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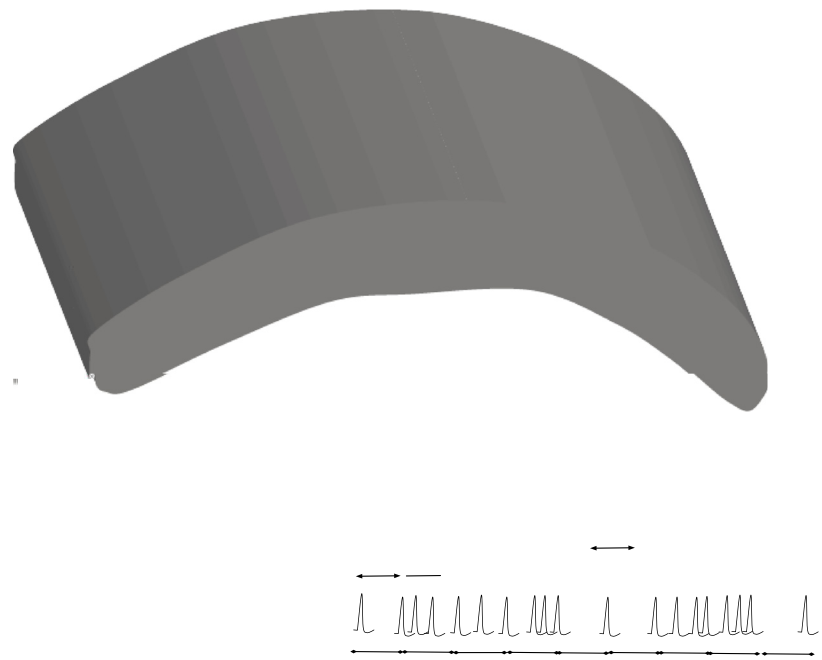
Brain oscillations in perception, timing and action

CrossM

Figure 1



coupling causes information to be coherently processed in distributed circuits, supporting the tight temporal coupling between various aspects of a sensorimotor task. The degree of this coupling depends on the demands of the task. For example, catching a faster-moving object requires a tighter coupling between various sensorimotor functions that occurs over shorter sub-second durations.

The information resulting from the activities of local circuits can be described by Shannon entropy, i.e., the amount of uncertainty about whether a neuron that represents an information source, such as the primary visual cortex, will or will not fire within a particular temporal window [23,24]. Information or entropy in the proposed multidimensional domain is a consequence of the stochastic nature of the neuronal responses to a stimulus [25,26,27•]. Other sources of information for multidimensional processing may include higher functional areas, such as the somatosensory areas, multimodal areas, motor areas and the anterior association area in the prefrontal cortex. Note that the information resulting from the coherent neuronal activities that are responsible for sensorimotor tasks can be quantified by different analyses, including wavelet information analysis and the study of spike structures in terms of complexity and randomness [26,27•,28].

In one study in which primates were presented with naturalistic scenes, a positive correlation was observed between high-gamma local field potential (LFP) (60–100 Hz) and spikes, along with a strong positive correlation within high-gamma LFPs in the primary visual cortex [16]. These findings suggest that high-gamma LFPs and spikes are generated within the same network [16]. Another study revealed significant phase correlations in approximately 60% of the multiunit activities of neurons and LFP recordings from visual cortices during a specific visual stimulation in addition to phase correlations between oscillatory events at different frequencies [15]. As such, the information in spike structure [27•] during multidimensional processing is indicative of sensorimotor responses.

