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# Who dominates who in the dark basements of the brain?

A commentary on Bjorn Merker "Consciousness without a cerebral cortex: A challenge for neuroscience and medicine", *Behavioral and Brain Sciences*, 2007. (Merker, 2007)

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## ABSTRACT

Subcortical substrates for behavioural integration include the fore/midbrain nuclei of the basal ganglia and the hindbrain medial reticular formation. The midbrain superior colliculus requires basal ganglia disinhibition in order to generate orienting movements. The colliculus should therefore be seen as one of many competitors vying for control of the body's effector systems with the basal ganglia acting as the key arbiter.

Understanding the brain's functional architecture is certainly key to unlocking the mystery of the coherence of behaviour, and even, perhaps, consciousness. In this regard, Merker usefully draws our attention to subcortical systems as critical loci for behavioural integration that may instantiate some form of supra-cortical control. As we have previously argued (Prescott et al., 1999), combining Penfield's notion of a centrencephalic dimension to brain organization with a view of the brain as a layered control system provides a powerful set of explanatory concepts for understanding how the vertebrate brain architecture has adapted, with little change to its basic "groundplan," to many different body types and ecological niches. The particular set of brainstem substrates that Merker has chosen to emphasize seems, however, somewhat curious. The roles of the colliculus in orienting, the periaquaductal grey in behavioural patterning, and the hypothalamus in motivation are not controversial, but the promotion of the colliculus to the "functional apex" of processing for target selection is surprising, as is the suggestion of the zona incerta (ZI) as a key locus for action selection. In our view, other centres, either side (i.e., both more rostral and more caudal) of Merker's "selection triangle," may be more important in subserving these important aspects of behavioural integration.

One such group of structures are the basal ganglia (BG). This collection of fore- and mid-brain nuclei, identified by (Thompson, 1993) as a major component of the centrencephalic core, is located in such a way that its principal input structure (striatum) is rostral, and its output structure, substantia nigra (SNr), caudal to Merker's "synencephalic bottleneck." The BG are therefore ideally placed to provide the required funnel from distributed cortical processing to sequential brainstem operation. Merker discusses the functional role of the BG, primarily in relation to this "data reduction" context, as providing actionrelated information to the colliculus. However, the BG appear to be doing something more significant than simply providing the colliculus with one of its several sources of afferent input. Specifically, the tonic inhibition provided by the SNr maintains a veto over the capacity of the colliculus to generate orienting movements (Hikosaka et al., 2000). In the case of a visual stimulus, for example, this veto is only removed when there is sufficient excitatory input onto the oculomotor region of the striatum to cause inhibition of SNr and, thence, disinhibition of the collicular motor layer. The colliculus itself provides afferent input (via thalamus) to relevant striatal neurons that, together with convergent signals from cortex, the limbic system, and elsewhere, determine the significance of the stimulus (McHaffie et al., 2005). It is therefore the BG, not the colliculus, that sees the full gamut of pertinent, contextual information and is thus the dominant partner. Without BG gating, the colliculus would initiate orienting to any target that generated a strong, spatially localized phasic stimulus. The BG add intelligence to this reactive process by preventing orienting to high-amplitude but uninteresting stimuli, and enabling it to weaker, but potentially more significant, triggers. A broad range of empirical studies, theoretical proposals, and computational models (for reviews see (Gurney et al., 2004; Redgrave et al., 1999)) support the proposal that the BG operate as an action selection mechanism, not just for collicular control of orienting, but for competing sensorimotor systems throughout the brain. From this perspective, the colliculus is just one of many competitors vying for control of the body's effector mechanisms, with the BG as the key arbiter.

A remarkable feature of the BG is the homogeneity of their intrinsic circuitry. This observation adds weight to the hypothesis that these nuclei implement a consistent function despite the functional diversity of brain areas to which they interface. In contrast, the ZI, highlighted by Merker as a possible action selection locus, is a very heterogeneous structure (Mitrofanis, 2005). Furthermore, evidence from functional studies suggests other possible modulating roles: for instance, (Trageser et al., 2006) reported ZI's involvement in gating ascending sensory inputs according to the animal's current state of arousal.

Although the BG instantiate a dominant integrative centre in the intact adult brain, studies of infant and decerebrate rats suggest the presence of an alternative locus for action integration further down the neuraxis. A possible candidate, first suggested by the Scheibels (Scheibel and Scheibel, 1967), is the medial core of the reticular formation (mRF). This hindbrain structure receives input from many cortical and subcortical brain systems and directs its output to movement generators in the brainstem and spinal cord. We recently sought to promote interest in the mRF by elucidating its anatomy (Humphries et al., 2006), and by developing new simulation and robotic models of this structure viewed as an action selection mechanism (Humphries et al., 2007). The mRF is organized as a set of linearly arranged cell clusters, likened by the Scheibels to a "stack of poker chips." In Humphries et al. (2007) we proposed, and demonstrated in simulation, that activity in individual clusters may represent sub-actions – component parts of a complete behavior. Effective control by the mRF would therefore involve simultaneous activation of clusters representing compatible subactions and inhibition of clusters representing incompatible ones. The mRF is a major target of BG output (via the pedunculopontine nucleus) and, in the intact adult brain, both systems are likely to cooperate in determining what behaviour is expressed at a given time. The relationship between the two systems may combine aspects of layered and hierarchical decomposition of control. Layered, because developmental and lesion studies suggest that the mRF can operate, to some degree, without modulation from higher brain structures (including BG). Hierarchical, because patterns of mRF coordinated behavior could be selected in toto by BG focal disinhibition.

For Wilson (Wilson, 1925), the BG, lying towards the base of the brain, had "the characteristic of all basements, i.e. darkness." Although many windows have been opened onto BG function since Wilson's era, other subcortical nuclei still reside in subterranean obscurity. Despite the gaps in our knowledge, Merker is right to try to discern some structure amidst the gloom. With regard to his specific hypotheses, however, there is no compelling reason for viewing the ZI as the central arbiter, or the colliculus as the target selector. In the dark basements of the brain the basal ganglia dominate both.

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