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BETA OSCILLATIONS AND THEIR FUNCTIONAL ROLE IN MOVEMENT PERCEPTION

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Abstract

Neuronal oscillations refer to periodic changes of neuronal activity. A prominent neuronal oscillation, especially in sensorimotor areas, is the beta-frequency-band (~ 13-29 Hz). Sensorimotor beta oscillations are predominantly linked to motor-related functions such as preparation and/or execution of movements. In addition, beta oscillations have been suggested to play a role in long-range communication between multiple brain areas. In this review, we assess different studies that show that sensorimotor beta oscillations are additionally involved in the visual perception and imagery of biological movements. We propose that sensorimotor beta oscillations reflect a mechanism of attempted matching to internally stored representations of movements. We additionally, provide evidence that beta oscillations play a role for the integration of visual and sensorimotor areas to a functional network that incorporates perceptual components at specific spatial-temporal profiles and transmits information across different areas.

Keywords

• Cross-frequency coupling • Neuronal oscillations • Biological movement • Beta • Point-light displays

Neuronal oscillations

Neuronal oscillations are a ubiquitous phenomenon observed in multiple cortical and subcortical areas across a wide range of species [1]. Neuronal oscillations are often generated in neuronal networks that influence each other via excitatory and inhibitory connections. As a result, neurons are rhythmically stimulated and inhibited [2]. Neuronal oscillations have been described on several levels, ranging from single cells to cell assemblies of several thousand neurons. Accordingly, several methods exist to measure neuronal oscillations. On the level of single cells or small cell assemblies neuronal oscillations can be measured invasively by single cell or multi-unit recordings. If thousands of neurons oscillate synchronously, the resulting signal might be strong enough to be recorded non-invasively outside the skull using electroencephalography (EEG) and magnetoencephalography (MEG) [3,4].

Using EEG, the first to observe such rhythmic fluctuations non-invasively in the living human brain was Hans Berger [5]. In his seminal work, he first described rhythmic patterns in the EEG in the 8-12 Hz range; the famous alpha waves. Since then, investigators have revealed a wide range of oscillatory activity in several different frequency bands ranging from slow (0.1 Hz) to ultra-fast (~ 500 Hz) oscillations [4].

Neuronal oscillations can be found in local neuronal groups, but oscillations have also been suggested as a mechanism for long-range communication between neuronal groups. Long-range communication is a process in which one area transfers certain characteristics of its current functional state to another area [6] or in which spatially distinct cortical areas are bound to one functional network [7]. In general, high frequencies are believed to reflect neuronal activity over small spatial regions and short temporal windows, while low frequencies are believed to modulate activity over large spatial regions and long temporal windows [8,9]. These relations between spatial and temporal patterns allow brain processes to be carried out simultaneously at multiple spatial and temporal scales [10-12].

Neuronal oscillations have been classified in mainly five distinct frequency bands: delta (1.5-4 Hz), theta (5-7 Hz), alpha (8-12 Hz), beta (13-29 Hz) and gamma (30-80 Hz). Within the same neuronal network each frequency band is usually associated with different cognitive states [13] or sensory, motor and cognitive processes [14-20]. Delta oscillations are often seen during deep sleep, but recently they have also been linked to cognitive functions such as motivational and reward processes [21-23]. Theta-band is often associated with working memory [24,25], while alpha oscillations have been suggested to reflect cortical idling states [26]. In recent years however, the role of alpha oscillations has also been linked to active inhibition [27] as well as cortical excitability [28-30]. Oscillations in the beta-band have been more characteristically related to sensorimotor functions [31,32], whilst gamma oscillations have been associated to a broad range of cognitive functions that include working memory, attention, object recognition, and perceptual learning [33-39]. In addition to these local occurrences of oscillations, oscillations in several different frequency bands can temporally co-exist within the same or different brain areas and interact with one another [12,40].

