

2002). Lack of a clear differentiation among processes in primary consciousness and in other levels of mental functioning may add to confusion and slow the development of scientific interest in the subject. Merker's target article presents a strong challenge to the prevailing notion of cognitive primacy in emotion processes and in emotion-cognition-behavior-relations (cf. Zajonc 1980).

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Target selection, attention, and the superior colliculus

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Abstract: Consistent with the target article, recent evidence indicates that the superior colliculus (SC) is somehow involved in target selection. However, it is not yet known whether this function is inherent to the SC or inherited from its inputs, how the selection process occurs for different movements, or how target selection by the SC is related to covert selection (i.e., attention).

It has been recognized for some time that the intermediate and deep layers of the superior colliculus (SC) in primates plays some role in target selection, at least for saccadic eye movements. For example, the preparation of saccades is correlated with increases in the activity of SC neurons that can begin hundreds of milliseconds before any movement and this activity appears to play a role in representing possible targets (Glimcher & Sparks 1992). Changing the probability that a visual stimulus will be the target – for example, by adding a variable number of irrelevant stimuli – changes the visual and tonic activity of many SC neurons (Basso & Wurtz 1997; Dorris & Munoz 1998). When the subject must search for a uniquely colored target stimulus amidst other colored distracters, many SC neurons discriminate the target from the distracter with a delay that is time-locked to stimulus onset, rather than saccade onset, suggesting that they play a role in target selection in addition to saccade preparation (McPeck & Keller 2002).

Perhaps the most compelling evidence for a role of the SC in target selection, as distinguished from saccade selection, comes from studies of the other type of voluntary eye movement made by primates – smooth pursuit. The SC has long been known to contain a motor map for saccades, but more recent studies have shown that the activity of many saccade-related SC neurons is also modulated during pursuit eye movements. These neurons show a somewhat complicated temporal pattern of activity during pursuit – and also fixation – but this pattern can be explained fairly simply by considering the location of the tracked target within the neurons' retinotopically organized response fields (Krauzlis et al. 1997, 2000). The distribution of activity across the SC motor map therefore appears to provide a real-time estimate of the position of the target in oculocentric or retinotopic coordinates, not restricted to saccades but for orienting movements in general. This "target position map" hypothesis provides what we consider to be a parsimonious alternative to the widely discussed "fixation zone/saccade zone" hypothesis (Munoz & Fecteau 2002), but the issue remains controversial.

The activity of many SC neurons also predicts the subject's choice of target for pursuit as well as for saccades. During

a visual search task, many SC neurons exhibit a preference for the target stimulus over irrelevant distracters that emerges over the course of ~100 ms prior to the initiation of pursuit and saccades (Krauzlis & Dill 2002). By interpreting the preference for the target stimulus as a "decision signal," we showed that SC activity could account for the target choices made by pursuit and saccades. We also inferred that pursuit uses a less stringent decision criterion than saccades, perhaps because errant saccades are more costly in their disruption to vision than mistakes by pursuit. These physiology results have been recently corroborated by behavioral studies in human subjects showing evidence that pursuit and saccade choices are guided by a common decision signal, and that the decision to trigger pursuit involves a threshold that is generally lower than that for saccades (Liston & Krauzlis 2003; 2005). The idea of a common decision signal is consistent with the integrative viewpoint put forward in the target article, but these issues are also not yet settled. For example, an alternative viewpoint is that target selection involves a serial linkage between saccades and pursuit, with pursuit simply adopting the choice made by the saccade system (Gardner & Lisberger 2002).

A pair of studies has recently demonstrated the idea that the SC is causally involved in target selection. The first study, focusing on saccadic eye movements, used a visual search task and found that when the region of the SC representing the target was focally inactivated, saccades were often misdirected to distracters appearing in unaffected areas of the visual field (McPeck & Keller 2004). The second study examined both saccades and pursuit using a luminance discrimination task and found that subthreshold microstimulation of the SC biased the selection of targets toward the stimulated location for both types of eye movements (Carello & Krauzlis 2004). The results for pursuit were especially revealing. Because the targets for pursuit initially appeared at a location opposite to its direction of motion, the experiment was able to distinguish between effects on the motor commands (i.e., which direction to move) and effects on the position of the target (i.e., which stimulus to follow). The results showed that altering SC activity changed which stimulus was chosen, regardless of the type or direction of eye movement that was needed to acquire the target. These experimental results provide strong support for the interpretation put forward in the target article that the primate SC plays an integrative role in target selection and decision-making, beyond its conventional role in the motor control of saccades.

What remains unclear from these studies is the extent to which target selection is a function that is inherent to the superior colliculus, a point that is central to the "mesodiencephalic" theory of consciousness put forward in the target article. A fairly common view of these recent findings is that the SC functions as a conduit for selection signals that are generated in other places, such as the cerebral cortex. Unfortunately for the theory, it is difficult to rule out this interpretation, because the extensive cortical and subcortical network involved in target selection makes it difficult to isolate the contribution of individual brain regions. Nonetheless, one crucial test is to determine how the inactivation of various cortical areas involved in target selection alters the properties of neurons elsewhere in the network, including the SC. These experiments would most likely identify multiple sources of support for target selection, but they might also help identify how the basic form of target selection putatively accomplished by the SC is extended in functional scope by the addition of signals from the forebrain.