It was observed that stimulus-driven excitability variations in local cortical ensembles are related to the phases of brain oscillations within the setting of a hierarchical cross-frequency coupling — amplitude of a higher frequency oscillation is coupled with the phase of a lower frequency oscillation [29••,30]. Accordingly, we propose that synchronized long-range low-frequency oscillations provide a temporal window of integration (TWI) in the framework multidimensional processing. The TWI may manifest as a peak or trough of a low-frequency brain oscillation because coupling has been observed between the high gamma power and the peak phases of alpha (8–12 Hz) oscillations in a working memory task [31] and the troughs of theta (4–8 Hz) oscillations in motor, sensory and cognitive tasks [5]. Moreover, the TWI is likely to be related to the periodicity of the low-frequency oscillations. Typical integrations of auditory and visual events occur within a time window of 100 ms, for example, those observed during the sound-induced double-flash illusion [32]. The sound-induced double-flash illusion may be explained by the coupling of the activities of the auditory and visual circuits to the same phase of a slow wave oscillation in the framework of multidimensional processing. An important supporting piece of evidence comes from spatial ventriloquism in which a visual object can attract the perceived location of a spatially discordant but temporally synchronous sound [33•,34•]. This attraction can be understood as a phase-amplitude coupling of the circuits processing the sound to the synchronized low-frequency oscillations that are devoted to processing different features of the visual object.

Although spatial ventriloquism is an example of the integration of spatially separate events, phase-amplitude coupling is observed in the integration of information associated with inputs arising from a single source. For example, during simple visual tasks, alpha/high gamma coupling preferentially increases in the visual cortical regions [8]. A recent study provides the causal evidence that the temporal window of integration associated with sound-induced double-flash illusion is constrained by the frequency of occipital oscillations in the alpha band [34•]. Faster alpha frequencies also predict vision with a finer temporal resolution, which is consistent with the hypothesis that faster alpha oscillations provide more cycles for the separate rather than combined integration, which results in better resolution [35].

In another study of the integration of two stimuli (i.e., audio and tactile), the alpha power recorded over the superior and inferior parietal lobules was relatively increased in a pre-tactile stimulus time-window of approximately 330 ms prior to the subsequent perception of an integrated rather than segregated stimulus [36]. Due to the lack of a post-stimulus effect in this study, the integrated/segregated perception was likely an effect of a network comprising 'multisensory integration' areas with unisensory areas rather than a specific multisensory area [36]. This interpretation is consistent with the multidimensional processing of auditory and tactile stimuli within a network.

The increase in alpha power during the integration of two stimuli can be understood in terms of multidimensional processing. For multisensory integration to occur, the alpha oscillations modulating both unisensory circuits, i.e., tactile and auditory, must synchronize, producing an increase in alpha power. Therefore, one may argue that the processing of multiple sensory stimuli (as depicted in Figure 1) within successive but discrete TWIs results in the integration of sensory information from multiple sources in a dynamic network of circuits over a time period. This integration forms the basis of successful sensorimotor interactions with the external physical environment.

Multidimensional processing in apparent visual motion

In this section, we argue that pre-stimulus alpha power and spontaneous brain oscillations influence apparent motion perception [37•]. Apparent motion is a visual illusion in which motion is perceived when two spatially distinct static objects alternate in sequence. Apparent motion illusions are robust at presentation frequencies of approximately 3 Hz. Apparent motion has been deemed to be dependent on the ability to use predictive feedback signals in the processing of 'fragmented' sensory information [38,39]. The perception of good apparent motion follows an optimal range of presentation frequencies. Lower alpha power predicts percepts between apparent motion and flickering at high presentation frequencies. In a study, higher alpha power predicts apparent motion percepts of visual objects with low presentation frequencies [37•]. Specifically, apparent motion perception depends on both local neural synchronization (i.e., the power within the frontal and occipital regions of interests) and long-distance neural synchronization (i.e., frontal-occipital connectivity) in the pre-stimulus alpha oscillations [37•].