In this review, we will focus on one specific band, namely the beta-band. Beta oscillations

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are classically considered as an oscillation of the sensorimotor system, typically related to movement execution and/or preparation. Beta oscillations and their modulations by specific tasks and/or stimuli however, are also observed in several other cortical and subcortical areas. We will review evidence for the functional role of beta oscillations in local neuronal groups but also in long-range communication between local neuronal groups that goes beyond the classical view of movement execution. We will outline that the local oscillations and the long-range communication become most evident for the visual perception of movements as this process incorporates both the visual and the sensorimotor systems and their effective interaction. Finally, we will suggest how disturbances of the neuronal network for movement perception by non-invasive and reversible brain stimulation or by pathological dysfunctions can affect the visual perception of movements.

Beta oscillations in sensorimotor areas during movement execution and movement perception

Changes in beta power are mostly found in sensorimotor areas and striatal-motor networks. These changes in the beta frequency band, therefore, have been associated classically with movement preparation and execution: voluntary movement causes a decrease in beta power, while an increase in beta power in sensorimotor areas reflects active inhibition of the motor system [41-45]. For example, Pfurtscheller and colleagues [46] observed a decrease in beta power during the preparation of voluntary finger (thumb and index) and wrist movements, similar to that observed by Salmelin and colleagues [47] during self-paced finger movements. In addition, beta activity has also been suggested to play a role in recalibrating the sensorimotor system following a movement, in preparation of the next [48].

In contrast to healthy subjects, patients suffering from Parkinson's disease (PD), who find it difficult to instigate or change movement, show abnormal levels of beta power compared to healthy subjects [49]. Several studies have shown synchronized beta activity in the subthalamic nucleus and globus pallidus [50-52]. This has led to the notion that excessive beta activity might cause akinesia in PD patients. The use of medication, such as levodopa, effectively suppresses beta activity in the above areas and strongly correlates with clinical improvement [53]. Additionally, coherence in the beta-band has been shown to provide a mechanism to couple the sensorimotor system with peripheral systems such as spinal cord and muscles [48,54-57].

In addition to their relevance in movement execution and motor impairments, beta oscillations in the sensorimotor cortex have also been shown to be modulated by both imagery and visual perception of movements in the absence of any movement execution [58-61]. While motor imagery refers to the internal formation of a movement, visual perception of a movement on the other hand, involves the interpretation of the observed movement.

For example, Schnitzler and colleagues [62] used MEG to show that imagination of finger movements led to a reduction of beta power in human primary motor cortex similar to that observed during the execution of finger movements, although less strong in magnitude. Likewise, an EEG study by Pfurtscheller and colleagues [63] revealed that imagination of either left or right movements localized unilateral changes in low beta power in sensorimotor cortices, similar to that observed during the planning of voluntary movements (Figure 1; [63]).

Similarly, when subjects observed finger movements performed by another actor during an EEG study beta power was reduced in sensors over sensorimotor cortex [58]. Another EEG study reported that beta power in primary motor cortex was decreased by observation of somatosensory stimulation and by observation of goal-directed movements, but not by the observation of aimless finger movements [60]. These studies clearly show that the human sensorimotor cortex is not only engaged in movement execution, but also in observation and imagination of movements. This engagement is reflected by a decrease of local beta power.

In addition, modulations of sensorimotor beta power have also been observed during the observation of correct vs. incorrect movements [64]. A stronger suppression of beta power was

