Multi-frequency coordination of cortical oscillations

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Introduction

Rhythmic bimanual tapping is a paradigmatic example where close agreement between theory and experiment has been established. Both iso- and multi-frequency (n:m, e.g. 2:3 and 3:5) tapping has been modeled by two coupled oscillators operating at the movement frequency (Haken *et al.*, 1985; Haken *et al.*, 1996). These oscillators are thought to be instantiated by neuronal circuits but their biophysical implementation has not been established. Electrophysiological studies on tapping indicate that cortical activity operates at much faster time-scales. In particular, many studies found beta activity (15-30Hz) to be functionally relevant in rhythmic motor performance (Boonstra *et al.*, 2007; Houweling *et al.*, 2010). In this study, we sought to establish a neurobiological mechanisms that describes how n:m coupling at the movement frequencies (1-3Hz) can arise from neural activity at timescales an order of magnitude faster.

Methods

Cortical activity was modeled by systems of coupled oscillators with neurobiologically informed connection topologies and phase interaction functions (Breakspear *et al.*, 2010). In broad regions of parameter space, such systems robustly exhibit a form of winnerless competition known as heteroclinic cycles, characterized by slow transitions between partially synchronized cluster states (Ashwin *et al.*, 2007; Rabinovich *et al.*, 2008). Whereas the individual phase oscillators operate at a fast time-scale, the switching between different cluster states evolves much slower. We therefore developed a computational model of coupled phase oscillators to exploit heteroclinic cycles to achieve multi-frequency coordination between cortex and movement. The system consists of two ensembles of coupled oscillators, representing activity in each motor cortex with bidirectional coupling. Switching dynamics were investigated for different intrinsic switching rates (which was modulated by the detuning between oscillators) and coupling strengths. The dynamics were visualized using weighted order parameters, equivalent to local field potentials in neural systems. To assess the model, we compared the dynamics at both the fast and slow timescale to previously acquired empirical data.

Results

We observed robust switching between different configurations of clustered phase-locked oscillators. This switching resulted in a temporal desynchronization of phase oscillators and a concomitant reduction in the beta amplitude of the simulated local field potential. Hence, the amplitude of the faster beta rhythm was coupled to the phase of a slower movement rhythm, in accordance with electrophysiological studies. The bilateral coupling at the slow time scale was assessed by the mode locking structure (n:m frequency locking) between the two ensembles. Specific mode locking regimes were observed for particular coupling strengths and ratios of the intrinsic switching rates. These show the appearance of stable regions of higher order n:m frequency locking (e.g., 2:3 and 3:5) with increasing coupling strength, resembling a devil's staircase.

Conclusions
Whereas previous heuristic models have captured n:m bimanual tapping at the movement frequency, we present for the first time, a neurobiologically-informed computational model of the neural dynamics underlying bimanual tapping that describes and links both the fast and slow timescales. At the movement frequency, the mode locking structure reflected a devil's staircase with stable regions of n:m frequency locking in keeping with behavioral data. The simulated local field potential revealed amplitude modulations at the beta frequency (~20Hz) that were coupled to the phase of the slow frequency. The model agrees with empirical findings and provides an explicit implementation for nested cortical oscillations. On a physiological level, the phase dispersion of the beta oscillators can be interpreted as partially synchronized local inhibition.

References

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