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Brain oscillations in perception, timing and action

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Catching a thrown ball requires a tight coupling between perception and motor control. In this review, we examine multidimensional information processing across various perceptual and motor tasks. We summarize how perception, timing and action can be understood in terms of the coupling of gamma band oscillations, which represent the local activities of brain circuits, to a specific phase of long-range low-frequency oscillations. We propose a temporal window of integration that emerges from cross-frequency coupling that serves to produce optimized action.

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Introduction

To hit a pitched baseball requires that the batter generates accurate estimates of the position, speed, and timing of the moving ball and use this information to produce a coordinated movement. Humans are adept in compensating for their own sensorimotor uncertainty in the execution of skilled actions [1,2••,3]; however, the neural mechanisms underlying the temporal coordination between perception and action have not been fully established.

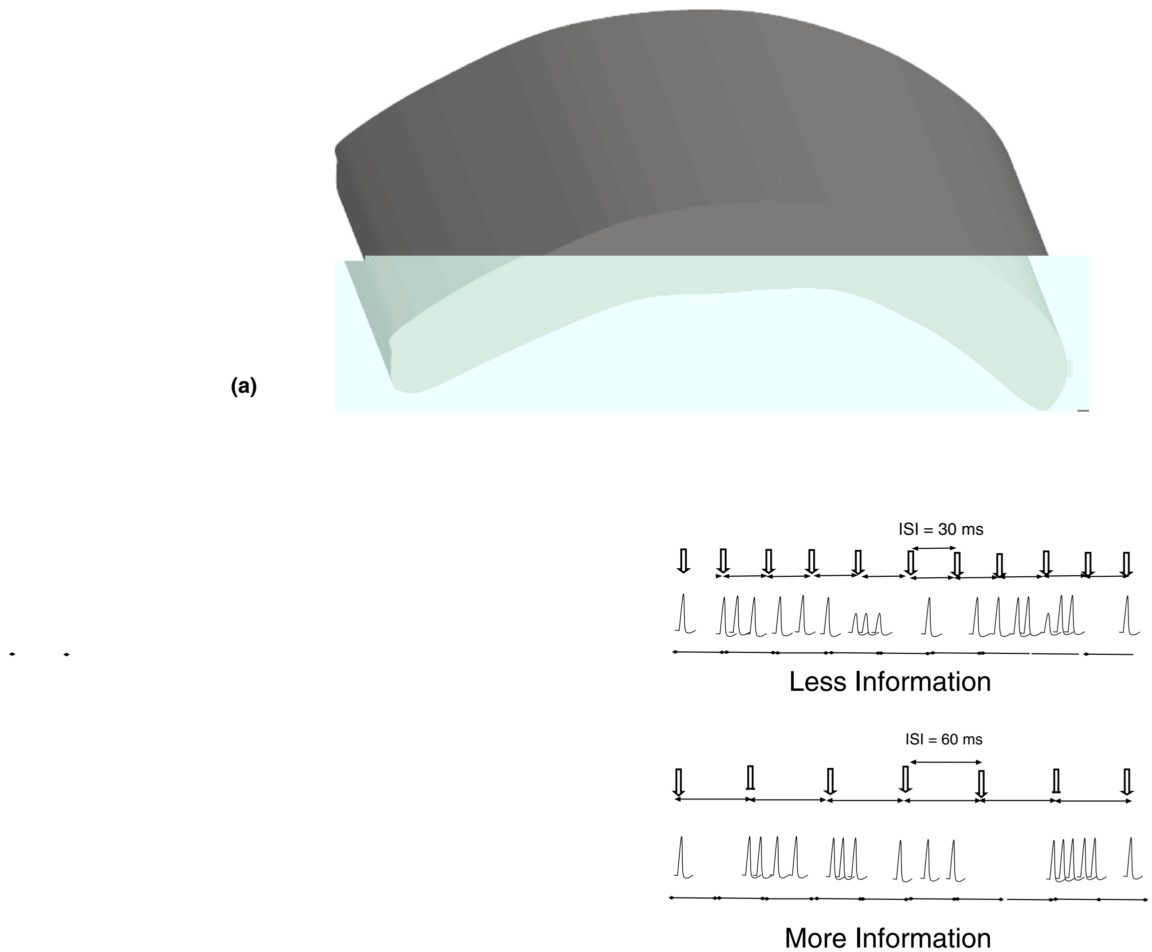
Different lines of evidence have facilitated our understanding of the computations and physiological underpinnings that are involved in the coupling of perception and action. For example, a recent computational modeling study revealed that the internal representations of observers' spatial visuomotor errors (in visuomotor decision tasks) are best described by a mixture of distributions that differ in location and scale [2••]. This indicates that the internal probability density functions of their own visuomotor error distributions are discrete [2••]. These results suggest that discrete neurophysiological processes may be responsible for various sensorimotor tasks. In this review, we propose that the processing of multidimensional information by neuronal populations occurs in separate epochs and that these epochs represent different facets of the interaction between perception and action (Figure 1).

Multidimensional processing of sensorimotor information

ver the last decade, there has been considerable interest in the roles of cross-frequency phase-amplitude coupling in various cognitive functions [4••]. Cross-frequency phase-amplitude coupling is a phenomenon in which the phase of a lower frequency brain oscillation modulates the amplitudes, i.e., the differences in the maxima and minima of oscillation waves, of a higher frequency oscillation to create 'packets' of those higher frequency waves [4••]. Coupling of the phases of low-frequency theta (4–8 Hz) and alpha (8–12 Hz) oscillations to the amplitudes of high-frequency gamma (30–150 Hz) oscillations [5,6,7•,8,9,10••,11,12•,13,14,15] has been observed in various sensory and motor tasks. In one study, visual processing is found to reflect local activity, whereas working memory retention and mental imagery, which likely involve multiple, distributed cortical areas, are related to theta (4–8 Hz) and alpha (8–12 Hz) frequency oscillations [11]. Furthermore, gamma band neuronal oscillations that relate to the spiking activities of neurons [9,15,16] in response to stimulus characteristics, including intensity and duration, have been observed in many cortical and subcortical structures [17•,18,19,20,21]. Additionally, a recent study demonstrated zero and non-zero lags between the phases of gamma oscillations in spatially separate sites in the primary visual cortex [22]. These non-zero lags are modulated by the stimulus, suggesting that gamma oscillations can also dynamically influence the exchange of information among local populations of neurons [22].

In contrast to gamma oscillations, low-frequency oscillations generally synchronize larger areas of the cortex and play a role in long-range interactions [4••,15]. Thus, as a result of phase-amplitude coupling, gamma-band oscillations reflect local activities, whereas low-frequency oscillations help to engage their long-range interactions [4••,15]. In the framework of multidimensional processing, the amplitudes of high-frequency oscillations that synchronize the processing of information in multiple local circuits are modulated by the phases of synchronous long-range low-frequency brain oscillations. This phase-amplitude

Figure 1



(a) **(b)** **(c)**

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•]. ther 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 (LF) (60–100 Hz) and spikes, along with a strong positive correlation within high-gamma LF s in the primary visual cortex [16]. These findings suggest that high-gamma LF s and spikes are generated within the same network [16]. Another study revealed significant phase correlations in approximately 60% of the multiunit

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

hase-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 LF s were recorded in monkeys that were performing a synchronization-continuation task. The LF s 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 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

Van ullen 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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