

Below is the copyedited final draft of a BBS target article that has been accepted for publication. This updated preprint has been prepared for formally invited commentators. Please DO NOT write a commentary unless you have been formally invited.

---

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

**Bjorn Merker**

Gamla Kyrkvagen 44, SE-14171 Segeltorp, Sweden  
gyr694c@tninet.se

**Abstract:** 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 can be seen to form a centralized functional design in which an upper brain stem system organized for conscious function performs a penultimate step in action control. It retained this key role throughout the evolutionary process by which an expanding forebrain – culminating in the cerebral cortex of mammals – came to serve as a medium for the elaboration of conscious contents. This 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. It maintains special connective relations with cortical territories implicated in attentional and conscious functions, but is not rendered nonfunctional in the absence of cortical input. This helps explain 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 are integral to the constitution of 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

### 1. Introduction

The four semiindependent pacemakers of the noncephalized 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 (Adrian et al. 1954; Baars 1988; James 1890; Mandler 1975).

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 on any particular level or degree of complexity of the processes or contents that constitute the conscious state, but only on 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 on 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, and so forth, as cogently argued by Dretske (1993; see also Merker 1997; Searle 1992). 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.

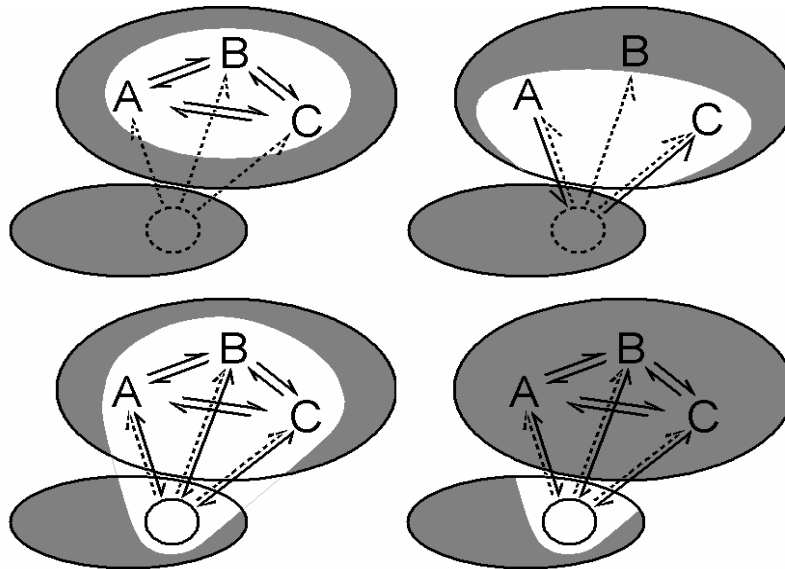
With some notable exceptions (e.g., Bogen 1995; Brown 1989; Panksepp 1982; Parvizi & Damasio 2001; Scheibel & Scheibel 1977; Sowards & Sowards 2000; Thompson 1993; Watt 2000), brainstem mechanisms have not figured prominently in the upsurge of interest in the nature and organization of consciousness that was ushered in with cognitivism in psychology and neuroscience (Baars 1988; Mandler 1975; Miller 1986). Few cognitivists or neuroscientists would today object to the assertion that “cortex is the organ of consciousness.”<sup>1</sup> 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 reexamine the routine assumption that another “higher function,” closely allied to that of sleep and wakefulness, namely consciousness, is an exclusively cortical affair (Penfield & 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). In that 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

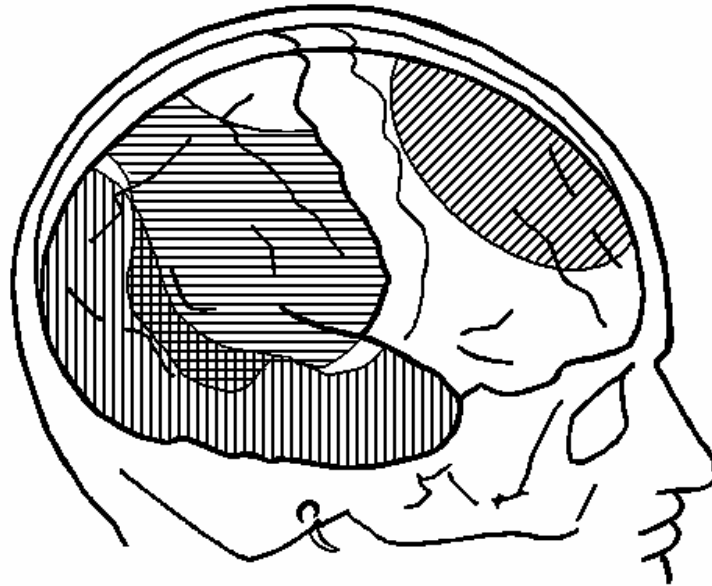
extension into what was then known as the “nonspecific” thalamus (a nuclear grouping encompassing the midline, intralaminar, and reticular thalamic nuclei). They regarded this anatomically subcortical system to be functionally supracortical in the sense of occupying a superordinate position relative to the cerebral cortex in functional or control terms (Penfield & Jasper 1954, pp. 28, 77; see Sections 3 and 4, following). 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 earlier (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 “corticentric” 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 corticentric, 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 Figure 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 (Devlin et al. 2003; Penfield & Jasper 1954, p. 477). 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, because 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, in that 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). Although 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 (Blumenfeld & Taylor 2003; Danober et al. 1998; Derensart et al. 2001; McCormick & Contreras 2001; Stefan & Snead 1997; Strafstrom 2006). We shall return to this matter in Section 4.5.3.

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, see Penfield & Jasper 1954, p. 43, and Figs. on p. 145 & 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 raphé, 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, 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 (Graf et al. 2002; Kuypers & Martin 1982; Nudo & Masterton 1988; Ugolini 1995), 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 (Kyupers 1968; Lang & Schieber 2003; Lawrence & Kuypers 1982; 1987). In such a setting, the idea that the output of a subcortical structure might override a cortical one, and in this sense could exercise supracortical 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 supracortical 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 (Sherman 1974; Sprague 1966; 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 (Sherman 1977; Sprague 1966; 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 (Berson & McIlwain 1983; Harting et al. 1992; Palmer et al. 1972; Sprague 1975), but it 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 (McHaffie et al. 1993; Sprague 1996; Wallace et al. 1990; 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 visually guided behavior as a result.

The point is underscored by the analogous circumstances pertaining to the neglect of one half of space (unilateral neglect) 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 also lifts on 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, in that 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**

Although 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 (May 2005; Keller et al. 2005; Krauzlis et al. 2004; Sparks 1999). 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 multieffector 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 (Basso & Wurtz 1998; 2002; Carello & Krauzlis 2004; Cavanaugh & Wurtz 2004; Fecteau & Munoz 2006; Glimcher & Sparks 1992; Horowitz & Newsome 1999; Krauzlis et al. 2004; McPeck & Keller 2004; Schlag-Rey et al. 1992; Wurtz & Mohler 1974; 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 1980; Edwards et al. 1979) and visual as well as nonvisual cortical sources (Collins et al. 2005; Harting et al. 1992; 1997; Kawamura & Konno 1979; Sherman et al. 1979). 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 there are contributions from both the dorsal (parietal cortex) and the ventral (temporal cortex) “streams” of the visual system (Fries 1984; Steele & Weller 1993; Webster et al. 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), electroceptive (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 (Behan & Kime 1996; Bell et al. 2003; Binns 1999; Doubell et al. 2003; Lee et al. 1997; Meredith & King 2004; Meredith & Ramoa 1998; Mize et al. 1994; Özen et al. 2000; Zhu & Lo 2000). There is thus no dearth of complex intrinsic collicular circuitry – only beginning to be systematically charted – for collicular decision-making based on 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). This would place the colliculus at the functional top 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 (Allport 1987; Tyrrell 1993; Brooks 1994; Dean & Redgrave 1984; Isa & Kobayashi 2004; McFarland & Sibly 1975; see Fecteau & Munoz 2006 for collicular “priority mapping” in relation to action).

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 (Lomber et al. 2001; Schall 1997; Schiller et al. 1979; Tehovnik et al. 1994), 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 (Albano & Wurtz 1978; Casagrande & Diamond 1974; Denny-Brown 1962; Goodale & Murison 1975; Merker 1980; Mort et al. 1980; Schiller et al. 1979; Schiller & Lee 1994; Schneider 1967). 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 supracortical*.

#### **4. Integration for action**

As noted in Section 3, 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, because 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), whereas 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 that 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 (Butler & Hodos 1996; Holland & Holland 1999; Northcutt 1996b). 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 prevertebrate 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, constituted the functionally highest and also anatomically most rostral subdivision of the neuraxis (Holland & Holland 1999; 2001; Holland et al. 1994; Lacalli 1996; 2001; Wicht 1996). 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 (Butler 2000; Holland et al. 1994).

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 just mentioned 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” (preectum) 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 the hypothalamus, ventral thalamus, dorsal thalamus, preectum, 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* (see Figure 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. Between these two is wedged additional integrative machinery in the form of the midbrain reticular formation, ventral thalamus, the periaqueductal gray, the ventral tegmental/substantia nigra pivot of the striatal system, as well as "locomotor centers" and basic mechanisms serving navigation. I will return to some of these in subsequent sections.

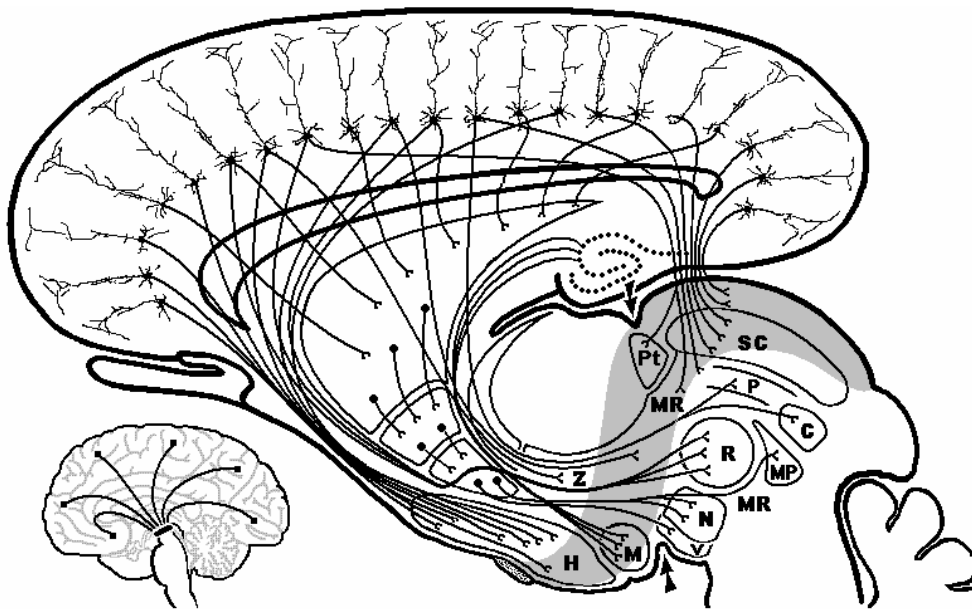
This concentration of conserved integrative machinery to the mesodiencephalon, I suggest, reflects the costs and benefits of evolving image-forming eyes in the ancestors of vertebrates (cf. Northcutt 1996a). Full use of the potential powers of visual guidance meant evolving solutions to an intricate set of sensorimotor problems. The confounding of sensory information by the sensory consequences of movement ("reafference", from 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 counterrotation 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 evolved in the immediate ancestors of true vertebrates (Braun 1996, p. 272; Fritsch et al. 1990; Wicht 1996, p. 253). 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 (Carpenter 1991; Windle & Baxter 1936).

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 prevertebrate 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 (Braun 1996; Northcutt & Wicht 1997; Wicht & Northcutt 1992). 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 preexisting 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 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 (Allport 1987; Baars 1993; Cabanac 1996; Cowan 2001; Mandler 1975; 2002, chapt. 2; McFarland & Sibly 1975; Tyrrell 1993).



**Figure 3.** Schematic sagittal 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, pedunculopontine 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,” the principle of which 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 (Baerends 1976; Tinbergen 1951). The tasks set by these goals compete for an animal’s behavioral resources, and because 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 that entail sometimes incompatible tasks or behaviors requiring sequencing/selection, entered the so-called behavior-based approach to robotics under the name “action selection” (Brooks 1986; Blumberg 1994; McFarland & Houston, 1981; Maes 1990; Prescott et al. 1999; Tyrell 1993; 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 (Altman & Kien 1989; Brooks 1986). But from the inherent functional relationship just sketched, that is, 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) allowing their separate momentary states to interact with and constrain one another. This extends to such a tripartite interaction, the principle already derived for the efficient management of motivational trade-offs, namely, the convertibility of different motives through a motivational “common currency” and their convergence among themselves at some point in the system (McFarland & Sibly 1975; see also Cabanac 1992, and more later).

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 centerpiece. Evolving such an interface is far from a trivial problem, all the more so as 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 (Gallistel 1999; Kawato et al. 1993). 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 might the former be compared 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, that is, what we normally call reality.<sup>2</sup> 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).

