available evidence”. As in the case of collicular target selection, the loss of such a high-level function need not generate conspicuous behavioral deficits, and does not appear to do so in rats with incertal lesions (Thompson & Bachman 1979). Rather, it would be expected to issue in suboptimal levels of resource allocation relative to shifting patterns of multiply interacting opportunities and needs. Preliminary indications regarding the great diversity and complexity of neuronal response properties in the *zona incerta* are worthy of note in this connection (Crutcher et al. 1980; Kendrick et al. 1991; Nicolelis et al. 1993; Ma 1996; Mungarndee et al. 2002).

Finally, the *zona incerta* lies in immediate anterior continuity with the prerubral field and rostral interstitial nucleus of the medial longitudinal fasciculus, i.e. with the rostral-most pole of the intermediate control system for orienting organized in spherical coordinates mentioned in Section 4.3, above. This rostral pole is specialized for vertical movement, while the system’s horizontal components are found farther caudally, in paramedian reticular structures extending into the pons. Could it be that the *zona incerta* supplies a kind of origin for this coordinate system, a midline-straddling point of unity connected directly and *via* the colliculus to the rest of the coordinate space (Leichnetz et al. 1987; Kolmac et al. 1998; Giolli et al. 2001)? Its population of omnipause neurons are at least compatible with such an eventuality (Hikosaka & Wurtz 1983; Ma 1996). Nothing would be more elegant than to lodge the final arbitration of “what to do next” in a winner-take-all self-inhibitory network supplying the origin of the coordinate system that controls the orienting movements which execute that decision once made. As a primary perspectival viewpoint charged with changing motives it would possess the essential attributes of a self (see Section 4.3 above). Prominent incertal afference from cingulate cortex would fit such a role (cf. Northoff et al. 2006 for medial cortex and self), but short of further evidence, the suggestion must remain speculative.

4.5.1. Collicular gamma oscillations and cortical “binding”

The superior colliculus is the only place outside of the cerebral cortex in which fast oscillations in the gamma range have been shown to occur and to behave in a manner paralleling in all significant respects that of the cortex (Brecht et al. 1998, 1999, 2001). At the cortical level such oscillatory activity has been proposed to serve a “binding” function for consciousness (in the sense of integrating disparate elements of unitary conscious percepts) on circumstantial grounds (Engel et al. 1999; Engel and Singer 2001; Singer 2001). As we shall see one need not, however, ascribe a unique role to gamma oscillations in either binding or consciousness to recognize that they may have consequences for cortico-collicular integration nevertheless.

Though sometimes portrayed as “the” problem of consciousness, the acuteness of the cortical binding problem must not be exaggerated. The pyramid architecture of point-to-point interareal connectivity within topographically organized cortical sensory domains ensures that corresponding points on areal topographies featuring different functional content (e.g. contour and color) are *connectively* and thus coherently related even though the areas themselves occupy separate locations in the cortical sheet (Felleman & VanEssen 1991; Merker 2004a, Fig. 2 and footnote 2 of that paper).

The laminar superposition of numerous cortical areas in the colliculus takes this principle further. Here the joining of corresponding points on different cortical maps takes place by direct laminar superposition of topographic projections of different cortical areas within a unified collicular topography. Thus the output of

different cortical areas are brought within the compass of the dendritic trees of single collicular neurons, which often straddle collicular laminar boundaries (Langer & Lund 1974; Laemle 1983; Ma et al. 1990; Albers & Meek 1991). Tight temporal synchrony of neuronal firing in separate cortical loci (through coupling to gamma oscillations) increases the probability that their joint activity will fall within the temporal window of integration of any neuron – whether cortical or subcortical – to which they project convergently (Abeles 1982; König 1996). Synchronous activation of corresponding loci on separate cortical maps would accordingly assist such activity in crossing collicular thresholds by summation *via* the dendritic trees of convergently innervated collicular cells.

In crossing the collicular threshold – whether assisted by gamma synchrony or not – cortical activity would gain access to the mesodiencephalic system in all its ramifications, projections to the cortex included (see Fig. 6). This, according to the present account, would be a principal step by which such activity enters awareness. If so, it follows that *no change in conscious contents should take place without involvement of the mesodiencephalic system (centered on the superior colliculus) as outlined here, even when that change is unaccompanied by eye movements*. This prediction is specific to the present perspective, and accordingly renders it testable. The means for doing so are exemplified by a recent functional imaging study of a visual-auditory illusion in humans (Watkins et al. 2006). That study revealed collicular activation associated with awareness of the illusion, though stimuli were identical on trials in which the illusion was not perceived, and central fixation was maintained throughout, confirming the above prediction in this particular instance.