Multidimensional processing in timing and action

Phase-amplitude coupling provides a plausible mechanism for the calibration of modular clocks. This calibration involves endogenous oscillators within various networks, modules that calibrate the oscillators, and downstream circuits that process task-specific time intervals. These components are connected via flexible connections as proposed by Gupta (2014) [40•]. The modular clock mechanism is calibrated by circuits, such as those in the cerebellum and posterior parietal cortex, which are important for feedback control during various sensorimotor tasks [40•]. During complex sensorimotor tasks, such as catching a flying ball or lifting a cup, irregular spike bursts are produced during feedback processes and reflect unequal temporal epochs that separate the activities of individual muscles during these movements. Furthermore, the irregular changes in the neuronal activities during a sensorimotor task mirror the changes in the physical time-related parameters, such as speed and duration. The input from feedback circuits to endogenous oscillatory mechanisms aid in the transfer of the physical time information. Note that phase-amplitude coupling preserves the temporal relationship between the parallel inputs of irregular activities that arrive at the oscillator/local clock mechanism from a calibration module. Additionally, motor and sensory task-modulated changes in the activities of neurons are observed in parts of the brain, such as the inferior temporal lobe and prefrontal cortex, which are not directly responsible for the feedback control of external sensorimotor tasks [41,42]. These changes may influence the effects of feedback processes and could also be responsible for the calibration of endogenous oscillators.

Several recent studies have also suggested the role of beta band oscillations in the representation of various time durations in the brain [43,44,45•]. Interestingly, in a recent study by Bartolo and Merchant (2015), putaminal LFPs were recorded in monkeys that were performing a synchronization-continuation task. The LFPs exhibited an initial burst of beta band oscillation that was followed by another increase during the continuation phase of the task [45•]. This latter increase depends on internally generated cues [45•]. The dependence on internally generated cues suggests the involvement of other calibration modules, such as those arising from the basal ganglia circuit as previously proposed by Gupta (2014) [40•], which may be responsible for the observed increase in the beta power via an increase in the number of long-range beta-oscillation interactions during the continuation phase of the task.

Consistent with the role of low-frequency oscillations in the modulation of the amplitudes of high-frequency oscillations by long-range oscillations, previous studies utilizing motor tasks have demonstrated phase-amplitude coupling between movement-selective high gamma and alpha oscillations in humans [14] and between gamma and theta oscillations in the motor cortical areas of rats during distinct movement states [12•]. Another study suggests a saccade-related phase-amplitude coupling between theta and low gamma activities [13]. Thus, the amplitudes of gamma oscillations in motor areas, which represent motor information including the time of the onset, performance and execution [46,47], nested within the low-frequency oscillations are likely to play an important role in the processing of information for the execution of sensorimotor tasks.

A recent study simultaneously recorded neuronal activities in multiple cortical regions in monkeys that were trained to report the color or motion of the stimuli. This study revealed complex dynamics of information flow [48]. When information reaches one part of the brain from another, the phase of the synchronized low-frequency oscillations connecting the two regions is advanced [49]. This delay in phase affects the processing of the arriving information by altering the available size of the TWI. The effect of long-range oscillations on information flow has been indicated by an analysis of intracranial EEG data that revealed that power changes in different frequency bands significantly contribute to the late components of the event-related potentials [50]. The micro-stimulation of V1 (i.e., the primary visual area) generates gamma oscillations in the feedforward direction, whereas such stimulation of V4 (i.e., a downstream visual area) generates alpha oscillations in the feedback direction [49]. These findings suggest that during the multidimensional procesgni could also modulate the flow of information between lower and higher visual areas. Thus, phase-amplitude coupling could form one of the important bases of sensorimotor choices in flexible visuomotor tasks; such choices are believed to result from the integration of opposite flows of sensory and task information [48].

Summary

VanRullen and Koch (2003) proposed that cross-frequency interactions between gamma and alpha oscillations constrain perception [51]. We extend this proposal to include motor functions to understand the role of the multidimensional processing of information during sensorimotor tasks. The multidimensional processing provides an important basis for understanding how different circuits of the brain can be temporally coupled during various sensorimotor tasks.

Conflict of interest statement

Nothing declared.

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