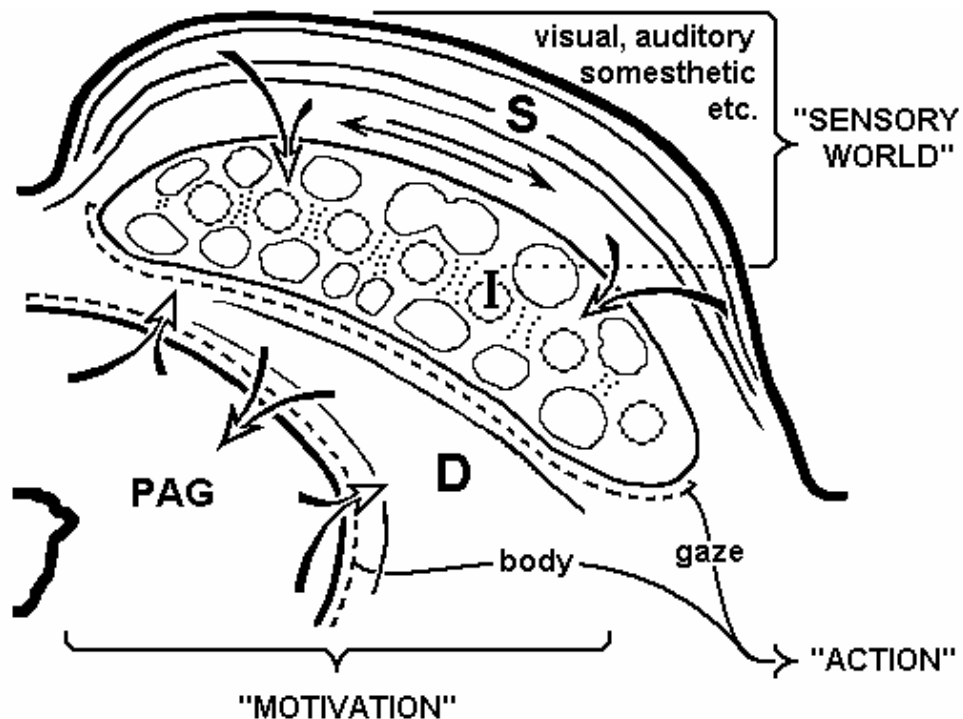
We have already seen in Sections 3.2 and 4.1 that the roof of the midbrain of vertebrates houses a sophisticated laminar superposition of the spatial senses in a premotor framework for orienting. It appears to contain the essential signals for bringing these senses into registry (Groh & Sparks 1996; Jay & Sparks 1987; Krauzlis 2001; Populin & Yin 1998; Van Opstal et al. 1995; 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. Guillaume & Pélisson 2001; Hirai et al. 1982;

May et al. 1990; Niemi-Junkola & Westby 2000). 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 (Goto et al. 2005; see refs. 36, 37, 39, 222, & 256 in Swanson 2000).

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 (Adams 1979; Behbehani 1995; Fernandez de Molina & Hunsperger 1962; Holstege et al. 1996; Jurgens 1994; Kittelberger et al. 2006; Lonstein et al. 1998; Mouton 1999; Panksepp 1982; 1998; Watt 2000). 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 (Heath 1975; Iacono & Nashold 1982; Nashold et al. 1969). Functionally the periaqueductal gray is continuous and reciprocally interconnected with the immediately overlying deep layers of the superior colliculus (Bittencourt et al. 2005; Cadusseau & Roger 1985; Gordon et al. 2002; Grofova et al. 1978; Harting et al. 1992, Fig. 27; Sprague et al. 1961; Wiberg 1992). 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 (Jiang et al. 2003; Mana & Chevalier 2001; see also Sections 3.1 & 3.2). Here the final distillate of basal ganglia action-related information is interdigitated with the latticework of histochemically defined compartments that organize the input-output relations of the intermediate colliculus (Graybiel 1978; Harting et al. 1997; Illing 1992; Illing & Graybiel 1986). 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 discussion, and it is hereby proposed to do so. The elements of this scheme are sketched in Figure 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. 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 Courjon et al 2004; Jackson et al. 2005; Schneider & Deubel 2002; Stuphorn et al. 2000; Werner et al. 1997). Nor is the output of the tecto-periaqueductal system limited to the species-specific orienting reflex. It includes escape behavior (Dean et al. 1989; Merker 1980; Sprague et al. 1961) 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 on input to the tectum from the region of the caudal thalamus and pretectum, just anterior to the tectum (Ewert 1968; Ingle 1973). 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

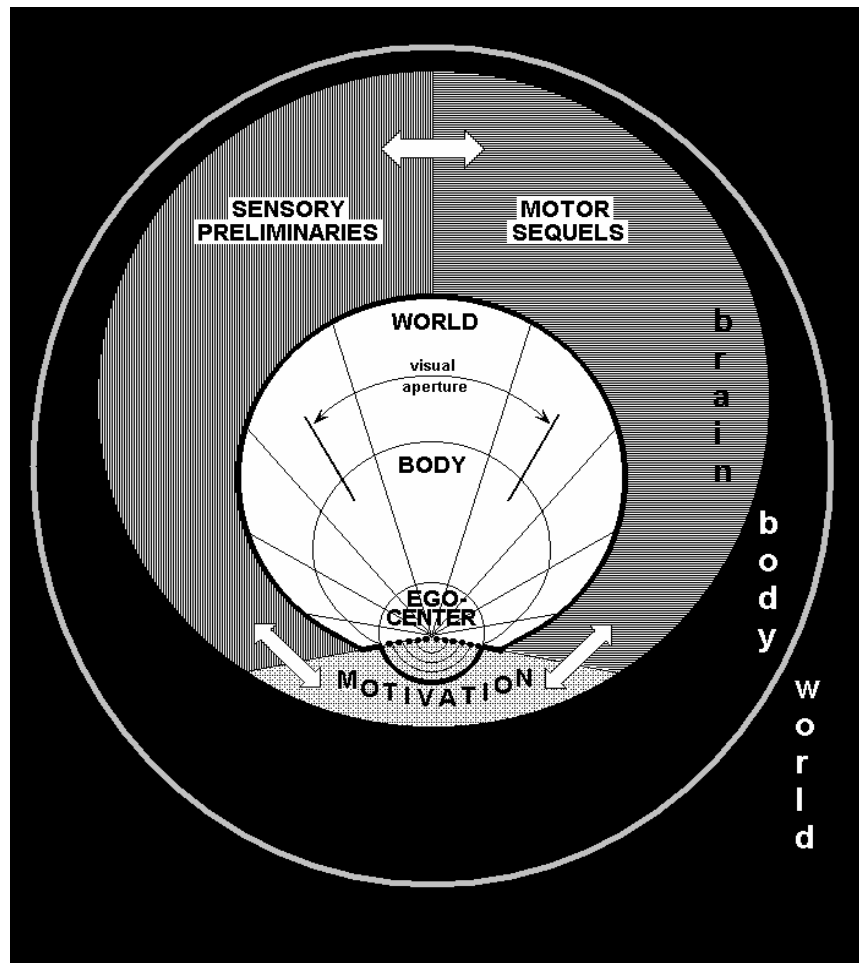
Whether primitive or advanced, the fundamental simplifying device of the proposed simulation space is to associate the origin of its shared body-world coordinate system for orienting with the head representation of its analog body. This does *not* mean that the coordinate system itself is head centered (i.e., moves with the head). At brainstem levels it appears, rather, to be oculocentric (Klier et al. 2001; Moschovakis 1996; Moschovakis & Highstein 1994). 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, that is, spherical, coordinates (Grobstein 1989; Masino 1992; Masino & Grobstein 1989; Masino & Knudsen 1990; see also Isa & Sasaki 2002). In humans, covert orienting of attention, as well as the visuomotor map for reaching (Gawryszewski et al. 2005; Vetter et al. 1999), appear to be framed in spherical coordinates,<sup>3</sup> perhaps reflecting collicular involvement in both functions (Müller et al. 2004; Werner et al. 1997).

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. note 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 that 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, whereas vision is only partially mapped in this way. 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 (Cox 1999; Hering 1879; Howard & Templeton 1966; Neelon et al. 2004; Roelofs 1959). 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 Figure 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, that is, phenomena such as inattention blindness, change blindness, and allied effects (O’Reagan et al. 2000; Rensink 2002; Rensink et al. 1997; Simon & Chabris 1999). Such “deletions from consciousness” can be countered by appropriately placed microstimulation of the superior colliculus (Cavanaugh & Wurtz 2004; see also Müller et al. 2005). 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. Cabanac 1992; Panksepp 1982; 1998;). 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 discussion. 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.

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 scaffolding supporting all further elaboration of conscious contents in phylogeny. Centered on the colliculus extending into periaqueductal gray, it will be further defined in Section 4.5. A felicitous term for the functional state supported by the basic (mesodiencephalic) 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 of this article is supported by a number of empirical findings that receive a unified interpretation in this 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, whereas stimulation at more rostral or caudal levels tends to evoke more fragmentary or incomplete behaviors (Adams 1979; Bandler & Keay 1996; Bard 1928; Brandao et al. 1999; Carrive et al. 1989; Fernandez de Molina & Hunsperger 1962; Hess 1954; Hess & Brugger 1943; Holstege & Georgiadis 2004; Hunsperger 1956; 1963; Hunsperger & Bucher 1967; Kaada 1951; Orlovsky & Shik 1976; Schaefer & Schneider 1968; Schuller & Radtke-Schuller 1990).

All of the behaviors just mentioned have also been exhibited by experimental animals after their cerebral cortex has been removed surgically, either in adulthood or neonatally. Best studied in this regard are rodents (Wishaw 1990; Woods 1964). 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, although an experienced observer would be able to do so on the basis of cues in posture, movement, and appearance (Whishaw 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 (Panksepp et al. 1994; Pellis et al. 1992), 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 & 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 (Bjursten 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 on basal ganglia and basal forebrain functions remaining after the loss of their principal (cortical) source of afference (Wishaw 1990, p. 246), whereas 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; Holstege & Georgiadis 2004; Masino 1992; Maskos et al. 2005; Panksepp 1982; Sakuma & Pfaff 1979; Swanson 2000). The particulars of the dependence of these behaviors on key structures located in the mesodiencephalic region has been repeatedly reviewed (Bassett & Taube 2001; Behbehani 1995; Groenewegen 2003; Haber & Fudge 1997; Horvitz 2000; Houk 1991; Jurgens 1994; Mouton 1999; Padel 1993; Panksepp 1998; Prescott et al. 1999; Swanson 1987; 2000; ten Donkelaar 1988; Watt 2000; Watt & Pincus 2004; Winn 1998; Zahm 2006).

It is into the premotor circuitry of these ancient and highly conserved upper brainstem mechanisms 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 discussion and sketched in Figure 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.

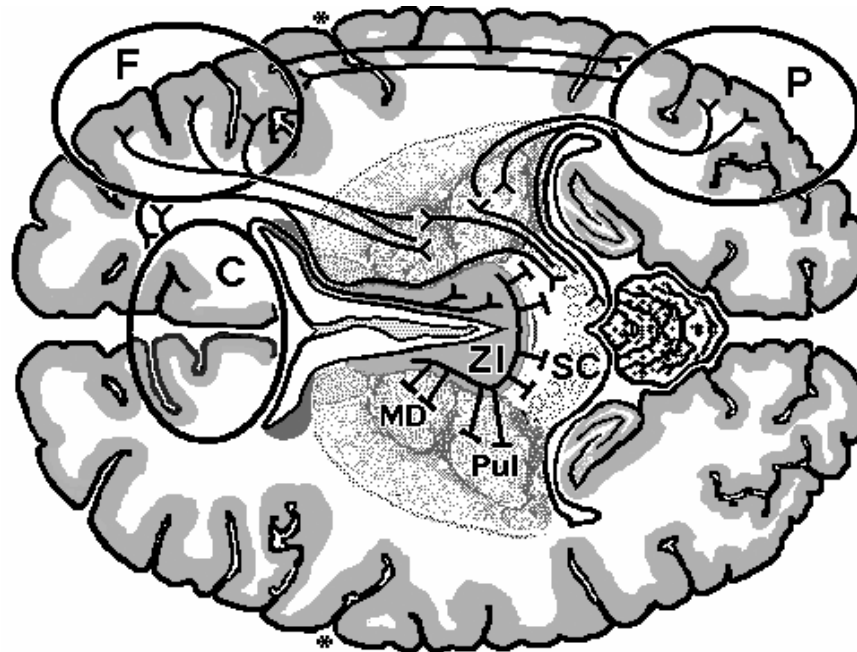
#### 4.5. Including the forebrain

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 (Baars et al. 2003, Fig. 1; Blumenfeld & Taylor 2003; Clower et al. 2001; Corbetta 1998; Han et al. 2003; Lynch et al. 1994; Mesulam 1999; Posner & Petersen 1990; Raz & Buhle 2006; Rees & Lavie 2001; ). A special connective and functional relationship exists between these three cortical territories and the mesodiencephalic system outlined in the foregoing discussion. 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 extralencephalic 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, whereas 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 (Harting et al. 1992; Sherman et al. 1979;), 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 a 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 (Barthó et al. 2002; Lavallée et al. 2005; Power et al. 1999; Trageser & Keller 2004).