This, then, would be the identity of the so far unidentified threshold featured in a recent programmatic proposal regarding conscious function (Crick & Koch 2003). Its above identification with the threshold for access to the mesodiencephalic system centered on the colliculus (Figs. 4 & 6) is reinforced by the fact that only cortical layer V pyramidal cells project to the colliculus. They exhibit a number of notable specializations: they do *not* give off collaterals to the thalamic reticular nucleus on passing through it (Jones 2002), their local intra-cortical connectivity appears stereotyped (Kozloski et al. 2001), and their apical dendrites branch in cortical layer I and carry specialized conductance mechanisms activated by top-down (feedback) connections in the superficial cortical layers (Larkum et al. 2004). This may ensure that activation of both the feedforward and feedback cortical system is typically required for the cortico-mesencephalic threshold to be crossed, such concurrent activation having been proposed as an essential condition for cortical information to reach awareness (Lamme & Spekreijse 2000; see also Merker 2004a, p. 566).

4.5.2 Consciousness and cortical memory

Penfield and Jasper proposed a role for the centrencephalic system in both consciousness and the laying down of cortical memories across the life span. A rationale for such a memory role is suggested by the present perspective. The perpetual and cumulative nature of cortical memory recording (Standing 1973; Merker 2004a, b) puts a premium on economy of storage, i.e. on concentrating memory recording to significant information (Haft 1998). A criterion for doing so is available in the system of integration for action as outlined here: information that is important enough to capture control of behavior (i.e. by triggering an orienting movement placing its target in focal awareness) is also important enough to be consigned to permanent cortical storage. The focal presence of the target obviously will be the greater part of ensuring such an outcome, but it is likely to be actively supported as well by the system of dual colliculo-thalamic relays to cortex (cf. Fig. 6). From its parietal and frontal target areas, accessed in part via so called matrix cell projections from the thalamus to the superficial cortical layers (Jones 1998), the mesodiencephalic influence would then propagate and spread through the cortex *via* intracortical top-down feedback connectivity.

The evidence for a “general learning system” (which includes the superior colliculus: Thompson 1993), mentioned in the introduction to Section 3 above, would seem to bear on this proposal as well. In fact, the severe capacity limitations of so called working memory (Baddeley 1992; Cowan 2001) are likely to derive in large part from the mesodiencephalic bottleneck which all attended (i.e. conscious) information must access according to the present proposal, just at the point where the parallel distributed data format of the

forebrain *requires* conversion to a serial, limited capacity format to serve behavior.

