which has been shown not only to be a relay station for sensory input, but also a center for transmitting and integrating information transmitted between cortical regions (Sherman & Guillery 1996) and plays a key mediating role in gamma-linked processes. B&Y have made an important contribution by highlighting the potential role of anatomically distributed thalamocortical processes and gamma resonances in the emergence of hallucinations.

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## A possible role for non-gamma oscillations in conscious perception: Implications for hallucinations in schizophrenia

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**Abstract:** Behrendt & Young (B&Y) propose a useful theoretical framework for the study of processes underlying perception and hallucinations. It focuses on gamma oscillations in thalamocortical networks and the role of the reticular thalamic nucleus in modulating these oscillations. I suggest that their theoretical model might also be applied to the investigation of temporal encoding deficits in disorders such as dyslexia. I further suggest, however, that a role for slower rhythms, such as theta, might also be considered when investigating perceptual experience.

Behrendt & Young (B&Y) propose that conscious perception is subserved by synchronization of gamma-frequency oscillations in recurrent thalamocortical networks, and that hallucinations that occur in schizophrenia, for example, result from underconstrained activation in this circuitry. As the authors note, the idea that gamma activity in thalamocortical networks subserves perception has been suggested previously by Llinas and colleagues (Llinas et al. 1994), and that dysfunction in thalamic nuclei may result in hallucinations has also been proposed (e.g., Gruzelier 1999). However, although resting heavily on prior work, the stated aim of the authors is to provide a "unified pathophysiological framework for hallucinations in neurological and psychiatric conditions" (target article, Abstract), and in that they have succeeded admirably.

B&Y argue that hallucinations differ from "normal" perceptions only in the degree to which they are constrained by sensory input. They argue that this constraint is mediated by inhibition of specific thalamic nuclei by the reticular thalamic nucleus (and modulation of gamma activity). Hallucinations arise when the constraint is compromised, by dysfunction of the reticular nucleus, or indeed compromised sensory input to specific thalamic nuclei. The authors support their proposal with an impressive array of suggestions as to how arousal and attentional mechanisms modulate thalamocortical gamma activity, and how clinical findings regarding hallucinations may be explained by their model.

The potential future utility of B&Y's proposed framework remains to be seen, however. There is apparently, as yet, a lack of anatomical evidence (either gross or micro) that would support the presence of a dysfunction in the reticular thalamus in those prone to hallucinations, and, as the authors themselves note, functional imaging studies showing, for example, coactivation of auditory thalamus and auditory cortex during both speech perception and verbal hallucinations are required.

Nevertheless, B&Y's proposals deserve to be more fully explored in the variety of conditions they mention, and indeed, their general framework may also be applied to other populations as well. For example, it has been proposed that language- and reading-impaired individuals (such as those with dyslexia) have fundamental difficulties with temporal processing (Hautus et al. 2003; Lovegrove et al. 1990; Stein 1994; Tallal et al. 1996; Wright et al. 1997). With auditory processing at least, this is usually attributed to an abnormality in the magnocellular system. An analogous abnormality is usually assumed for deficits in temporal processing in the visual domain as well (Habib 2000). As B&Y note, however, the reticular nucleus participates in time-dependent analysis of auditory input, and thus a dysfunction of this nucleus might also be hypothesized. Magnetoencephalographic investigation of gamma activity during temporal processing tasks (paradigmatically similar to investigations of the auditory P50 discussed by the authors) has indeed shown clear differences between good and poor readers (Nagarajan et al. 1999). Of interest here, as well, is that it has been proposed that dyslexia and schizophrenia may be considered to be representatives of a related spectrum of disorders (Stein 1994). Although the degree of atypical magnocellular development and atypical cerebral asymmetry was proposed to determine the manifestations and severity of these disorders, abnormal reticular thalamus function might also be proposed as a common factor. Of course, the rather different extents to which dyslexics and schizophrenics are prone to hallucinations would have to be explained by other factors.

Finally, and more generally, it might be argued that, although necessary for conscious perception, gamma activity in thalamocortical networks may not be sufficient for a full contextual integration of perceptual information. Certainly, Llinas et al. (e.g., 1994) and Crick & Koch (1990) suggest that gamma frequency oscillation may be the fundamental feature responsible for conscious experience. However, it has also been suggested that different frequencies of oscillation may be required for different scales of cortical integration (von Stein & Sarthein 2000). In this view, gamma frequency oscillation may be required for integration in relatively local networks (or local cell assembly formation), whereas slower oscillation, in the theta range, for example (4–7 Hz), might underlie longer-range integration, or indeed the formation of global cell assemblies. It is conceivable that the content of perception is represented in local assemblies formed by gamma activity, whereas integration of this information into a context may require interaction within a global assembly maintained by lower-frequency oscillations. Lisman and Idiart (1995), for example, have suggested how gamma oscillations "nested" in theta oscillations might subserve mnemonic processing in hippocampus. Thus, gamma might simultaneously occur in local nodes of a global network, but integration is maintained by simultaneous theta-rhythmic activity across the global network. It is possible that global integration is required for the "substantiality, richness, and clarity" (sect. 2, para. 4) of perceptual (or indeed hallucinatory) experience. In this regard, it has recently been shown that theta-rhythmic EEG increases over left superior temporal cortex during hallucinations in a schizophrenic (Ishii et al. 2000).

It has been recently proposed that theta performs a role in integrating activity in hippocampal, thalamic, and cortical sites during mnemonic processing (Kirk & MacKay 2003). Critical thalamic nuclei appear to be the anterior thalamic complex and mediodorsal thalamus (see also Aggleton & Brown 1999). It is interesting that volume reductions in the medial dorsal thalamus are commonly reported in schizophrenia (e.g., Danos et al. 2003). Thus, perhaps, abnormalities in nuclei in addition to the reticular thalamus should be examined when considering manifestations of schizophrenic symptoms such as hallucinations.



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