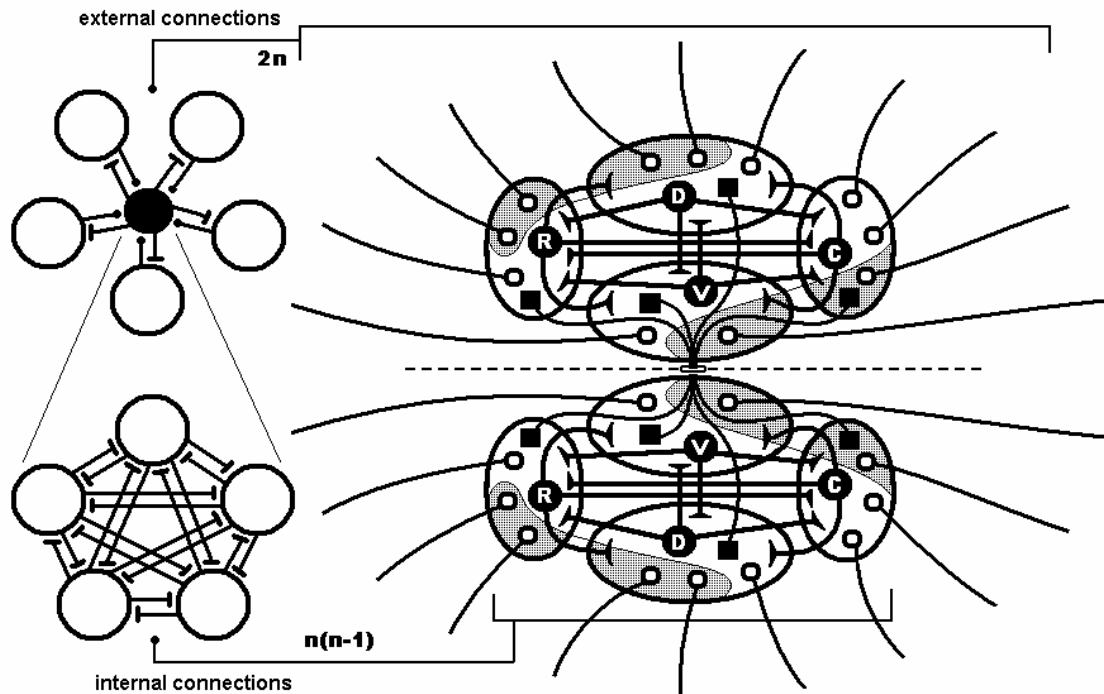
Collicular input to the higher-order nuclei is excitatory, whereas their incertal input is inhibitory. This implies dynamic competition between colliculus and zona incerta for influence over the two principal thalamic dependencies of the prefrontal and the posterior parietal cortex. In this competition 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 Figure 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 Figure 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 profuse 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 internal mutual inhibition is the theoretically optimal solution for implementing global competitive interaction among structures separated by long distances (see McFarland 1965; Snaith & 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 Figure 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 nonmammals – 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 – 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 nontopographic, 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; Ma 1996; Mungarndee et al. 2002; Nicolelis et al. 1993).

Finally, the zona incerta lies in immediate anterior continuity with the prerubral field and rostral interstitial nucleus of the medial longitudinal fasciculus, that is, with the rostral-most pole of the intermediate control system for orienting organized in spherical coordinates, mentioned in Section 4.3. This rostral pole is specialized for vertical movement, whereas 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 (Giolli et al. 2001; Kolmac et al. 1998; Leichnetz et al. 1987)? Incertal omnipause neurons are at least compatible with such an eventuality (Hikosaka & Wurtz 1983; Ma 1996). Nothing would be more elegant than to entrust the final arbitration of “what to do next” to a self-inhibitory “winner-take-all” or other decision network (Richards et al. 2006) lodged at the origin of the coordinate system that controls the orienting movements that 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). 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 & Singer 2001; Singer 2001). As we will 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 article).

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 (Albers & Meek 1991; Laemle 1983; Langer & Lund 1974; Ma et al. 1990). 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 of 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 *one conscious content will not be replaced by another 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 prediction just made, 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 identification with the threshold for access to the mesodiencephalic system centered on the colliculus (Figs. 4 & 6) is reinforced by the fact that layer V pyramidal cells supply the sole cortical projection 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 intracortical 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 (Merker 2004a; 2004b; Standing 1973) puts a premium on economy of storage, that is, 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.

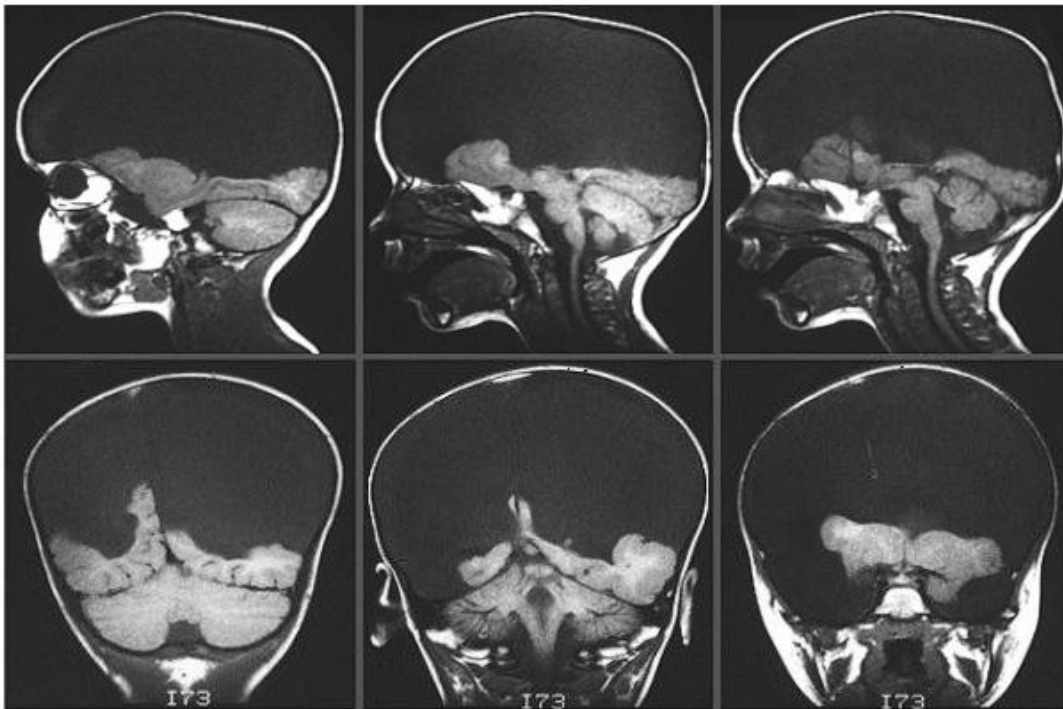
The evidence for a “general learning system” (which includes the superior colliculus: Thompson 1993), mentioned in the introduction to Section 3, would seem to bear on this proposal, as well. In fact, the severe capacity limitations of so called working memory (Baddeley 1992; Cowan 2001; Mandler 1975) 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). The fluttering of the eyelids that often occurs in the same situation is also easily accommodated by the functional anatomy of this region (Morcuende et al. 2002; Schmidtke & Buttner-Ennever 1992).

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 reexamined 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 reevaluation 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 reexamination to identify the zona incerta as the perfect anatomical centerpiece 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, for example, 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 Figure 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 Figure 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 (Marin-Padilla 1997; Takada et al. 1989). As Figure 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 (Baars et al. 2003; Sporns et al. 2000).

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 that 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 (Counter 2005; Covington et al. 2003; Hoffman & Liss 1969; McAbee et al. 2000).

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 on 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. (1999) 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. Since February of 2003 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 Figure 9 for an illustration), most readily to sounds, but also to salient visual stimuli (optic nerve status varies widely in hydranencephaly, discussed later). 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 on 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 parents 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, would 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, so is it rare for any auditory cortex to be spared. Yet, sensory responsiveness in hydranencephaly shows the opposite asymmetry. Hearing is generally preserved, whereas 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 that 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 (Provine & Yong 1991; van Hooff 1972). 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 postmortem 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, that is, 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 on cumulative integration of individual experience across the lifetime (see Merker, 2004a). Now as then, this brainstem system performs for the cortex, as for the rest of the brain, a basic function: that 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 was found 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 article, 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, but 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 such a framework can be developed into a comprehensive account of the neural organization of consciousness will depend upon resolving a number of the empirical and theoretical questions left unanswered in the foregoing discussion. Preliminary though it may be, that discussion suggests that part of the endeavor to resolve these questions will require close scrutiny of conserved and convergently innervated upper brainstem mechanisms as potential key components of a neural mechanism of consciousness.

## ACKNOWLEDGMENTS

My gratitude goes first to all the members of the hydranencephaly internet group founded by Barb Aleman. To them and their children I owe not only this article, but a precious enrichment of my life. To Karen Krueger my thanks for permission to use photos of her daughter Heather Joy. I am grateful as well to Bernard Baars for his personal encouragement, and to him, Douglas Watt, Alan Shewmon, Jaak Panksepp, and Sunny Anand for most helpful comments on an earlier version of this manuscript. The comments and suggestions provided by five referees helped me to further improve this article. Finally, my intellectual debt to the late Eugene Sachs is gratefully acknowledged.

## NOTES

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 this sense, and “brainstem” will refer 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 things like 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 on additional neural structures whose operations presuppose those described here. The purpose of the “analog simulation” defined here 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,” that is, a system of spherical coordinates.

## References

Abeles, M. (1982) Role of the cortical neuron: Integrator or coincidence detector? *Israel Journal of Medical Science* 18:83–92.

Adams, D.B. (1979) Brain mechanisms for offense, defense and submission. *The Behavioral and Brain Sciences* 2:201–41.

Adrian, E. D., Bremer F., & Jasper, H. H., eds. (1954) Brain mechanisms and consciousness. Springfield, IL: Charles C. Thomas.

Albano, J. E. & Wurtz, R. H. (1978) Modification of the pattern of saccadic eye movements

following ablation of the monkey superior colliculus. *I* 4:161.

Albers, F. J. & Meek, J. (1991) Dendritic and synaptic properties of collicular neurons: A quantitative light and electron microscopical study of Golgi-impregnated cells. *Anatomical Record* 231:524–37.

Allport, D. A. (1987) Selection for action: Some behavioral and neurophysiological considerations of attention and action. In: *Perspectives on perception and action*, ed. H. Heuer & A. F. Sanders, pp. 395–419. Erlbaum.

Altman, J. S. & Kien, J. (1989) New models for motor control. *Neural Computation* 1:173–83.

An, X., Bandler, R., Öngür, D. & Price, J. L. (1998) Prefrontal cortical projections to longitudinal columns in the midbrain periaqueductal gray in macaque monkeys. *The Journal of Comparative Neurology* 401:455–79.

Anand, K. J. S. & Hickey, P. R. (1987) Pain and its effects in the human neonate and fetus. *New England Journal of Medicine* 317:1321–29.

Andre, M., Plenat, F., Floquet, J. & Picard, L. (1975) Major cerebral lesions with normal neonatal neurologic behavior. *Archives Francaises de Pediatrie* 32:915–924 (in French).

Appell, P. P. & Behan, M. (1990) Sources of subcortical GABAergic projections to the superior colliculus in the cat. *Journal of Comparative Neurology* 302:143–58.

Baars, B. J. (1988) *A cognitive theory of consciousness*. Cambridge University Press.

Baars, B. J. (1993) How does a serial, integrated and very limited stream of consciousness emerge from a nervous system that is mostly unconscious, distributed, parallel and of enormous capacity? In: *Theoretical and experimental studies of consciousness, Ciba Foundation Symposium 174*, ed. G. Bock and J. Marsh, pp. 282–90. Wiley.

Baars, B. J., Ramsøy, T. Z. & Laureys, S. (2003) Brain, conscious experience and the observing self. *Trends in Neurosciences* 26:671–75.

Baddeley, A. D. (1992) Consciousness and working memory. *Consciousness and Cognition* 1:3–6.

Baerends, G. P. (1976) The functional organization of behaviour. *Animal Behaviour* 24:726–38.

Bagchi, A. (1975) *Indian definition of mind*. Sanskrit College Research Series nr. XCVIII, Calcutta, Sanskrit College.

Bandler, R. & Keay, K. A. (1996) Columnar organization in the midbrain periaqueductal gray and the integration of emotional expression. *Progress in Brain Research* 107:285–300.

Bard, P. (1928) A diencephalic mechanism for the expression of rage with special reference to the sympathetic nervous system. *American Journal of Physiology* 84:490–515.

- Bard, P. & Rioch, D. M. (1937) A study of four cats deprived of neocortex and additional portions of the forebrain. *Bulletin of the Johns Hopkins Hospital* 60:73–148.
- Bartho, P., Freund, T. F. & Acsady, L. (2002) Selective GABAergic innervation of thalamic nuclei from zona incerta. *European Journal of Neuroscience* 16:999–1014.
- Bassett, J. P. & Taube, J. S. (2001) Neural correlates for angular head velocity in the rat dorsal tegmental nucleus. *Journal of Neuroscience* 21:5740–51.
- Basso, M. A. & Wurtz, R. H. (1998) Modulation of neuronal activity in superior colliculus by changes in target probability. *Journal of Neuroscience* 18:7519–34.
- Basso, M. A. & Wurtz, R. H. (2002) Neuronal activity in substantia nigra pars reticulata during target selection. *Journal of Neuroscience* 22:1883–94.
- Bastian, J. (1982) Vision and electroreception: Integration of sensory information in the optic tectum of weakly electric fish *Apteronotus albifrons*. *Journal of Comparative Physiology* 147:287–98.
- Behan, M. & Kime, N. M. (1996) Intrinsic circuitry in the deep layers of the cat superior colliculus. *Visual Neuroscience* 13:1031–42.
- Behbehani, M. M. (1995) Functional characteristics of the midbrain periaqueductal gray. *Progress in Neurobiology* 46:575–605.
- Beitz, A. J. (1982) The organization of afferent projections to the midbrain periaqueductal gray of the rat. *Neuroscience* 7:133–59.
- Bell, A. H., Corneil, B. D., Munoz, D. P. & Meredith, M. A. (2003) Engagement of visual fixation suppresses sensory responsiveness and multisensory integration in the primate superior colliculus. *European Journal of Neuroscience* 18:2867–73.
- Benevento, L. A. & Fallon, J. H. (1975) The ascending projections of the superior colliculus in the rhesus monkey (*Macaca mulatta*). *Journal of Comparative Neurology* 160:339–62.
- Benson, D. L., Isackson, P. J., Hendry, S. H. & Jones, E. G. (1991) Differential gene expression for glutamic acid decarboxylase and type II calcium-calmodulin-dependent protein kinase in basal ganglia, thalamus, and hypothalamus of the monkey. *Journal of Neuroscience* 11:1540–64.
- Benson, D. L., Isackson, P. J., Gall, C. M. & Jones, E. G. (1992) Contrasting patterns in the localization of glutamic decarboxylase and Ca<sup>2+</sup>/calmodulin protein kinase gene expression in the rat central nervous system. *Neuroscience* 46:825–49.
- Berson, D. M. & McIlwain, J. T. (1983) Visual cortical input to deep layers of cat's superior colliculus. *Journal of Neurophysiology* 50:1143–55.
- Binns, K. E. (1999) The synaptic pharmacology underlying sensory processing in the superior

colliculus. *Progress in Neurobiology* 59:129–59.