4.5.3 The zona incerta and the seizures of absence epilepsy

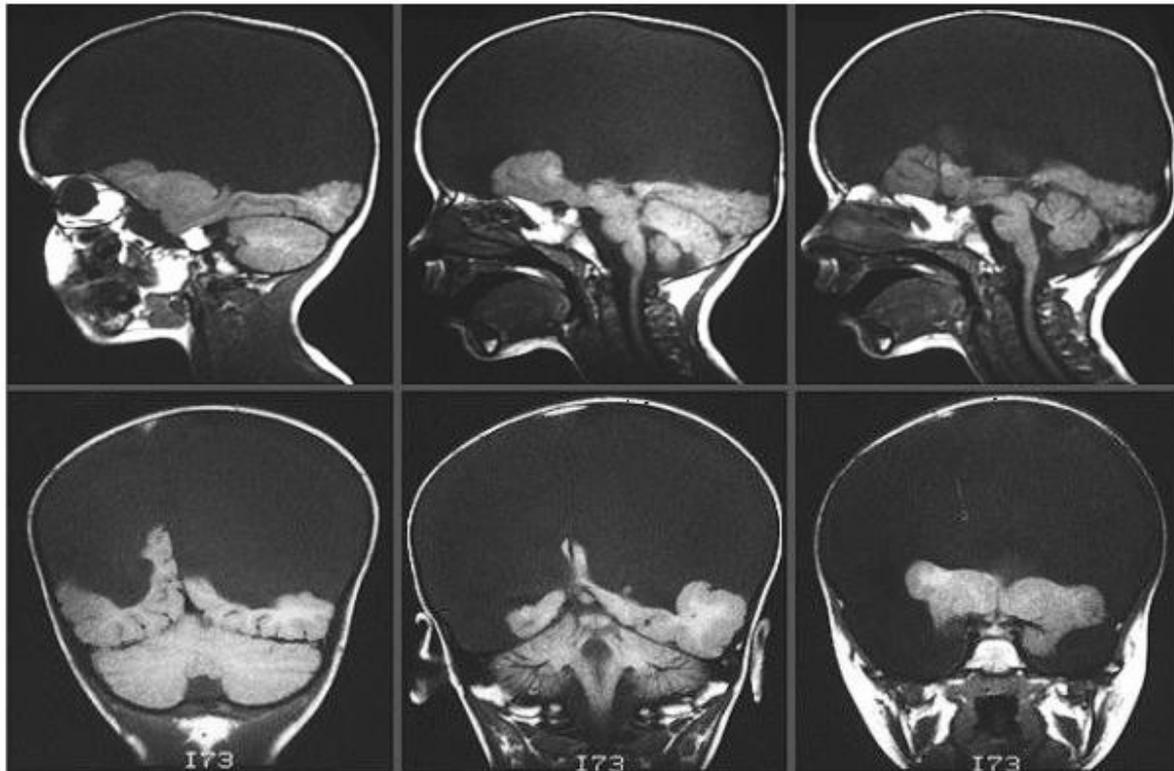
It is to be noted, finally, that the Penfield and Jasper postulation of a centrencephalic system *symmetrically related to both cerebral hemispheres* was motivated in part by observations on the generalized seizures of absence epilepsy. The *zona incerta* sends a rich complement of commissural fibers across the midline not only to itself, but to the association nuclei of the dorsal thalamus (Power & Mitrofanis 1999, 2001). It is also a prime locus for the induction of generalized epileptic seizures, being more sensitive than any other brain site to their induction by local infusion of carbachol (Brudzynski et al. 1995; see also Gioanni et al. 1991; Hamani et al. 1994). A number of phenomena that may accompany absence seizures can be readily related to the *zona incerta*. Thus a forward bending or dropping of the head (or bending of the whole body to the ground; Penfield & Jasper, 1954, p. 28) may relate to the already mentioned fact that the transition between the zona incerta and midbrain contains mechanisms for vertical control of eyes and head (Holstege & Cowie 1989; Waitzman et al. 2000; cf. Section 4.2, above). The fluttering of the eyelids that often occurs in the same situation is also easily accommodated by the functional anatomy of this region (Schmidtke & Buttner-Ennever 1992; Morcuende et al. 2002).

The Penfield and Jasper definition of their proposed centrencephalic system always included explicit reference to the midbrain reticular formation. The *zona incerta* resembles a forward extension of the midbrain reticular formation beneath the thalamus (Ramón-Moliner & Nauta 1966), and much of the functional anatomy of the diencephalon needs to be re-examined in light of its unusual connectivity. As noted by Barthó et al. (2002), the identification of a second, incertal, source of GABAergic innervation of the dorsal thalamus in addition to that of the thalamic reticular nucleus necessitates a re-evaluation of the entire issue of the nature of thalamic involvement in seizure generation and oscillatory thalamocortical activity (McCormick & Contreras 2001; Steriade 2001). This is all the more so since the even more recent discovery of a third source of powerful GABAergic thalamic inhibition, originating in the anterior pretectal nucleus (Bokor et al. 2005). One need not, however, await the outcome of such re-examination to identify the *zona incerta* as the perfect anatomical center-piece for the Penfield and Jasper centrencephalic hypothesis, though its obscurity at the time kept it from being recognized as such.

5. Consciousness in children born without cortex.

Anencephaly is the medical term for a condition in which the cerebral hemispheres either fail to develop for genetic-developmental reasons or are massively compromised by trauma of a physical, vascular, toxic, hypoxic-ischemic or infectious nature at some stage of their development. Strictly speaking the term is a misnomer. The brain consists of far more than cerebral hemispheres or prosencephalon, yet various conditions of radical hemispheric damage are historically labelled anencephaly. When the condition is acquired, e.g. by an intrauterine vascular accident (stroke) of the fetal brain, the damaged forebrain tissue may undergo wholesale resorption. It is replaced by cerebrospinal fluid filling otherwise empty meninges lining a normally shaped skull, as illustrated in Fig. 8. The condition is then called hydranencephaly (Friede 1989), and is unrelated to the far more benign condition called hydrocephalus, in which cortical tissue is compressed by enlarging ventricles but is present in anatomically distorted form (Sutton et al. 1980).

