



dependent reset partially resolves this issue. One might expect that the problem of spike timing is overcome completely when considering biophysically more detailed models, such as Hodgkin–Huxley or compartment models; but even for arbitrarily refined, high-dimensional differential equation models, any reasonable time scale described must be much larger than intrinsic time scales characterizing, e.g., individual ion channels, because otherwise the very description by differential equations loses its meaning.

The study of Cessac and Viéville (2008), pushing further an alternative discrete-time view onto the world of biological neural network modeling, naturally raises more questions than it answers: in their model, discrete spike times themselves are defined arbitrarily precise (namely on the lattice) such that it remains debatable in how far the above precision problem is actually solved. More generally, how does noise affect the spike timing in networks and what is the impact of the dynamics of action potential initiation (cf. Naundorf et al., 2006)? We also need to reconsider related questions about creating (or removing) additional spikes by small perturbations and about the reliability of spikes (Jahnke et al., 2008; Teramae and Fukai, 2008). For computations in neural systems it finally seems most relevant how precisely spike times can actu-

ally be detected by neurons and read out for further processing (Tiesinga et al., 2008). We definitely need to take some time to precisely think about timing before recording, simulating or analyzing the timing of action potentials in neural circuits.

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Cross-frequency coupling in parieto-frontal oscillatory networks during motor imagery revealed by magnetoencephalography

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A commentary on

Interactions between posterior gamma and frontal alpha/beta oscillations during imagined actions

by Floris P. de Lange, Ole Jensen, Markus Bauer and Ivan Toni

Movement execution is the end-product of multiple intricate neural processes including action selection and planning. Although the neural dynamics involved in such internal processes are generally investigated during the build-up to movement execution, the study of motor imagery provides an alternative window on the

large-scale cortical dynamics mediating formation of motor plans. Indeed, motor imagery is associated with oscillatory power modulations widely distributed in sensorimotor cortical networks (Pfurtscheller and Neuper, 1997). However, the functional role of such oscillations and the putative inter-regional coupling within and across



multiple frequency bands are still unresolved issues.

The study by de Lange et al. (2008) addresses these timely questions by using whole-head magnetoencephalography (MEG) to investigate oscillatory brain dynamics in subjects performing a motor imagery task. The participants were required to judge the handedness of drawings of a left hand or a right hand presented at various angles. Such a task elicits internal simulations of rotating one's own hands. With frequency domain analysis and MEG source estimation, the authors evaluate modulations of various rhythmic components induced by the hand motor imagery task demands. While task-related suppressions in oscillatory power were found in the alpha (8–12 Hz) and beta (16–24 Hz) bands over occipitoparietal and precentral areas, significant increases in gamma-range (50–80 Hz) power were revealed over occipitoparietal cortex. Interestingly, when compared to right-hand motor imagery, left hand imagery was associated with stronger suppressions in contralateral motor areas. A further significant novelty of the study is the usage of cross-frequency amplitude correlation to specifically investigate oscillatory interactions between posterior parietal

and frontal regions during formation of a motor plan. The authors therefore provide evidence for a significant long-range anti-correlation between parietal gamma power and frontal beta power at specific periods during mental simulation of action.

Viewed in the broader context of the previous work, the findings are of particular significance. Firstly, because the findings provide novel insights into the local and long-range oscillatory dynamics within the parieto-frontal network during motor imagery, and secondly, because of the important questions raised by the findings for future research. Acknowledging the fact that behavior arises from the integrative action of large-scale brain networks (Varela et al., 2001), earlier electrophysiological studies have assessed long-range interactions between distant structures of the human brain during different experimental paradigms by using various measures of coupling (e.g., Hummel and Gerloff, 2006; Jerbi et al., 2007; Lachaux et al., 1999; Schoffelen and Gross, 2009; Sehatpour et al., 2008; von Stein et al., 2000). These studies suggest that coupling between distinct neural structures at certain frequencies might provide an efficient mechanism for inter-regional communica-

tion in the brain (Fries, 2005). A growing body of research in recent years extends this view by pointing to cross-frequency coupling as a further putative mechanism mediating complex hierarchies of integrated neural ensembles at various scales (Jensen and Colgin, 2007). The study by de Lange et al. (2008) provides evidence for cross-frequency inter-areal amplitude coupling adding to a list of reported inter-frequency relations such as cross-frequency phase synchrony (Palva et al., 2005) or nested oscillations. The latter findings are observed as a locking between amplitude fluctuation of faster oscillations and the phase of slower oscillations, and have been observed during active tasks as well as in spontaneous brain activity (Bruns and Eckhorn, 2004; Canolty et al., 2006; Lakatos et al., 2008; Monto et al., 2008; Mormann et al., 2005; Osipova et al., 2008; Schack et al., 2002). Finally, in order to better understand the functional role of these mechanisms, future studies will have to monitor the putative relationship between interaction measures and behavioral performance. Investigating the alteration of cross-frequency coupling in pathology will also enhance the shift from descriptions of correlations to causal inference.

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