Bisti, S., Maffei, L. & Piccolino, M. (1972) Variations of the visual responses of the superior colliculus in relation to body roll. *Science* 175:456–57.

Bittencourt, A. S., Nakamura-Palacios, E. M., Mauad, H., Tufik, S. & Schenberg, L. C. (2005) Organization of electrically and chemically evoked defensive behaviors within the deeper collicular layers as compared to the periaqueductal gray matter of the rat. *Neuroscience* 133:873–92.

Bjursten, L.-M., Norrsell, K. & Norrsell, U. (1976) Behavioral repertory of cats without cerebral cortex from infancy. *Experimental Brain Research* 25:115–30.

Blumberg, B. (1994) Action-selection in Hamsterdam: Lessons from ethology. In: *The Third International Conference on the Simulation of Adaptive Behavior*, ed. D. Cliff, P. Husbands, J. A. Meyer & S. W. Wilson, pp. 108–17. MIT Press.

Blumenfeld, H. & Taylor, J. (2003) Why do seizures cause loss of consciousness? *The Neuroscientist* 9:301–10.

Bogen, J. E. (1995) On the neurophysiology of consciousness. Part 1: Overview. *Consciousness and Cognition* 4:52–62.

Bokor, H., Frere, S. G., Eyre, M. D., Slezia, A., Ulbert, I., Luthi, A. & Acsady, L. (2005) Selective GABAergic control of higher-order thalamic relays. *Neuron* 45:929–40.

Brandão, M. L., Anseloni, V. Z., Pandóssio, J. E. De Araújo, J. E. & Castilho, V. M. (1999) Neurochemical mechanisms of the defensive behavior in the dorsal midbrain. *Neuroscience and Biobehavioral Reviews* 23:863–75.

Braun, C. B. (1996) The sensory biology of the living jawless fishes: A phylogenetic assessment. *Brain, Behavior and Evolution* 48:262–76.

Brecht, M., Singer, W. & Engel, A. K. (1998) Correlation analysis of cortico-tectal interactions in the cat visual system. *Journal of Neurophysiology* 79:2394–07.

Brecht, M., Singer, W. & Engel, A. K. (1999) Patterns of synchronization in the superior colliculus of anesthetized cats. *The Journal of Neuroscience* 19:3567–79.

Brecht, M., Goebel, R., Singer, W. & Engel, A. K. (2001) Synchronization of visual responses in the superior colliculus of awake cats. *Neuroreport* 12:43–47.

Brooks, R. A. (1986) A robust layered control system for a mobile robot. *IEEE Journal on Robotics and Automation* 2:14–23.

Brooks, R. A. (1989) A robot that walks: Emergent behaviour from a carefully evolved network. *Neural Computation* 1:253–62.

- Brooks, R. A. (1994) Coherent behaviour from many adaptive processes. In: *From animals to animats 3: Proceedings of the Third International Conference on Simulation of Adaptive Behavior*, ed. D. Cliff, P. Husbands, J.-A. Meyer & S. W. Wilson, pp. 22–29. MIT Press.
- Brown, J. W. (1989). Essay on perception. In: *Neuropsychology of perception*, ed. J. W. Brown, pp. 233–56. Erlbaum.
- Brudzynski, S. M., Cruickshank, J. W. & McLachlan, R. S. (1995) Cholinergic mechanisms in generalised seizures: importance of the zona incerta. *Canadian Journal of Neurological Sciences* 22:116–20.
- Butler, A. B. (2000) Sensory system evolution at the origin of craniates. *Philosophical Transactions of the Royal Society (London B)* 355:1309–13.
- Butler, A. B. & Hodos, W. (1996) *Comparative vertebrate neuroanatomy: Evolution and adaptation*. Wiley-Liss.
- Cabanac, M. (1992) Pleasure: The common currency. *Journal of Theoretical Biology* 155:173–200.
- Cabanac, M. (1996) The place of behavior in physiology. In: *Handbook of physiology, environmental physiology*, ed. M. J. Fregly & C. Blatteis, pp. 1523–36. Oxford University Press.
- Cadusseau, J. & Roger, M. (1985) Afferent projections to the superior colliculus in the rat, with special attention to the deep layers. *Journal für Hirnforschung* 26:667–81.
- Carello, C. D. & Krauzlis, R. J. (2004) Manipulating intent: Evidence for a causal role of the superior colliculus in target selection. *Neuron* 43:575–83.
- Carpenter, R. H. S. (1991) The visual origins of ocular motility. In: *Vision and visual dysfunction. Vol 8: Eye movements*, ed. R. H. S. Carpenter, pp. 1–10. MacMillan.
- Carrive, P., Bandler, R. & Dampney, R. A. (1989) Somatic and autonomic integration in the midbrain of the unanesthetized decerebrate cat: A distinctive pattern evoked by excitation of neurones in the subtentorial portion of the midbrain periaqueductal grey. *Brain Research* 483: 251–58.
- Carter, C. S., Witt, D. M., Kolb, B. & Wishaw, I. Q. (1982) Neonatal decortication and adult female sexual behavior. *Physiology and Behavior* 29:763–66.
- Casagrande, V. A. & Diamond, I. T. (1974) Ablation study of the superior colliculus in the tree shrew (*Tupaia glis*). *Journal of Comparative Neurology* 156: 207–38.
- Cavanaugh, J. & Wurtz, R. H. (2004) Subcortical modulation of attention counters change blindness. *The Journal of Neuroscience* 24:11236–243.
- Clower, D. M., West, R. A., Lynch, J. C. & Strick, P. L. (2001) The inferior parietal lobule is the target of output from the superior colliculus, hippocampus, and cerebellum. *Journal of*

*Neuroscience* 21:6283–91.

Collins, C. E., Lyon, D. C. & Kaas, J. H. (2005) Distribution across cortical areas of neurons projecting to the superior colliculus in New World monkeys. *I 285A:619–27.*

Corbetta, M. (1998) Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proceedings of the National Academy of Sciences, USA* 95:831–38.

Counter, S. A. (2005) Music stirred her damaged brain. *The Boston Globe, Health/Science*, March 29, 2005.  
[http://www.boston.com/news/globe/health\\_science/articles/2005/03/29/music\\_stirred\\_her\\_damaged\\_brain](http://www.boston.com/news/globe/health_science/articles/2005/03/29/music_stirred_her_damaged_brain)

Covington, C., Taylor, H., Gill, C., Padaliya, B., Newman, W., Smart, J. R. 3rd & Charles, P. D. (2003) Prolonged survival in hydranencephaly: A case report. *Tennessee Medicine* 96:423–24.

Courjon, J.-H., Olivier, E. & Pélisson, D. (2004) Direct evidence for the contribution of the superior colliculus in the control of visually guided reaching movements in the cat. *Journal of Physiology* 556:675–81.

Cowan, N. (2001) The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences* 24:87–185.

Cox, P. H. (1999) *An initial investigation of the auditory egocenter: Evidence for a “cyclopean ear.”* Doctoral dissertation, North Carolina State University, Raleigh, NC.

Crick, F. & Koch, C. (2003) A framework for consciousness. *Nature Neuroscience* 6:119–26.

Crutcher, M. D., Branch, M. H. DeLong, M. R. & Georgopoulos, A. P. (1980) Activity of zona incerta neurons in the behaving primate. *Society for Neuroscience Abstracts* 6:676.

Danober, L., Deransart, C., Depaulis, A., Vergnes, M. & Marescaux, C. (1998) Pathophysiologic mechanisms of genetic absence epilepsy in the rat. *Progress in Neurobiology* 55:27–57.

Dean, P., Porrill, J. & Stone, J. V. (2002) Decorrelation control by the cerebellum achieves oculomotor plant compensation in simulated vestibulo-ocular reflex. *Proceedings of the Royal Society of London, Series B* 269:1895–1904.

Dean, P., Porrill, J. & Stone, J. V. (2004) Visual awareness and the cerebellum: Possible role of decorrelation control. The roots of visual awareness. *Progress in Brain Research* 144:61–75.

Dean, P. & Redgrave, P. (1984) Superior colliculus and visual neglect in rat and hamster. III. Functional implications. *Brain Research Reviews* 8:155–63.

Dean, P., Redgrave, P. & Westby, G. M. W. (1989) Event or emergency – 2 response systems in the mammalian superior colliculus. *Trends In Neurosciences* 12:137–47.

- Denny-Brown, D. (1962) The midbrain and motor integration. *Proceedings of the Royal Society of Medicine* 55:527–38.
- Deransart, C., Le-Pham, B.-T., Hirsch, E., Marescaux, C. H., & Depaulis, A. (2001) Inhibition of the substantia nigra suppresses absences and clonic seizures in audiogenic rats, but not tonic seizures: Evidence for seizure specificity of the nigral control. *Neuroscience* 105:203–11.
- Devlin, A. M., Cross, J. H., Harkness, W., Chong, W. K., Harding, B., Vargha-Khadem, F. & Neville, B. G. R. (2003) Clinical outcomes of hemispherectomy for epilepsy in childhood and adolescence. *Brain* 126:556–66.
- Doubell, T. P., Skaliora, I., Baron, J. & King, A. J. (2003) functional connectivity between the superficial and deeper layers of the superior colliculus: An anatomical substrate for sensorimotor integration. *The Journal of Neuroscience* 23:6596–607.
- Dretske, F. (1993) Conscious experience. *Mind* 102:1–21.
- Driver, J. & Vuilleumier, P. (2001) Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition* 79:39–88.
- Durmer, J. S. & Rosenquist, A. C. (2001) Ibotenic acid lesions in the pedunculo-pontine region result in recovery of visual orienting in the hemianopic cat. *Neuroscience* 106:765–81.
- Eccles, J. C. ed. (1966) *Brain and conscious experience*. Springer Verlag.
- Edwards, S. B. (1980) The deep layers of the superior colliculus: Their reticular characteristics and organization. In: *The reticular formation revisited*. ed. A. Hobson & M. A. B. Brazier, pp. 193–209. Raven Press.
- Edwards, S. B., Ginsburgh, C. L., Henkel, C. K. & Stein, B. E. (1979) Sources of subcortical projections to the superior colliculus in the cat. *Journal of Comparative Neurology* 184:309–29.
- Engel, A. K, Fries, P., König, P., Brecht, M. & Singer, W. (1999) Temporal binding, binocular rivalry, and consciousness. *Consciousness and Cognition* 8:128–51.
- Engel, A. K. & Singer, W. (2001) Temporal binding and the neural correlates of sensory awareness. *Trends in Cognitive Sciences* 5:16–25.
- Ewert, J.-P. (1968) Der Einfluss von Zwischenhirndefekten auf die Visuomotorik im Beutefang- und Fluchtverhalten der Erdkröte (*Bufo bufo* L.). *Zeitschrift für Vergleichende Physiologie* 61:41–70.
- Fecteau, J. H. & Munoz, D. P. (2006) Saliency, relevance, and firing: a priority map for target selection. *Trends in Cognitive Sciences* 10:382–90.
- Felleman, D. J. & Van Essen, D. C. (1991) Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex* 1:1–47.



- Fernandez de Molina, A. & Hunsperger, R. W. (1962) Organization of the subcortical system governing defense and flight reactions in the cat. *Journal of Physiology* 160:200–13.
- Fessard, A. E. (1954) Mechanisms of nervous integration and conscious experience. In: *Brain mechanisms and consciousness*, ed. E. D. Adrian, F. Bremer & H. H. Jasper, pp. 200–36. Blackwell.
- Ficalora, A. S. & Mize, R. R. (1989) The neurones of the substantia nigra and the zona incerta which project to the cat superior colliculus are GABA immunoreactive: A double label study using GABA immunocytochemistry and lectin retrograde transport. *Neuroscience* 29:567–81.
- Findlay, J. M. & Walker, R. (1999) A model of saccade generation based on parallel processing and competitive inhibition. *Behavioral and Brain Sciences* 22:661–74.
- Floyd, N. S., Price, J. L., Ferry, A. T., Keay, K. A. & Bandler, R. (2000) Orbitomedial prefrontal cortical projections to distinct longitudinal columns of the periaqueductal gray in the rat. *Journal of Comparative Neurology* 422:556–78.
- Friede, R. L. (1989) *Developmental neuropathology*, pp. 31–39. Springer-Verlag.
- Fries, W. (1984) Cortical projections to the superior colliculus in the macaque monkey: A retrograde study using horseradish peroxidase. *Journal of Comparative Neurology* 230:55–76.
- Fritsch, B., Sonntag, R., Dubuc, R., Ohta, Y. & Grillner, S. (1990) Organization of the six motor nuclei innervating the ocular muscles in lamprey. *Journal of Comparative Neurology* 294:491–506.
- Gallistel, C. R. (1999) Coordinate transformations in the genesis of directed action. In *Cognitive science*, ed. B. O. M. Bly & D. E. Rummelhart, pp. 1–42. Academic Press.
- Gamper, E. (1926) Bau und Leistungen eines menschlichen Mittelhirnwesen (Arhinencephalie mit Encephalocoele). *Zeitschrift für die gesamte Neurologie und Psychiatrie* 102:154–235, and 104: 49–120.
- Gawryszewski, L. G., Carreiro, L. R. R. & Magalhães, F. V. (2005) Early and late inhibitions elicited by a peripheral visual cue on manual response to a visual target: Are they based on Cartesian coordinates? *Psicológica* 26:121–37.
- Gibbs, F. A., Gibbs, E. L. & Lennox, W. G. (1937) Epilepsy: A paroxysmal cerebral dysrhythmia. *Brain* 60:377–88.
- Gibbs, F. A., Lennox, W. G. & Gibbs, E. L. (1936) Localizable features of the electrical activity of the brain in petit mal epilepsy. *American Journal of Physiology* 116:61.
- Gioanni, Y., Gioanni, H. & Mitrovic, N. (1991) Seizures can be triggered by stimulating non-cortical structures in the quaking mutant mouse. *Epilepsy Research* 9:19–31.
- Giolli, R. A.; Gregory, K. M.; Suzuki, D. A.; Blanks, R. H.; Lui, F. & Betelak, K. F. (2001)

Cortical and subcortical afferents to the nucleus reticularis tegmenti pontis and basal pontine nuclei in the macaque monkey. *Visual Neuroscience* 18:725–40.