Figure 8. Sagittal and frontal magnetic resonance images of the head of a child with hydranencephaly. Spared ventromedial occipital and some midline cortical matter overlies an intact cerebellum and brainstem, while the rest of the cranium is filled with cerebrospinal fluid. Reprinted with the kind permission of the American College of Radiology (ACR Learning File, Neuroradiology, Edition 2, 2004).



The loss of cortex must be massive to be designated hydranencephaly, but it is seldom complete (see Fig. 8). It typically corresponds to the vast but somewhat variable forebrain expanse supplied by the anterior cerebral circulation (Myers 1989; Wintour et al. 1996). Variable remnants of cortex supplied by the posterior circulation, notably inferomedial occipital, but also basal portions of temporal cortex, and midline cortical tissue along the falx extending into medial frontal cortex, may be spared. The physical presence of such cortical tissue, clearly visible in Fig. 8, need not mean, however, that it is connected to the thalamus (white matter loss often interrupts the visual radiations, for instance) or that it is even locally functional. On autopsy such tissue may be found to be gliotic on microscopic examination or to exhibit other structural anomalies indicating loss of function (Takada et al. 1989; Marin-Padilla 1997). As Fig 8 shows, most cortical areas are simply missing in hydranencephaly, and with them the organized system of corticocortical connections that underlie the integrative activity of cortex and its proposed role in functions such as consciousness (Sporns et al. 2000; Baars et al. 2003).

An infant born with hydranencephaly may initially present no conspicuous symptoms (Andre et al. 1975), and occasionally the condition is not diagnosed until several months postnatally, when developmental milestones are missed. In the course of the first year of life, which is often though not invariably difficult, these infants typically develop a variety of complications which always include motoric ones (tonus, spasticity, cerebral palsy), and often include seizures, problems with temperature regulation, reflux/aspiration with pulmonary sequelae and other health problems occasioning medical emergencies and attended by a high mortality rate. Were one to confine one's assessment of the capacities of children with hydranencephaly to their presentation at this time – which for natural reasons is the period in the lives of these children to which the medical profession has the most exposure – it would be all too easy to paint a dismal picture of incapacity and unresponsiveness as the hydranencephaly norm. When, however, the health problems are brought under control by medication and other suitable interventions such as shunting to relieve intracranial pressure, the child tends to stabilize and with proper care and stimulation can survive for years and even decades (Hoffman & Liss 1969; McAbee et al. 2000; Covington et al. 2003; Counter 2005).

When examined after such stabilization has taken place, and in the setting of the home environment upon which these medically fragile children are crucially dependent, they give proof of being not only awake, but of the kind of responsiveness to their surroundings that qualifies as conscious by the criteria of ordinary neurological examination (Shewmon et al. 1999). The report by Shewmon and colleagues is the only published account based upon an assessment of the capacities of children with hydranencephaly under near optimal conditions, and the authors found that each of the four children they assessed was conscious. For detail, the reader is referred to the case reports included in the Shewmon et al. publication. Anecdotal reports by medical professionals to the same effect occasionally see print (Counter, 2005), but compared to its theoretical and medical importance the issue remains woefully underexplored.

To supplement the limited information available in the medical literature on the behavior of children with hydranencephaly, the present author joined a worldwide internet self-help group formed by parents and primary caregivers of such children in February of 2003. Since then he has read more than 26,000 e-mail messages passing between group members. Of these he has saved some 1,200 messages containing informative observations or revealing incidents involving the children. In October 2004 he joined five of these families for one week as part of a social get-together featuring extended visits to DisneyWorld with the children, who ranged in age from 10 months to 5 years. The author followed and observed their behavior in the course of the many private and public events of that week, and documented it with four hours of video recordings.

The author's impression from this first-hand exposure to children with hydranencephaly roundly confirms the account given by Shewmon and colleagues. These children are not only awake and often alert, but show responsiveness to their surroundings in the form of emotional or orienting reactions to environmental events (see Fig. 9 for an illustration), most readily to sounds but also to salient visual stimuli (optic nerve status varies widely in hydranencephaly, see below). They express pleasure by smiling and laughter, and aversion by "fussing", arching of the back and crying (in many gradations), their faces being animated by these emotional states. A familiar adult can employ this responsiveness to build up play sequences predictably progressing from smiling, over giggling to laughter and great excitement on the part of the child. The children respond differentially to the voice and initiatives of familiars, and show preferences for certain situations and stimuli over others, such as a specific familiar toy, tune or video program, and apparently can even come to expect their regular presence in the course of recurrent daily routines.