A better test of the theory is suggested by the strongest prediction put forward in the article, namely 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" (sect. 4.5.1, para. 4, emphasis in original). Testing the contents of consciousness in animal subjects poses serious

challenges, but some recent studies have shown that stimulation in the SC alters performance in ways that mimic visual attention (Cavanaugh & Wurtz 2004; Muller et al. 2005). It is premature to conclude from this evidence that the SC plays a causal role in determining the contents of perceptual awareness, first because “attention” is not synonymous with “awareness,” but also because the effects of the stimulation likely extend to a network of areas connected to the SC, including several cortical areas that are themselves implicated in the control of attention. However, similar tests of visual attention can be conducted using selective inactivation of SC neurons, as has been done for target selection. Such experiments would provide an important test of the “mesodiencephalic” theory, and indicate whether further tests seem worthwhile.

In summary, the target article presents a provocative and contrarian theory of consciousness, but one that is supported by recent experimental findings about the role of the primate SC in target selection. Even more importantly, the theory makes specific predictions about the role of the SC in the control of perceptual awareness that could be tested experimentally.

Consciousness is more than wakefulness

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Abstract: Merker’s definition of consciousness excludes self-reflective thought, making his proposal for decorticate consciousness not particularly ground-breaking. He suggests that brainstem sites are neglected in current theories of consciousness. This is so because broader definitions of consciousness are used. Split-brain data show that the cortex is important for full-blown consciousness; also, behaviors exhibited by hydranencephaly patients and decorticated rats do not seem to require reflective consciousness.

In the target article Merker wisely starts by explaining what his view of consciousness is. He defines consciousness as “a state of wakefulness . . . which typically involves seeing, hearing, feeling, or other kinds of experience” (sect. 1, para. 1) but excludes reflective awareness (i.e., being “aware that one is seeing, hearing, and so forth”; sect. 1, para. 6). As such, consciousness is equated with wakefulness and responsiveness to one’s environment, and the reader is indeed tempted to concur with the author that consciousness results from activity of subcortical and brainstem mechanisms. In other words, the proposal that consciousness, as defined here, is possible without a cortex does not seem particularly ground-breaking and has been supported by neurophysiological evidence for quite some time now (as Merker extensively documents in the target article).

Merker states that “Few cognitivists or neuroscientists would today object to the assertion that ‘cortex is the organ of consciousness’” (sect. 1, para. 7). “With some notable exceptions [. . .], 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” (sect. 1, para. 7). This is not surprising, since what most researchers today are interested in is not “consciousness in its most basic and general sense, that is, as the state or condition presupposed by any experience whatsoever” (sect. 1, para. 2), but in full-blown introspective consciousness – which *does* depend on cortical activity. More than forty-five years of split-brain research has convincingly shown that surgically isolating the cerebral hemispheres alters consciousness (Gazzaniga 2005). At least six main interpretations

of commissurotomy have been put forward (Morin 2001) – of which only one suggests that consciousness is unaltered by the surgical procedure; the other five views (pre- and post-operation dual consciousness, equal and unequal division of consciousness, and dual personhood in the intact brain) all ascribe a key role to the cerebral hemispheres (and thus to the cortex) in consciousness. The fact that Merker does not mention this large body of work in the target article is rather disconcerting.

Hydranencephaly is used by the author to support his view of decorticate consciousness. He reports his first-hand experience with children afflicted by this condition and proposes that “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” (sect. 5, para. 6). This is followed by a description of behaviors that these children can engage in, including expressing pleasure and aversion, differentially responding to the voice of familiars, showing preferences for situations, and taking behavioral initiatives. It is further observed that decorticated rats can “stand, rear, climb, hang from bars, and sleep with normal postures” (sect. 4.4, para. 2). They can also swim, eat, mate, and defend themselves. The question, of course, is: How should one interpret such behaviors in relation to consciousness? Does expressing emotions or swimming entail “consciousness” as defined by Merker? Certainly. Do these behaviors necessitate self-awareness? Most probably not. This represents a challenge reminiscent of the one primatologists face when trying to determine if apes possess Theory-of-Mind, auto-noetic, or metacognitive abilities (see Terrace & Metcalfe 2005). For instance, one can ask animals to recall food locations or past personal events to test auto-noetic consciousness. Monkeys can indeed exhibit such behaviors (Menzel 2005; Schwartz 2005), but again, the point is that such behaviors most likely imply wakefulness and responsiveness, but not reflective consciousness.

Merker cites Baars (1988), Mandler (1975), and Miller (1986) as examples of theorists who do not focus on subcortical brain areas in their attempts to explain consciousness. The reason for this is simple: their definition of consciousness is much broader than the one proposed in the target article. To illustrate, Baars’ definition of consciousness (1988) includes one’s private experience of reading a word, remembering what one had for breakfast yesterday, and the feeling of a toothache – that is, instances of visual and auditory images, inner speech, bodily feelings, and so forth. Consciousness also contains “peripheral” information at the fringe of conscious experience – for example, the vague awareness one has of surrounding noises. Consciousness also encompasses one’s access to current beliefs, intentions, meanings, knowledge, and expectations, as well as voluntary control. Baars’ more operational definition of consciousness requires that (1) the organism can testify that it was conscious of something following the conscious experience, and (2) an independent effort at verifying the accuracy of the experience reported by the organism be made. Interestingly, Baars rightly notes that in reporting its experience the organism engages in a metacognitive act. Clearly, such a view of consciousness goes far beyond wakefulness and incorporates auto-noetic consciousness (access to one’s autobiography and mental time travel), self-description, verbal report, metacognition, and self-agency. These various facets of consciousness are reflective in essence.

If one defines consciousness simply as a state of wakefulness and responsiveness, then of course only brainstem sites are necessary, and Merker’s careful analysis is very useful in that respect. However, if one embraces the more common view of consciousness which includes self-reflection (e.g., Dennett 1991; Schooler 2002; Zelazo 1999), then obviously cortical areas are involved (e.g., Craik et al. 1999; Goldberg et al. 2006; Johnson et al. 2002; Kjaer et al. 2002), and Merker’s thesis does not apply.