Glimcher, P. W. & Sparks, D. L. (1992) Movement selection in advance of action in the superior colliculus. *Nature* 355:542–45.

Goodale, M. A. & Murison, R. C. C. (1975) The effects of lesions of the superior colliculus on locomotor orientation and the orienting reflex in the rat. *Brain Research* 88:243–61.

Gordon, N. S., Kollack-Walker, S., Akil, H., & Panksepp, J. (2002) Expression of c-fos gene activation during rough and tumble play in juvenile rats. *Brain Research Bulletin* 57:651–59.

Goto, M., Canteras, N. S., Burns, G. & Swanson, L. W. (2005) Projections from the subfornical region of the lateral hypothalamic area. *Journal of Comparative Neurology* 493:412–38.

Graf, W., Gerrits, N., Yatim-Dhiba, N. & Ugolini, G. (2002) Mapping the oculomotor system: The power of transneuronal labeling with rabies virus. *European Journal of Neuroscience* 15:1557–62.

Graybiel, A. M. (1978) A stereometric pattern of distribution of acetylthiocholinesterase in the deep layers of the superior colliculus. *Nature* 272:539–41.

Grillner, S. (2003) The motor infrastructure: From ion channels to neuronal networks. *Nature Reviews, Neuroscience* 4:573–86.

Grillner, S., Georgopoulos, A. P. & Jordan, L. M. (1997) Selection and initiation of motor behavior. In *Neurons, networks, and motor behavior*, ed. P. S. G. Stein, S. Grillner, A. I. Selverston & D. G. Stuart, pp. 1–19). MIT Press.

Grobstein, P. (1988) Between the retinotectal projection and directed movement: Topography of a sensorimotor interface. *Brain, Behavior and Evolution* 31:34–48.

Grobstein, P. (1989) Organization in the sensorimotor interface: A case of increased resolution. In *Visuomotor coordination*, ed. J.-P. Ewert & M. A. Arbib, pp. 537–68. Plenum.

Groenewegen, H. J. (2003) The basal ganglia and motor control. *Neural Plasticity* 10:107–20.

Grofova, I., Ottersen, O. P. & Rinvik, E. (1978) Mesencephalic and diencephalic afferents to the superior colliculus and periaqueductal gray substance demonstrated by retrograde axonal transport of horseradish peroxidase in the cat. *Brain Research* 146:205–20.

Groh, J. M. & Sparks, D. L. (1996) Saccades to somatosensory targets. III. Eye-dependent somatosensory activity in primate superior colliculus. *Journal of Neurophysiology* 75:439–53.

Guillaume, A. & Pélisson, D. (2001) Gaze shifts evoked by electrical stimulation of the superior colliculus in the head-unrestrained cat. II. Effect of muscimol inactivation of the caudal fastigial nucleus. *European Journal of Neuroscience* 14:1345–59.

- Haber, S. N. & Fudge, J. L. (1997) The primate substantia nigra and VTA: Integrative circuitry and function. *Critical Reviews in Neurobiology* 11:323–42.
- Haft, M. (1998) Robust “topological” codes by keeping control of internal redundancy. *Physical Review Letters* 81:4016–19.
- Hamani, C., Sakabe, S., Bortolotto, Z. A., Cavalheiro, E. A. & Mello, L. (1994) Inhibitory role of the zona incerta in the pilocarpine model of epilepsy. *Epilepsy Research* 49:73–80.
- Han, C. J., O’Tuathaigh, C. M., van Trigt, L., Quinn, J. J., Fanselow, M. S., Mongeau, R., Koch, C. & Anderson, D. J. (2003) Trace but not delay fear conditioning requires attention and the anterior cingulate cortex. *Proceedings of the National Academy of Sciences (USA)* 100:13087–92.
- Harding, D. E. (1961) *On having no head*. Arkana.
- Harting, J. K., Updyke, B. V. & Van Lieshout, D. P. (1992) Corticotectal projections in the cat: Anterograde transport studies of twenty five cortical areas. *Journal of Comparative Neurology* 328:379–414.
- Harting, J. K., Feig, S & Van Lieshout, D. P. (1997) Cortical somatosensory and trigeminal inputs to the cat superior colliculus: Light and electron microscopic analyses. *Journal of Comparative Neurology* 388:313–26.
- Harting, J. K., Huerta, M. F., Frankfurter, A. J., Strominger, N. L. & Royce, G. J. (1980) Ascending pathways from the monkey superior colliculus: An autoradiographic analysis. *Journal of Comparative Neurology* 192:853–82.
- Hartline, P. H., Kass, L. & Loop, M. S. (1978) Merging of modalities in the optic tectum: Infrared and visual integration in rattlesnakes. *Science* 199:1225–29.
- Heath, R. G. (1975) Brain function and behavior: I. Emotion and sensory phenomena in psychotic patients and in experimental animals. *Journal of Nervous and Mental Disease* 160:159–75.
- Hering, E. (1879) *Spatial sense and movements of the eye*. trans. C. A. Radde. American Academy of Optometry, Baltimore, 1942.
- Hess, W. R. (1954) *Das Zwischenhirn. Syndrome, Lokalisationen, Funktionen*, 2nd edition. Benno Schwabe.
- Hess, W. R. & Brugger, M (1943) Das subkortikale Zentrum der affektiven Abwehrreaktion. *Helvetica Physiologica Acta* 1:33–52.
- Hess, W. R., Bürgi, S. & Bucher, V. (1946) Motorische Funktion des tektal- und tegmentalgebietes. *Monatschrift für Psychiatrie und Neurologie* 112:1–52.
- Hikosaka, O. & Wurtz, R. H. (1983) Visual and oculomotor functions of monkey substantia nigra pars reticulata. I. Relation of visual and auditory responses to saccades. *Journal of*

*Neurophysiology* 49:1230–53.

Hikosaka, O. & Wurtz, R. H. (1989) The basal ganglia. In *The neurobiology of saccadic eye movements*, ed. R. H. Wurts & M. E. Goldberg, pp. 257–81. Elsevier.

Hirai, T., Onodera, S. & Kawamura, K. (1982) Cerebellotectal projections studied in cats with horseradish peroxidase or tritiated amino acids axonal transport. *Experimental Brain Research* 48:1–12.

Hodgson, S. H. (1878) *The philosophy of reflection*. Longmans, Green.

Hoffman, J. & Liss, L. (1969) "Hydranencephaly". A case report with autopsy findings in a 7-year-old girl. *Acta Paediatrica Scandinavica* 58:297–300.

Holland, P. W. H., Garcia-Fernández, J., Williams, N. A. & Sidow, A. (1994) Gene duplication and the origins of vertebrate development. *Development, Suppl.*:125–33.

Holland, L. Z., & Holland, N. D. (1999) Chordate origins of the vertebrate central nervous system. *Current Opinion in Neurobiology* 9:596–602.

Holland, L. Z. & Holland, N. D. (2001) Evolution of neural crest and placodes: *Amphioxus* as a model for the ancestral vertebrate? *Journal of Anatomy* 199:85–98.

Holstege, J. C. (1991) Ultrastructural evidence for GABAergic brain stem projections to spinal motoneurons in the rat. *Journal of Neuroscience* 11:159–67.

Holstege, G. & Cowie, R. J. (1989) Projections from the rostral mesencephalic reticular formation to the spinal cord. An HRP and autoradiographical tracing study in the cat. *Experimental Brain Research* 75:265–79.

Holstege, G., Bandler, R. & Saper, C. B., eds. (1996) *The emotional motor system*. Elsevier.

Holstege, G. & Georgiadis, J. R. (2004) The emotional brain: neural correlates of cat sexual behavior and human male ejaculation. *Progress in Brain Research* 143:39–45.

Horowitz, G. D. & Newsome, W. T. (1999) Separate signals for target selection and movement specification in the superior colliculus. *Science* 284:1158–61.

Horowitz, S. S., Blanchard, J. & Morin, L. P. (2005) Medial vestibular connections with the hypocretin (orexin) system. *Journal of Comparative Neurology* 487:127–46.

Horvitz, J. C. (2000) Mesolimbocortical and nigrostriatal dopamine responses to salient non-reward events. *Neuroscience* 96:651–56.

Houk, J. C. (1991) Red nucleus: role in motor control. *Current Opinion in Neurobiology* 1:610–15.

Hovda, D. A. & Villablanca, J. R. (1990) Spraying of visual field perception in neonatal but not

adult cerebral hemispherectomized cats. Relationship with oxidative metabolism of the superior colliculus. *Behavioral Brain Research* 39:119–32.

Howard, I. P. & Templeton, W. B. (1966) *Human spatial orientation*. Wiley.

Hunsperger, R. W. (1956) Affektreaktionen auf elektrische reizung im Hirnstamm der Katze. *Helvetica Physiologica Acta* 14:70–92.

Hunsperger, R. W. (1963) Comportements affectifs provoqués par la stimulation électrique du tronc cérébral et du cerveau antérieur. *Journal de Physiologie* 55:45–97.

Hunsperger, R. W. & Bucher, V. M. (1967) Affective behaviour produced by electrical stimulation in the forebrain and brainstem of the cat. *Progress in Brain Research* 27:103–27.

Hydranencephaly group survey (2003) Unpublished questionnaire survey of 81 families conducted by Barb Aleman from September 2002 through February 2003. URL: <http://hydranencephaly.com/researchresults.htm>

Iacono, R. P. & Nashold Jr., B. S. (1982). Mental and behavioral effects of brain stem and hypothalamic stimulation in man. *Human Neurobiology* 1:273–79.

Illing, R.-B. & Graybiel, A. M. (1986) Complementary and non-matching afferent compartments in the cat's superior colliculus: Innervation of the acetylcholinesterase-poor domain of the intermediate gray layer. *Neuroscience*:18:373–94.

Illing, R.-B. (1992) Association of efferent neurons to the compartmental architecture of the superior colliculus. *Proceedings of the National Academy of Sciences (USA)* 89:10900–04.

Ingle, D. (1973) Two visual systems in the frog. *Science* 181:1053–55.

Isa, T. & Kobayashi, Y. (2004) Switching between cortical and subcortical sensorimotor pathways. *Progress in Brain Research* 143:299–305.

Isa, T. & Sasaki, S. (2002) Brainstem control of head movements during orienting: Organization of the premotor circuits. *Progress in Neurobiology* 66:205–41.

Iwahori, N., Kawawaki, T. & Baba, J. (1999) Neuronal organization of the optic tectum in the river lamprey, *Lampetra japonica*: A Golgi study. *Journal für Hirnforschung* 39:409–24.

Jackson, S. R., Newport, R., Mort, D. & Husain, M. (2005) Where the eye looks, the hand follows: Limb-dependent magnetic misreaching in optic ataxia. *Current Biology* 15:42–46.

Jay, M. F. & Sparks, D. L. (1987) Sensorimotor integration in the primate superior colliculus. II. Coordinates of auditory signals. *Journal of Neurophysiology* 57:35–55.

James, W. (1890/1983) *The principles of psychology*, with introduction by G. A. Miller. Harvard University Press.

Jasper, H. H. & Droogleever-Fortuyn, J. (1947) Experimental studies on the functional anatomy of petit mal epilepsy. *Proceedings of the Association for Research in Nervous and Mental Disease* 26:272–98.

Jasper, H. H., Proctor, L. D., Knighton, R. S., Noshay, W. C. & Costello, R. T., eds. (1958) *Reticular formation of the brain. Henry Ford Hospital International Symposium*. Little Brown.

Jennett, B. (2002) *The vegetative state. Medical facts, ethical and legal dilemmas*. Cambridge University Press.

Jiang, H., Stein, B. E. & McHaffie, J. G. (2003) Opposing basal ganglia processes shape midbrain visuomotor activity bilaterally. *Nature* 423:982–86.

Johansson, R. S., Westling, G., Bäckström, A. & Flanagan, J. R. (2001) Eye-hand coordination in object manipulation. *Journal of Neuroscience* 21:6917–32.

Jones, E. G. (1998) A new view of specific and nonspecific thalamocortical connections. In: *Consciousness: At the frontiers of neuroscience*, eds. H. H. Jasper, L. Descarries, V. F. Castellucci & S. Rossignol. *Advances in Neurology* 77:49–73.

Jones, E. G. (2002) Thalamic circuitry and thalamocortical synchrony. *Philosophical Transactions of the Royal Society, London, Series B* 357:1659–73.