Figure 9. The reaction of a three year old girl with hydranencephaly in a social situation in which her baby brother has been placed in her arms by her parents, who face her attentively and help support the baby while photographing.

Though behavior varies from child to child and over time in all these respects, some of these children may even take behavioral initiatives within the severe limitations of their motor disabilities, in the form of instrumental behaviors such as making noise by kicking trinkets hanging in a special frame constructed for the purpose ("little room"), or activating favorite toys by switches, presumably based upon associative learning of the connection between actions and their effects. Such behaviors are accompanied by situationally appropriate signs of pleasure or excitement on the part of the child, indicating that they involve the kind of coherent interaction between environmental stimuli, motivational-emotional mechanisms, and bodily actions for which the mesodiencephalic system outlined in this article is proposed to have evolved. The children are, moreover, subject to the seizures of absence epilepsy. Parents recognize these lapses of accessibility in their children, commenting on them in terms such as "she is off talking with the angels", and they have no trouble recognizing when their child "is back". As discussed earlier, episodes of absence in this form of epilepsy represent a basic affliction of consciousness (cf. Blumenfeld & Taylor 2003). The fact that these children exhibit such episodes would seem to be a weighty piece of evidence regarding their conscious status.

In view of the functional considerations reviewed in the foregoing, none of these behavioral manifestations in children with hydranencephaly ought to occasion any surprise, and no special explanations such as neural reorganization based on plasticity are needed to account for them. Rather, they are what the nodal position of mesodiencephalic mechanisms in convergent neural integration, along with the comparative evidence regarding the behavior of mammals in the absence of cerebral cortex, lead us to expect. Nor is there much warrant for attempting to attribute these behaviors to remnant cortical tissue. Besides the questionable functional status of spared cortex already alluded to, a significant functional asymmetry speaks directly against it. As common as it is for some occipital cortex to remain in these individuals, as rare is it for any auditory cortex to be spared. Yet sensory responsiveness in hydranencephaly shows the opposite asymmetry: hearing is generally preserved while vision tends to be compromised (Hydranencephaly group survey 2003). The pattern is easily accounted for by the intactness of the brainstem auditory system in these children (Lott et al. 1986; Yuge & Kaga 1998), crowned by a projection from inferior to superior colliculus. By contrast, vision in these children is liable to be compromised already at the level of the optic nerve. The latter's blood supply through the anterior cerebral circulation exposes it to damage in hydranencephaly, and its status varies widely in affected children (Jones & France 1978).

What is surprising, instead, is the routine classification of children with hydranencephaly into the diagnostic category of "vegetative state" (Multi-Society Task Force 1994), apparently in conformity with a theoretical identification between the cortex as an anatomical entity and consciousness as a function. It is this very identification which has been under critical examination in the present target article. To the extent to which the arguments and the evidence presented here have any merit such an identification is not tenable, and the routine attribution of a lack of awareness to children lacking cortex from birth would accordingly be inadmissible. The extent of awareness and other capacities in these children must be based on assessment in its own right, by appropriate neurological tests, and not by reference to the status of their cortical tissue (Shewmon 2004). Moreover, considering the medically fragile status of many of these children, such behavioral assessment must be performed under optimal circumstances.

Properly assessed, the behavior of children with early loss of their hemispheres opens a unique window on the functional capacities of a human brainstem deprived of its cerebral cortex early in intrauterine development. They tell us, for one thing, that the human brainstem is specifically human: these children smile and laugh in the specifically human manner, which is different from that of our closest relatives among the apes (van Hooff 1972; Provine & Yong 1991). This means that the human brainstem incorporates mechanisms implementing specifically human capacities, as shown long ago by the neurologist Gamper on the basis of his detailed cinematographically documented account of a congenitally anencephalic girl entrusted to his care (Gamper, 1926). In her case there is no possibility that remnant hemispheric tissue might account for her human smile, since detailed post-mortem histology disclosed that she had no neural tissue above the level of the thalamus, and even her thalamus was not functional.

The implication of the present account is that unless there are further complications such a child should be *expected* to be conscious, i.e. possessed of the primary consciousness by which environmental sensory

information is related to bodily action (such as orienting) and motivation/emotion through the brainstem system outlined in the foregoing. The basic features of that system evolved long before the cerebral hemispheres embarked on their spectacular expansion in mammals to supply it with a new form of information based upon cumulative integration of individual experience across the lifetime (for which see Merker, 2004a). Now as then this brainstem system performs for cortex, as for the rest of the brain, its basic function of integrating the varied and widely distributed information needed to make the best choice of the very next act. That function, according to the present account, is the essential reason for our being conscious in the first place. The integrated and coherent relationship it establishes between environmental events, motivation/emotion, and actions around the pivotal node of an egocenter would seem to offer a definition of a “being” in biological terms.

6. Implications for medical ethics

Needless to say, the present account has ramifying implications for issues in medical ethics. One of these concerns pain management in children with hydranencephaly and similar conditions. It is not uncommon for parents to encounter surprise on the part of medical professionals when requesting analgesia or anesthesia for their crying child during invasive procedures, a situation in some ways reminiscent of what obtained in the case of neonates only a few decades back (Anand & Hickey 1987). They also extend to more general issues pertaining to the quality of care appropriate to these children, and ultimately to questions such as the meaning of personhood and even medical definitions of death (see, e.g., Shewmon et al. 1989, and references therein). Such questions are decidedly beyond the scope of the present paper, which is meant only to raise those issues of a theoretical and empirical nature which are prior to and essential for finding reasoned and responsible answers to the ethical ones. Suffice it to say that the evidence surveyed here gives no support for basing a search for such answers on the assumption that “awareness” in the primary sense of coherent relatedness of a motivated being to his or her surroundings is an exclusively cortical function and cannot exist without it.

7. Conclusion

The evidence and functional arguments reviewed in this article are not easily reconciled with an exclusive identification of the cerebral cortex as the medium of conscious function. They even suggest that the primary function of consciousness – that of matching opportunities with needs in a central motion-stabilized body-world interface organized around an ego-center – vastly antedates the invention of neocortex by mammals and may in fact have an implementation in the upper brainstem without it. The tacit consensus concerning the cerebral cortex as the “organ of consciousness” would thus have been reached prematurely, and may in fact be seriously in error. This has not always been so, as indicated by the review of the Penfield and Jasper “centrencephalic” theory of consciousness and volitional behavior with which we began. As we have seen, their proposal has not only been strengthened by certain findings accumulating since it was first formulated more than half a century ago. Suitably updated it still appears capable of providing a general framework for the integration of a vast array of diverse facts spanning from the basics of the vertebrate brain plan to evidence for awareness in children born without a cortex. Whether the perspective presented here can be developed into a comprehensive account of the neural organization of consciousness will require much additional work of a theoretical and empirical nature to determine. The testable prediction made in Section 4.5.1 above should smooth the path to such a future verdict.

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Footnotes:

1. In what follows the term “cortex” will always be taken to mean all or part of the cerebral cortex along with its associated dorsal thalamic and claustral nuclear apparatus. The thalamic reticular nucleus, being functionally intrinsic to this thalamocortical complex is regarded as being part of it despite its embryological and phylogenetic origin in the ventral thalamus (it is directly continuous with the lateral margin of the zona incerta). Unless otherwise indicated, “subcortical” will refer to all central nervous system tissue that is not thalamocortical complex in the above sense, and “brainstem” to diencephalon and the rest of the entire neuraxis caudal to it.

2. To avoid possible misunderstanding of this key point, note that the analog “reality simulation” proposed here has nothing to do with a facility for simulating, say, alternate courses of action by, say, letting them unfold “in imagination”, or any other version of an “inner world”, “subjective thought”, “fantasy”, or the like. Such capacities are derivative ones, dependent upon additional neural structures whose operations presuppose those described here. The purpose of the “analog simulation” is first and foremost to veridically reflect states of the world, the body and needs at whatever level of sophistication a given species implements those realities. It is thus most directly related to the model of Philipona and colleagues (2003, 2004), as well as to the “situation room” analogy developed by Lehar (2002).

3. Note that in some of the animal and human studies cited in this passage the term “Cartesian” occurs as a misnomer for “spherical”. They all refer to a system organized in terms of “azimuth” and “elevation”, i.e. a system of spherical coordinates.

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