Jones, R. M. & France, T. D. (1978) Electrophysiological responses in hydranencephaly. *American Journal of Ophthalmology* 85:478–84.

Jordan, L. M. (1998) Initiation of locomotion in mammals. *Annals of the New York Academy of Sciences* 860:83–93.

Julesz, B. (1971) *Foundations of cyclopean perception*. University of Chicago Press.

Jurgens, U. (1994) The role of the periaqueductal grey in vocal behaviour. *Behavioral Brain Research* 62:107–17.

Kaada, B. R. (1951) Somato-motor, autonomic and electrocorticographic responses to electrical stimulation of rhinencephalic and other structures in primates, cat, and dog; a study of responses from the limbic, subcallosal, orbito-insular, piriform and temporal cortex, hippocampus-fornix and amygdala. *Acta Physiologica Scandinavica (Suppl.)* 24:1–262.

Kawamura, K. & Konno, T. (1979) Various types of corticotectal neurons of cats as demonstrated by means of retrograde axonal transport of horseradish peroxidase. *Experimental Brain Research* 35:161–75.

Kawato, M., Hayakawa, H. & Inui, T. (1993) A forward-inverse optics model of reciprocal connections between visual cortical areas. *Network: Computation in Neural Systems* 4:415–22.

Keay, K. A. & Bandler, R. (2002) Distinct central representations of inescapable and escapable pain: Observations and speculation. *Experimental Physiology* 87:275–79.

- Keller, E. L., Lee, K.-M. & McPeck, R. M. (2005) Readout of higher-level processing in the discharge of superior colliculus neurons. *Annals of the New York Academy of Sciences* 1039:1–11.
- Kendrick, K. M., Hinton, M. R. & Baldwin, B. A. (1991) GABA release in the zona incerta of the sheep in response to the sight and ingestion of food and salt. *Brain Research* 550:165–68.
- Kim, U., Gregory, E. & Hall, W. C. (1992) Pathway from the zona incerta to the superior colliculus in the rat. *Journal of Comparative Neurology* 321:555–75.
- Kittelberger, J. M., Land, B. R. & Bass, A. H. (2006) The midbrain periaqueductal gray and vocal patterning in a teleost fish. *Journal of Neurophysiology* 96:71–85.
- Klier, E. M., Wang, H. & Crawford, J. D. (2001) The superior colliculus encodes gaze commands in retinal coordinates. *Nature Neuroscience* 4:627–32.
- Kolmac, C. I.; Power, B. D. & Mitrofanis, J. (1998) Patterns of connections between zona incerta and brainstem in rats. *Journal of Comparative Neurology* 396:544–55.
- König, P., Engel, A. K. & Singer, W. (1996) Integrator or coincidence detector? The role of the cortical neuron revisited. *Trends in Neurosciences* 19:130–37.
- Körding, K. P. & Wolpert, D. M. (2006) Bayesian decision theory in sensorimotor control. *Trends in Cognitive Sciences* 10:319–26.
- Kozloski, J., Hamzei-Sichani, F. & Yuste R. (2001) Stereotyped position of local synaptic targets in neocortex. *Science* 293:868–72.
- Krauzlis, R. J. (2001) Extraretinal inputs to neurons in the rostral superior colliculus of the monkey during smooth-pursuit eye movements. *Journal of Neurophysiology* 86:2629–33.
- Krauzlis, R. J., Liston, D. & Carello, C. D. (2004) Target selection and the superior colliculus: Goals, choices and hypotheses. *Vision Research* 44:1445–51.
- Kuypers, H. G. J. M. (1982) A new look at the organization of the motor system. *Progress in Brain Research* 57:381–403.
- Kuypers, H. G. J. M. (1987) Some aspects of the organization of the output of the motor cortex. In: *Motor areas of the cerebral cortex, Ciba Foundation Symposium, 132*, ed. G. Bock, M. O'Connor & J. Marsh, pp. 63–82.
- Kuypers, H. G. J. M. & Martin, G. F., eds. (1982) *Anatomy of descending pathways to the spinal cord. Progress in brain research 57*. Elsevier Biomedical.
- Lacalli, T. C. (1996) Landmarks and subdomains in the larval brain of *Branchiostoma*: Vertebrate homologs and invertebrate antecedents. *Israel Journal of Zoology* 42:S131–46.

- Lacalli, T. (2001) New perspectives on the evolution of protochordate sensory and locomotory systems, and the origin of brains and heads. *Philosophical Transactions of the Royal Society (London B)* 356:1565–72.
- Laemle, L. K. (1983) A Golgi study of cell morphology in the deep layers of the human superior colliculus. *Journal für Hirnforschung* 24:297–306.
- Lamme, V. A. F. & Spekreijse, H. (2000) Modulations of primary visual cortex activity represent attentive and conscious scene perception. *Frontiers in Bioscience* 5:232–43.
- Lang, C. E. & Schieber, M. H. (2003) Differential impairment of individuated finger movements in humans after damage to the motor cortex or the corticospinal tract. *Journal of Neurophysiology* 90:1160–70.
- Langer, T. P. & Lund, R. D. (1974) The upper layers of the superior colliculus of the rat: A Golgi study. *Journal of Comparative Neurology* 158:418–35.
- Larkum, M. E., Senn, W. & Lüscher, H.-R. (2004) Top-down dendritic input increases the gain of layer 5 pyramidal neurons. *Cerebral Cortex* 14:1059–70.
- Lavallée, P., Urbain, N., Dufresne, C., Bokor, H., Acsady, L. & Deschenes, M. (2005) Feedforward inhibitory control of sensory information in higher-order thalamic nuclei. *Journal of Neuroscience* 25:7489–98.
- Lawrence, D. G. & Kuypers, H. G. J. M. (1968) The functional organization of the motor system in the monkey. I. The effects of bilateral pyramidal lesions. *Brain* 91:1–14.
- Lee, P. H., Helms, M. C., Augustine, G. J. & Hall, W. C. (1997) Role of intrinsic synaptic circuitry in collicular sensorimotor integration. *Proceedings of the National Academy of Sciences (USA)* 94:13299–304.
- Lehar, S. (2002) *The world in your head: A gestalt view of the mechanism of conscious experience*. Erlbaum.
- Leichnetz, G. R., Gonzalo-Ruiz, A., DeSalles, A. A. & Hayes, R. L. (1987) The origin of brainstem afferents of the paramedian pontine reticular formation in the cat. *Brain Research* 422:389–97.
- Lomber, S. G. & Payne, B. R. (1996) Removal of two halves restores the whole: Reversal of visual hemineglect during bilateral cortical and collicular inactivation in the cat. *Visual Neuroscience* 13:1143–56.
- Lomber, S. G., Payne, B. R. & Cornwell, P. (2001) Role of the superior colliculus in analyses of space: Superficial and intermediate layer contributions to visual orienting, auditory orienting, and visuospatial discriminations during unilateral and bilateral deactivations. *Journal of Comparative Neurology* 441:44–57.
- Lonstein, J. S., Simmons, D. A. & Stern, J. M. (1998) Functions of the caudal periaqueductal



- gray in lactating rats: kyphosis, lordosis, maternal aggression, and fearfulness. *Behavioral Neuroscience* 112:1502–18.
- Loop, M. S. & Sherman, S. M. (1977) Visual discriminations of cats with cortical and tectal lesions. *Journal of Comparative Neurology* 174:79–88.
- Lott, I. T., McPherson, D. L. & Starr, A. (1986) Cerebral cortical contributions to sensory evoked potentials: hydranencephaly. *Electroencephalography and Clinical Neurophysiology* 64:218–23.
- Lynch, J. C., Hoover, J. E. & Strick, P. L. (1994) Input to the primate frontal eye field from the substantia nigra, superior colliculus, and dentate nucleus demonstrated by transneuronal transport. *Experimental Brain Research* 100:181–86.
- Lyon, D. C., Nassi, J. J. & Callaway, E. M. (2005) Disynaptic connections from the superior colliculus to cortical area MT revealed through transsynaptic labeling with rabies virus (abstract). *Journal of Vision* 5:432a.
- Ma, T. P. (1996) Saccade-related omnivectoral pause neurons in the primate zona incerta. *Neuroreport* 7:2713–16.
- Ma, T. P., Cheng, H. W., Czech, J. A. & Rafols, J. A. (1990) Intermediate and deep layers of the macaque superior colliculus: A Golgi study. *Journal of Comparative Neurology* 295:92–110.
- Maes, P. (1990) Situated agents can have goals. In: *Designing autonomous agents*, ed. P. Maes, pp. 49–70. MIT Press.
- Magoun, H. W. (1954) The ascending reticular system and wakefulness. In: *Brain mechanisms and consciousness*, ed. E. D. Adrian, F. Bremer & H. H. Jasper, pp. 1–20. Blackwell.
- Mana, S. & Chevalier, G. (2002) The fine organization of nigro-collicular channels with additional observations of their relationships with acetylcholinesterase in the rat. *Neuroscience* 106:357–74.
- Mandler, G. A. (1975) Consciousness: Respectable, useful, and *probably* necessary. In: *Information processing and cognition: The Loyola Symposium*, ed. R. Solso, pp. 229–54. Erlbaum.
- Mandler, G. A. (2002) *Consciousness recovered. Psychological functions and origins of conscious thought*. Benjamins.
- Marin-Padilla, M. (1997) Developmental neuropathology and impact of perinatal brain damage. II: White matter lesions of the neocortex. *Journal of Neuropathology and Experimental Neurology* 56:219–35.
- Maskos, U., Molles, B. E., Pons, S., Besson, M., Guiard, B. P., Guilloux J. P., Evrard, A., Cazala, P., Cormier, A., Mameli-Engvall, M., Dufour, N., Cloez-Tayarani, I., Bemelmans, A. P., Mallet, J., Gardier, A. M., David, V., Faure, P., Granon, S. & Changeux, J. P. (2005) Nicotine reinforcement and cognition restored by targeted expression of nicotinic receptors. *Nature*

436:103–07.

Masino, T. (1992) Brainstem control of orienting movements: Intrinsic coordinate system and underlying circuitry. *Brain, Behavior and Evolution* 40:98–111.

Masino, T. & Grobstein, P. (1989) The organization of descending tectofugal pathways underlying orienting in the frog, *Rana pipiens*. I. Lateralization, parcellation, and an intermediate spatial representation. *Experimental Brain Research* 75:227–44.

Masino, T. & Knudsen, E. I. (1990) Horizontal and vertical components of head movement are controlled by distinct neural circuits in the barn owl. *Nature* 345:434–37.

May, P. J. (2005) The mammalian superior colliculus: Laminar structure and connections. *Progress in Brain Research* 151:321–78.

May, P. J., Hartwich-Young, R., Nelson, J., Sparks, D. L. & Porter, J. D. (1990) Cerebellotectal pathways in the macaque: Implications for collicular generation of saccades. *Neuroscience* 36:305–24.

May, P. J., Sun, W. & Hall, W. C. (1997) Reciprocal connections between the zona incerta and the pretectum and superior colliculus of the cat. *Neuroscience* 77:1091–14.

McAbee, G. N., Chan, A. & Erde, E. L. (2000) Prolonged survival with hydranencephaly: Report of two patients and literature review. *Pediatric Neurology* 23:80–84.

McCormick, D. A. & Contreras, D. (2001) On the cellular and network bases of epileptic seizures. *Annual Review of Physiology* 63:815–46.

McFarland, D. (1965) Flow graph representation of motivational systems. *British Journal of Mathematical and Statistical Psychology* 18:25–43.

McFarland, D. J. & Sibly, R. M. (1975) The behavioural final common path. *Philosophical Transactions of the Royal Society (London)* 270:265–93.

McFarland, D. & Houston, A. (1981) *Quantitative ethology: The state space approach*. Pitman.

McHaffie, J. G., Norita, M., Dunning, D. D. & Stein, B. E. (1993) Corticotectal relationships: Direct and “indirect” pathways. *Progress in Brain Research* 95:139–50.

McPeck, R. M. & Keller, E. L. (2004) Deficits in saccade target selection after inactivation of the superior colliculus. *Nature Neuroscience* 7:757–63.

Meeren, H., Van Luijckelaar, E. L., Lopes da Silva, F. H. & Coenen, A. (2005) Evolving concepts on the pathophysiology of absence seizures. *Archives of Neurology* 62:371–76.

Meredith, M. A. & Ramoa, A. S. (1998). Intrinsic circuitry of the superior colliculus: Pharmacophysiological identification of horizontally oriented inhibitory interneurons. *Journal of Neurophysiology* 79:1597–1602.

- Meredith, M. A. & King A. J. (2004) Spatial distribution of functional superficial–deep connections in the adult ferret superior colliculus. *Neuroscience* 128:861–70.
- Merker, B. (1980) *The sentinel hypothesis: A role for the mammalian superior colliculus*. Doctoral dissertation, Massachusetts Institute of Technology.
- Merker, B. (1997) *The common denominator of conscious states: Implications for the biology of consciousness*. Archived preprint: <http://cogprints.soton.ac.uk> (biology; theoretical biology).
- Merker, B. (2004a) Cortex, countercurrent context, and dimensional integration of lifetime memory. *Cortex* 40:559–76.
- Merker, B. (2004b) The local and the global in cortical phylogeny and function. Reply to Finlay and Lamme. *Cortex* 40:582–83.
- Merker, B. (2005) The liabilities of mobility: A selection pressure for the transition to cortex in animal evolution. *Consciousness and Cognition* 14:89–114.
- Mesulam, M.-M. (1999) Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society (London B)* 354:1325–46.
- Meyer, J.-A. & Wilson, S. W., eds. (1991) *From animals to animats: Proceedings of the First International Conference on Simulation of Adaptive Behavior*. MIT Press.
- Miller, G. A. (1986) Interview with George A. Miller. In: *The cognitive revolution in psychology*, ed. B. J. Baars, pp. 199–222. Guilford.
- Mitrofanis, J. (2005) Some certainty for the “zone of uncertainty”? Exploring the function of the zona incerta. *Neuroscience* 130:1–15.
- Mitrofanis, J. & Mikuletic, L. (1999) Organization of the cortical projection to the zona incerta of the thalamus. *Journal of Comparative Neurology* 412:173–185.
- Mize, R. R., Whitworth, H., Nunes-Cardozo, B. & van der Want, J. (1994) Ultrastructural organization of GABA in the rabbit superior colliculus revealed by quantitative postembedding immunocytochemistry. *Journal of Comparative Neurology* 341:273–87.
- Morcuende, S., Delgado-García, J.-M. & Ugolini, G. (2002) Neuronal premotor networks involved in eyelid responses: Retrograde transneuronal tracing with rabies virus from the orbicularis oculi muscle in the rat. *Journal of Neuroscience* 22:8808–18.
- Morin, A. (2006) Levels of consciousness and self-awareness: A comparison and integration of various neurocognitive views. *Consciousness and Cognition* 15:358–71.
- Mort, E., Cairns, S., Hersch, H. & Finlay, B. (1980) The role of the superior colliculus in visually guided locomotion and visual orienting in the hamster. *Physiological Psychology* 8:20–28.

Moruzzi, G. & Magoun, H. W. (1949) Brain stem reticular formation and activation of the EEG. *Electroencephalography and Clinical Neurophysiology* 5:1–22.

Moschovakis, A. K. (1996) Neural network simulations of the primate oculomotor system. II. Frames of reference. *Brain Research Bulletin* 40:337–45.

Moschovakis, A. E. & Highstein, S. M. (1994) The anatomy and physiology of primate neurons the control rapid eye movements. *Annual Review of Neuroscience* 17:465–88.

Mouton, L. J. (1999) *Spinal efferents and afferents of the periaqueductal gray: Possible role in pain, sex and micturition*. Doctoral dissertation, University of Groningen.

Müller, J. R., Philiastides, M. G. & Newsome, W. T. (2004) Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proceedings of the National Academy of Sciences (USA)* 102:524–29.

The Multi-Society Task Force on the Persistent Vegetative State. (1994) Statement on medical aspects of the persistent vegetative state (first of two parts). *New England Journal of Medicine* 330:1499–1508.

Mungarndee, S. S., Baldwin, B. A., Chindadoungratna C. & Kotchabhakdi, N. (2002) Hypothalamic and zona incerta neurons in sheep, initially only responding to the sight of food, also respond to the sight of water after intracerebroventricular injection of hypertonic saline or angiotensin II. *Brain Research* 925:204–12.

Myers, R. E. (1989) Cerebral ischemia in the developing primate fetus. *Biomedica Biochimica Acta* 48:S137–42.

Nashold, B. S., Wilson, W. P. & Slaughter, G. (1969) Sensations evoked by stimulation of the midbrain of man. *Journal of Neurosurgery* 30:14–24.

Neelon, M. F., Brungart, D. S. & Simpson, B. D. (2004) The isoazimuthal perception of sounds across distance: A preliminary investigation into the location of the audio egocenter. *Journal of Neuroscience* 24:7640–47.

Nemec, P., Altman, J., Marhold, S., Burda, H., & Oelschläger, H. H. A. (2001) Neuroanatomy of magnetoreception: The superior colliculus involved in magnetic orientation in a mammal. *Science* 294:366–68.

Nicolelis, M. A. L., Chapin, J. K. & Lin, R. C. (1992) Somatotopic maps within the zona incerta relay parallel GABAergic somatosensory pathways to the neocortex, superior colliculus and brainstem. *Brain Research* 577:134–41.

Niemi-Junkola, U. J. & Westby, G. W. M. (2000) Cerebellar output exerts spatially organised influence on neural responses in the rat superior colliculus. *Neuroscience* 97:565–73.

Nieuwenhuis, R., Ten Donkelaar, H. J. & Nicholson, C., eds. (1998) *The central nervous system*

*of vertebrates* (4 Vols). Springer-Verlag.

Northcutt, R. G. (1996a) The Agnathan ark: The origin of the craniate brain. *Brain, Behavior and Evolution* 48:237–47.

Northcutt, R. G. (1996b) The origin of craniates: neural crest, neurogenic placodes, and homeobox genes. *Israel Journal of Zoology* 42:S273–13.

Northcutt, R. G. & Wicht, H. (1997) Afferent and efferent connections of the lateral and medial pallia of the silver lamprey. *Brain, Behavior and Evolution* 49:1–19.

Nudo, R. J. & Masterton, R. B. (1988) Descending pathways to the spinal cord: a comparative study of 22 mammals. *Journal of Comparative Neurology* 277:53–79.

Oakley, D. A. (1983) The varieties of memory: A phylogenetic approach. In *Memory in animals and humans*, ed. A. Mayes, pp. 20–82. Van Nostrand Reinhold.

O'Regan, J. K., Deubel, H., Clark, J. J. & Rensink, R. A. (2000) Picture changes during blinks: Looking without seeing and seeing without looking. *Visual Cognition* 7:191–211.

Orlovsky, G. N. & Shik, M. L. (1976) Control of locomotion: A neurophysiological analysis of the cat locomotor system. *International Review of Physiology* 10:281–317.

Özen, G., Augustine, G. J. & Hall, W. C. (2000) Contribution of superficial layer neurons to premotor bursts in the superior colliculus. *Journal of Neurophysiology* 84:460–71.

Padel, Y. (1993) Magnocellular and parvocellular red nuclei. Anatomico-functional aspects and relations with the cerebellum and other nerve centres. *Revue Neurologique (Paris)* 149:703–15 (in French).

Palmer, L. A., Rosenquist, A. C. & Sprague, J. M. (1972) Corticotectal systems in the cat: Their structure and function. In: *Corticothalamic projections and sensorimotor activities*, ed. T. Frigyesi, E. Rinvik & M. D. Yahr, pp. 491–522. Raven Press.

Panksepp, J. (1982) Toward a general psychobiological theory of emotions. *The Behavioral and Brain Sciences* 5:407–67.

Panksepp, J. (1998) *Affective neuroscience: The foundations of human and animal emotions*. Oxford University Press.

Panksepp, J., Normansell, L., Cox, J. F. & Siviy, S. M. (1994) Effects of neonatal decortication on the social play of juvenile rats. *Physiology and Behavior* 56:429–43.

Parvizi, J. & Damasio, A. R. (2001) Consciousness and the brainstem. *Cognition* 79:135–60.

Parvizi, J. & Damasio, A. R. (2003) Neuroanatomical correlates of brainstem coma. *Brain* 126:1524–36.

- Pellis, S. M., Pellis, V. C. & Whishaw, I. Q. (1992) The role of the cortex in play fighting by rats: Developmental and evolutionary implications. *Brain, Behavior and Evolution* 39:270–84.
- Penfield, W. (1952) Epileptic automatisms and the centrencephalic integrating system. *Research Publications of the Association for Nervous and Mental Disease* 30:513–28.
- Penfield, W. & Jasper, H. H. (1954) *Epilepsy and the functional anatomy of the human brain*. Little, Brown.
- Petty, P. G. (1998) Consciousness: A neurosurgical perspective. *Journal of Consciousness Studies* 5:86–96.
- Philipona, D., O'Reagan, J. K. & Nadal, J.-P. (2003) Is there something out there? Inferring space from sensorimotor dependencies. *Neural Computation* 15:2029–49.
- Philipona, D., O'Regan, J. K., Nadal, J.-P. & Coenen, O. J.-M. D. (2004) Perception of the structure of the physical world using multimodal unknown sensors and effectors. *Advances in Neural Information Processing Systems* 16:945–52.
- Populin, L. C. & Yin, T. C. T. (1998) Sensitivity of auditory cells in the superior colliculus to eye position in the behaving cat. In: *Psychological and physiological advances in hearing*, ed. A. R. Palmer, A. Q. Summerfield & R. Meddis, pp 441–48. Whurr.
- Posner, M. I. & Petersen, S. E. (1990) The attention systems of the human brain. *Annual Review of Neuroscience* 13:25–42.
- Power, B. D. & Mitrofanis, J. (1999) Evidence for extensive inter-connections within the zona incerta in rats. *Neuroscience Letters* 267: 9–12.
- Power, B. D., Kolmac, C. I. & Mitrofanis, J. (1999) Evidence for a large projection from the zona incerta to the dorsal thalamus. *Journal of Comparative Neurology* 404:554–65.
- Power, B. D. & Mitrofanis, J. (2001) Zona incerta: Substrate for the contralateral interconnectivity in the thalamus of rats. *Journal of Comparative Neurology* 436:52–63.
- Prescott, T. J., Redgrave, P. & Gurney, K. N. (1999) Layered control architectures in robots and vertebrates. *Adaptive Behavior* 7:99–127.
- Provine, R. R. & Yong, Y. L. (1991) Laughter: A stereotyped human vocalization. *Ethology* 89:115–24.
- Ramón-Moliner, E. & Nauta, W. J. H. (1966) The isodendritic core of the brainstem. *Journal of Comparative Neurology* 126:311–35.
- Raz, A. & Buhle, J. (2006) Typologies of attentional networks. *Nature Reviews Neuroscience* 7:367-79.

- Rees, G. (2001) Neuroimaging of visual awareness in patients and normal subjects. *Current Opinion in Neurobiology* 11:150–56.
- Rees, G. & Lavie, N. (2001) What can functional imaging reveal about the role of attention in visual awareness? *Neuropsychologia* 39:1343–53.
- Rensink, R.A. (2002) Change detection. *Annual Review of Psychology* 53:245–77.
- Rensink, R.A., O'Regan, J. K. and Clark, J. J. (1997) To see or not to see: The need for attention to perceive changes in scenes. *Psychological Science* 8:368–73.
- Richards, W., Seung H. S. & Pickard, G. (2006) Neural voting machines. *Neural Networks* 19:1161-7.
- Rieck, R. W., Huerta, M. F., Harting, J. K. & Weber, J. T. (1986) Hypothalamic and ventral thalamic projections to the superior colliculus in the cat. *Journal of Comparative Neurology* 243:249–65.
- Roelofs, C. O. (1959) Considerations on the visual egocenter. *Acta Psychologica* 16:226–34.
- Sakuma, Y. & Pfaff, D. W. (1979) Facilitation of female reproductive behavior from mesencephalic central gray in the rat. *American Journal of Physiology* 237:R278–84.
- Satterlie, R. A. & Nolen, T. G. (2001) Why do cubomedusae have only four swim pacemakers? *Journal of Experimental Biology* 204:1413–19.
- Schaefer, K. P. & Schneider, H. (1968) Reizversuche im tectum opticum des Kaninchens. Ein experimenteller Beitrag zur sensorimotorischen Koordination des Hirnstammes. *Archiv für Psychiatrie und Nervenkrankheiten* 211:118–37.
- Schall, J. D. (1997) Visuomotor areas of the frontal lobe. *Cerebral Cortex* 12:527–638.
- Scheibel, M. E. & Scheibel, A. B. (1977) The anatomy of constancy. *Annals of the New York Academy of Sciences* 290:421–35.
- Schiller, P. H. & Koerner, F. (1971) Discharge characteristics of single units in superior colliculus of the alert Rhesus monkey. *Journal of Neurophysiology* 43:920–36.
- Schiller, P. H., True, S. D. & Conway, J. L. (1979) Effects of frontal eye field and superior colliculus ablations on eye movements. *Science* 206:590–92.
- Schiller, P. H. & Lee, K. (1994) The effects of lateral geniculate nucleus, area V4, and middle temporal (MT) lesions on visually guided eye movements. *Visual Neuroscience* 11:229–41.
- Schlag-Rey, M., Schlag, J. & Dassonville, P. (1992) How the frontal eye fields impose a saccade goal on superior colliculus neurons. *Journal of Neurophysiology* 67:1003–05.
- Schmidtke, K. & Buttner-Ennever, J. A. (1992) Nervous control of eyelid function. A review of

clinical, experimental and pathological data. *Brain* 115:227–47.

Schneider, G. E. (1967) Contrasting visuomotor functions of tectum and cortex in the golden hamster. *Psychologische Forschung* 31:52–62.

Schneider, W. X. & Deubel, H. (2002) Selection-for-perception and selection-for-spatial-motor-action are coupled by visual attention: A review of recent findings and new evidence from stimulus-driven saccade control. In: *Attention and performance XIX: Common mechanisms in perception and action*, ed. W. Prinz & B. Hommel, pp. 609–27. Oxford University Press.

Schopenhauer, A. (1819/1958) *The world as will and representation* (2 vols.), trans. E. F. J. Payne. Dover.

Schuller, G. & Radtke-Schuller, S. (1990) Neural control of vocalization in bats: Mapping of brainstem areas with electrical microstimulation eliciting species-specific echolocation calls in the rufous horseshoe bat. *Experimental Brain Research* 79:192–206.

Searle, J. R. (1992) *The rediscovery of the mind*. MIT Press.

Sewards, T. V. & Sewards, M. A. (2000). Visual awareness due to neuronal activities in subcortical structures: A proposal. *Consciousness and Cognition* 9:86–116.

Sherman, H. B., Caviness, Jr., V. S. & Ingle, D. J. (1979) Corticotectal connections in the gerbil. *Neuroscience Abstract* 9:120.

Sherman, S. M. (1974) Visual fields of cats with cortical and tectal lesions. *Science* 185:355–57.

Sherman, S. M. (1977) The effect of superior colliculus lesions upon the visual fields of cats with cortical ablations. *Journal of Comparative Neurology* 172:211–30.

Sherman, S. M. & Guillery, R. W. (2001) *Exploring the thalamus*. Academic Press.

Shewmon, A. D., Capron, A. M., Peacock, W. J. & Shulman, B. L. (1989) The use of anencephalic infants as organ sources. A critique. *Journal of the American medical Association* 261:1773–81.

Shewmon, D. A., Holmes, G. L. & Byrne, P. A. (1999) Consciousness in congenitally decorticate children: Developmental vegetative state as self-fulfilling prophecy. *Developmental Medicine and Child Neurology* 41:364–74.

Shewmon, D. A. (2004) The ABC of PVS. In: *Brain death and disorders of consciousness*, ed. C. Machado & D. A. Shewmon, pp. 215–28. Kluwer Academic/Plenum.

Simons, D. J. & Chabris, C. F. (1999) Gorillas in our midst: Sustained inattentive blindness for dynamic events. *Perception* 28:1059–74.

Singer, W. (2001) Consciousness and the binding problem. In: *Cajal and consciousness: Scientific approaches to consciousness on the centennial of Ramón y Cajal's Textura*, ed. P. C.



Marijuán. *Annals of the New York Academy of Science* 929:123–46.

Snaith, S. & Holland, O. (1990) An investigation of two mediation strategies suitable for behavioural control in animals and animats. In: *From animals to animats: Proceedings of the First International Conference on Simulation of Adaptive Behavior*, ed. J.-A. Meyer & S. Wilson, pp. 255–62). MIT Press.

Snodgrass, R. E. (1935) *Principles of insect morphology*. McGraw-Hill.

Sommer, M. A. & Wurtz, R. H. (2004) What the brain stem tells the frontal cortex. I. Oculomotor signals sent from superior colliculus to frontal eye field via mediodorsal thalamus. *Journal of Neurophysiology* 91:1381–1402.

Sparks, D. L. (1999) Conceptual issues related to the role of the superior colliculus in the control of gaze. *Current Opinion in Neurobiology* 9:698–707.

Sporns, O., Tononi, G. & Edelman, G. M. (2000) Theoretical neuroanatomy: Relating anatomical and functional connectivity in graphs and cortical connection matrices. *Cerebral Cortex* 10:127–41.

Sprague, J. M. Chambers, W. W. & Stellar, E. (1961) Attentive, affective, and adaptive behavior in the cat. *Science* 133:165–73.

Sprague, J. M. (1966) Interaction of cortex and superior colliculus in mediation of visually guided behavior in the cat. *Science* 153:1544–47.

Sprague, J. M. (1975) Mammalian tectum: Intrinsic organization, afferent inputs, and integrative mechanisms. In: *Sensorimotor function of the midbrain tectum*, ed. D. Ingle & J. M. Sprague. *Neurosciences Research Program Bulletin* 13:204–14. MIT Press.

Sprague, J. M. (1991) The role of the superior colliculus in facilitating visual attention and form perception. *Proceedings of the National Academy of Sciences (USA)* 88:1286–90.

Sprague, J. M. (1996) Neural mechanisms of the visual orienting response. *Progress in Brain Research* 112:1–15.

Standing, L. (1973) Learning 10,000 pictures. *Quarterly Journal of Experimental Psychology* 25:207–22.

Steele, G. E. & Weller, R. E. (1993) Subcortical connections of subdivisions of inferior temporal cortex in squirrel monkeys. *Visual Neuroscience* 10:563–83.

Stefan, H. & Snead, O. C. (1997) Absence seizures. In *Epilepsy: A comprehensive textbook*, ed. J. Jr., Engel & T. A. Pedley, pp. 579–90. Lippincott-Raven.

Steriade, M. (2001) Impact of network activities on neuronal properties in corticothalamic systems. *Journal of Neurophysiology* 86:1–39.

- Stoerig, P. & Barth, E. (2001) Low-level phenomenal vision despite unilateral destruction of primary visual cortex. *Consciousness and Cognition* 10:574–87.
- Strafstrom, C. E. (2006) Epilepsy: A review of selected clinical syndromes and advances in basic science. *Journal of Cerebral Blood Flow and Metabolism* 26:983–1004.
- Stuphorn, V., Bauswein, E. & Hoffmann, K.-P. (2000) Neurons in the primate superior colliculus coding for arm movements in gaze-related coordinates. *Journal of Neurophysiology* 83:1283–99.
- Sutton, L. N., Bruce, D. A. & Schut, L. (1980) Hydranencephaly versus maximal hydrocephalus: An important clinical distinction. *Neurosurgery* 6:34–38.
- Swanson, L. W. (1987) The hypothalamus. In: *Handbook of chemical neuroanatomy. Integrated systems of the CNS, Part 1, vol. 5*, ed. T. Hökfelt, A. Björklund & L. W. Swanson, pp. 1–124. Elsevier.
- Swanson, L. W. (2000) Cerebral hemisphere regulation of motivated behavior. *Brain Research* 886:113–64.
- Takada, K., Shiota, M., Ando, M., Kimura, M. & Inoue, K. (1989) Porencephaly and hydranencephaly: a neuropathological study of four autopsy cases. *Brain and Development*, 11:51–56.
- Tehovnik, E. J., Lee, K. & Schiller, P. H. (1994) Stimulation-evoked saccades from the dorsomedial frontal cortex of the rhesus monkey following lesions of the frontal eye fields and superior colliculus. *Experimental Brain Research* 98:179–90.
- ten Donkelaar, H. J. (1988) Evolution of the red nucleus and rubrospinal tract. *Behavioral Brain Research* 28:920.
- Thompson, R. (1993) Centrencephalic theory, the general learning system, and subcortical dementia. *Annals of the New York Academy of Sciences* 702:197–223.
- Thompson, R & Bachman, M. K. (1979) Zona incerta: A link between the visual cortical sensory system and the brainstem motor system. *Physiological Psychology* 7:251–53.
- Tinbergen, N. (1951) *The study of instinct*. Clarendon.
- Trageser, J. C. & Keller, A. (2004) Reducing the uncertainty: Gating of peripheral inputs by zona incerta. *Journal of Neuroscience* 24:8911–9005.
- Trevarthen, C. & Reddy, V. (in press) Consciousness in infants. In: *A companion to consciousness*, ed. M. Velmans & S. Schneider. Blackwell.
- Tyrrell, T. (1993) *Computational mechanisms for action selection*. Doctoral dissertation, University of Edinburgh, Centre for Cognitive Science.
- Ugolini, G. (1995) The specificity of rabies virus as a transneuronal tracer of motor networks:

- Transfer from hypoglossal motoneurons to connected second-order and higher order central nervous system cell groups. *Journal of Comparative Neurology* 356:457–80.
- Valentine, D. E. & Moss, C. F. (1997) Spatially selective auditory responses in the superior colliculus of the echolocating bat. *Journal of Neuroscience* 17:1720–33.
- van Hooff, J. A. R. A. M. (1972) A comparative approach to the phylogeny of laughter and smile. In: *Nonverbal communication*, ed. R. A. Hinde, pp. 209–41. Cambridge University Press.
- Van Opstal, A. J., Hepp, K., Suzuki, Y., & Henn, V. (1995) Influence of eye position on activity in monkey superior colliculus. *Journal of Neurophysiology* 74:1539–1610.
- Vanderwolf, C. H., Kolb, B. & Cooley, R. K. (1978) Behavior of the rat after removal of the neocortex and hippocampal formation. *Journal of Comparative and Physiological Psychology* 92:156–75.
- Vetter, P., Goodbody, S. J. & Wolpert, D. M. (1999) Evidence for an eye-centered spherical representation of the visuomotor map. *Journal of Neurophysiology* 81:935–39.
- von Holst, E. & Mittelstaedt, H. (1950) Das Reafferenzprinzip (Wechselwirkungen zwischen Zentralnervensystem und Peripherie). *Naturwissenschaften* 37:464–76.
- Waitzman, D. M., Silakov, V. L, DePalma-Bowles, S. & Ayers, A. S. (2000) Effects of reversible inactivation of the primate mesencephalic reticular formation. II. Hypometric vertical saccades. *Journal of Neurophysiology* 83:2285–99.
- Wallace, S. F., Rosenquist, A. C. & Sprague, J. M. (1989) Recovery from cortical blindness mediated by destruction of nontectotectal fibers in the commissure of the superior colliculus in the cat. *Journal of Comparative Neurology* 284:429–50.
- Wallace, S. F., Rosenquist, A. C. & Sprague, J. M. (1990) Ibotenic acid lesions of the lateral substantia nigra restore visual orientation behavior in the hemianopic cat. *Journal of Comparative Neurology* 296:222–52.
- Wang, S. & Redgrave, P. (1997) Microinjections of muscimol into lateral superior colliculus disrupt orienting and oral movements in the formalin model of pain. *Neuroscience* 81:967–88.
- Watkins, S., Shams, L., Tanaka, S., Haynes, J.-D. & Rees, G. (2006) Sound alters activity in human V1 in association with illusory visual perception. *NeuroImage* 31:1247–56.
- Watt, D. (2000) The centrencephalon and thalamocortical integration: Neglected contributions of periaqueductal gray. *Consciousness and Emotion* 1:91–114.
- Watt, D. F. & Pincus, D. I. (2004) Neural substrates of consciousness: implications for clinical psychiatry. In: *Textbook of biological psychiatry*, ed. J. Paanksepp, pp. 75–110. Wiley.
- Webster, M. J., Bachevalier, J. & Ungerleider, L. G. (1993) Subcortical connections of inferior temporal areas TE and TEO in macaque monkeys. *Journal of Comparative Neurology* 335:73–

*Webster's Third New International Dictionary of the English language unabridged*, 1961, ed. P. Babcock Gove. 1993 reprint. Könemann.

Weddell, R. A. (2004) Subcortical modulation of spatial attention including evidence that the Sprague effect extends to man. *Brain and Cognition* 55:497–506.

Wentzel, P. R., De Zeeuw, C. I., Holstege, J. C. & Gerrits, N. M. (1995) Inhibitory synaptic inputs to the oculomotor nucleus from vestibulo-ocular-reflex-related nuclei in the rabbit. *Neuroscience* 65:161–74.

Werner, W., Dannenberg, S. & Hoffmann, P. (1997) Arm-movement-related neurons in the primate superior colliculus and underlying reticular formation: Comparison of neuronal activity with EMGs of muscles of the shoulder, arm and trunk during reaching. *Experimental Brain Research* 115:191–205.

Whishaw, I. Q. (1990) The decorticate rat. In: *The cerebral cortex of the rat*, ed. B. Kolb & R. C. Tees, pp. 239–67. MIT Press.

Whishaw, I. Q. & Kolb, B. (1985) The mating movements of male decorticate rats: Evidence for subcortically generated movements by the male but regulation of approaches by the female. *Behavioural Brain Research* 17:171–91.

Whishaw, I. Q. & Kolb, B. (1988) Spraying of skilled forelimb reaching and corticospinal projections after neonatal motor cortex removal or hemidecortication in the rat: Support for the Kennard doctrine. *Brain Research* 451:97–114.

Wiberg, M. (1992) Reciprocal connections between the periaqueductal gray matter and other somatosensory regions of the cat midbrain: a possible mechanism of pain inhibition. *Uppsala Journal of Medical Science* 97:37–47.

Wicht, H. (1996) The brains of lampreys and hagfishes: Characteristics, characters, and comparisons. *Brain, Behavior and Evolution* 48:248–61.

Wicht, H. & Northcutt, R. G. (1992) The forebrain of the pacific hagfish: A cladistic reconstruction of the ancestral craniate forebrain. *Brain, Behavior and Evolution* 40:25–64.

Windle, W. F. & Baxter, R. E. (1936) Development of reflex mechanisms in the spinal cord of albino rat embryos. Correlations between structure and function, and comparisons with the cat and the chick. *Journal of Comparative Neurology* 63:189–209.

Winn, P. (1998) Frontal syndrome as a consequence of lesions in the pedunculopontine tegmental nucleus: A short theoretical review. *Brain Research Bulletin* 47:551–63.

Wintour, E. M., Lewitt, M., McFarlane, A., Moritz, K., Potocnik, S., Rees, S. & Tangalakis, K. (1996) Experimental hydranencephaly in the ovine fetus. *Acta Neuropathologica (Berlin)* 91:537–44.

Woods, J. W. (1964) Behavior of chronic decerebrate rats. *Journal of Neurophysiology* 27:635–44.

Wurtz, R. H. & Mohler, C. W. (1974) Selection of visual targets for the initiation of saccadic eye movements. *Brain Research* 71:209–14.

Yarrow, K., Johnson, H., Haggard, P. & Rothwell, J. C. (2004) Consistent chronostasis effects across saccade categories imply a subcortical efferent trigger. *Journal of Cognitive Neuroscience* 16:839–47.

Yuge, T. & Kaga, K. (1998) Brain functions of an infant with hydranencephaly revealed by auditory evoked potentials. *International Journal of Pediatric Otorhinolaryngology* 45:91–95.

Zahm, D. S. (2006) The evolving theory of basal forebrain functional-anatomical ‘macrosystems’. *Neuroscience and Biobehavioral Reviews* 30:148–72.

Zella, J. C., Brugge, J. F. & Schnupp, J. W. H. (2001) Passive eye displacement alters auditory spatial receptive fields of cat superior colliculus neurons. *Nature Neuroscience* 4:1167–69.

Zhu, J. J. & Lo, F. S. (2000) Recurrent inhibitory circuitry in the deep layers of the rabbit superior colliculus. *Journal of Physiology* 523:731–40.

Zompa, I. C. & Dubuc, R. (1996) A mesencephalic relay for visual inputs to reticulospinal neurones in lampreys. *Brain Research* 718:221–27.

<Refs end>