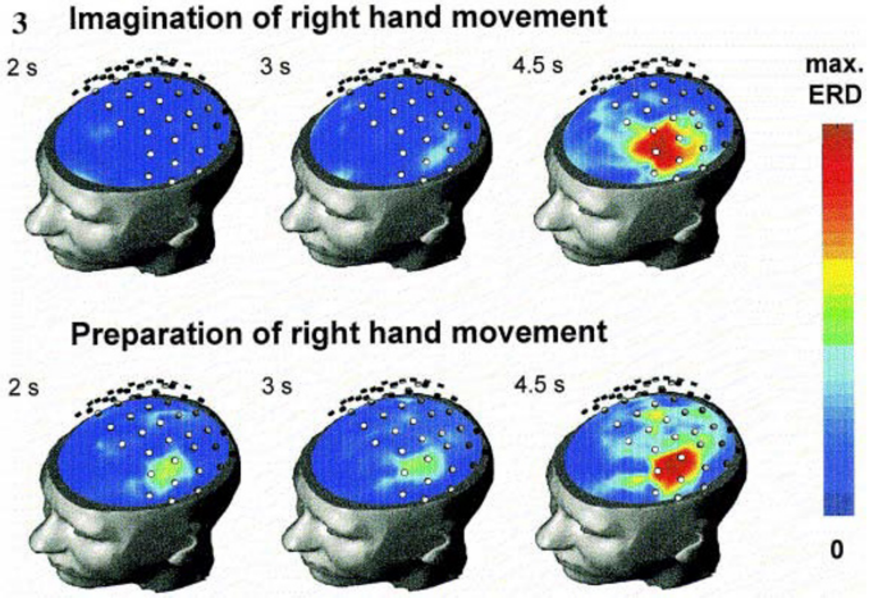

Figure 1. Beta power decrease maps of the same subject during the imagination/preparation of movements [63]. Upper panel shows beta power decrease during the imagination of right hand movements. Lower panel shows beta power decrease during the preparation of voluntary movements of the right index finger (execution of movement at 5.0 s [63]).

observed for incorrect movements, suggesting that sensorimotor beta might be engaged in the evaluation of the observed movements [64].

Orgs and colleagues [65], expanded this view further in an EEG study by reporting that a decrease of beta power during the observation of different movements was modulated by the degree of expertise. Professional dancers and non-dancers watched movies of everyday movements, as well as, complex dance movements. Both groups showed a similar and moderate decrease of beta power over sensorimotor areas while watching everyday movements. During the observation of complex dance movements however, a strong induced decrease in beta power was observed in dancers but hardly any decrease in non-dancers. The authors suggest that the beta-band decrease reveals the integration of visual and sensorimotor systems. Observed (dance) movements are matched to the individual's motor repertoire [65]. The motor repertoire of an individual is defined as the storage of all motor knowledge acquired throughout one's lifetime [66]. In line with this hypothesis, Lange and colleagues [67,68] proposed that the visual perception of movements might act via a "template-matching" approach where visual input of the movement is matched to the internally stored templates. These proposed templates might exist in one's motor repertoire. Therefore, each individual's motor or template repertoire is unique (e.g. dancers vs. non-dancers), and is limited by the biomechanics of the human figure (i.e. the bending of joints in one direction [69,70]). If the observer's motor repertoire is tuned to the observed movement, sensorimotor cortex becomes engaged into the action recognition process, as reflected by reduced beta power.

Recently, Pavlidou and colleagues [71,72] further pursued the hypothesis of matching visual input to the stored representations within one's motor repertoire as a mechanism for the interpretation of movements. The authors used point-light displays (PLD), a method which visually portrays a human figure with just a handful of moving dots [73], and presented normal biological human movements ("plausible" condition). In addition, Pavlidou and colleagues manipulated the spatial positioning of the PLD dots of these normal biological movements. This way, they created movements, which still represented a human figure but were biomechanically improbable ("implausible" condition) or so that they did not represent a human figure at all ("scrambled" condition). Analysis of MEG data revealed a widespread network of cortical areas showing changes in alpha, beta, and gamma oscillatory power during the visual presentation of these movements, mainly in visual and sensorimotor areas [71]. When studying differences between conditions, significant differences in beta power were found in visual and sensorimotor areas for plausible vs. implausible (Figure 2A, Figure 2B; [72]) and plausible vs. scrambled movements [71]. Notably, the decrease of sensorimotor

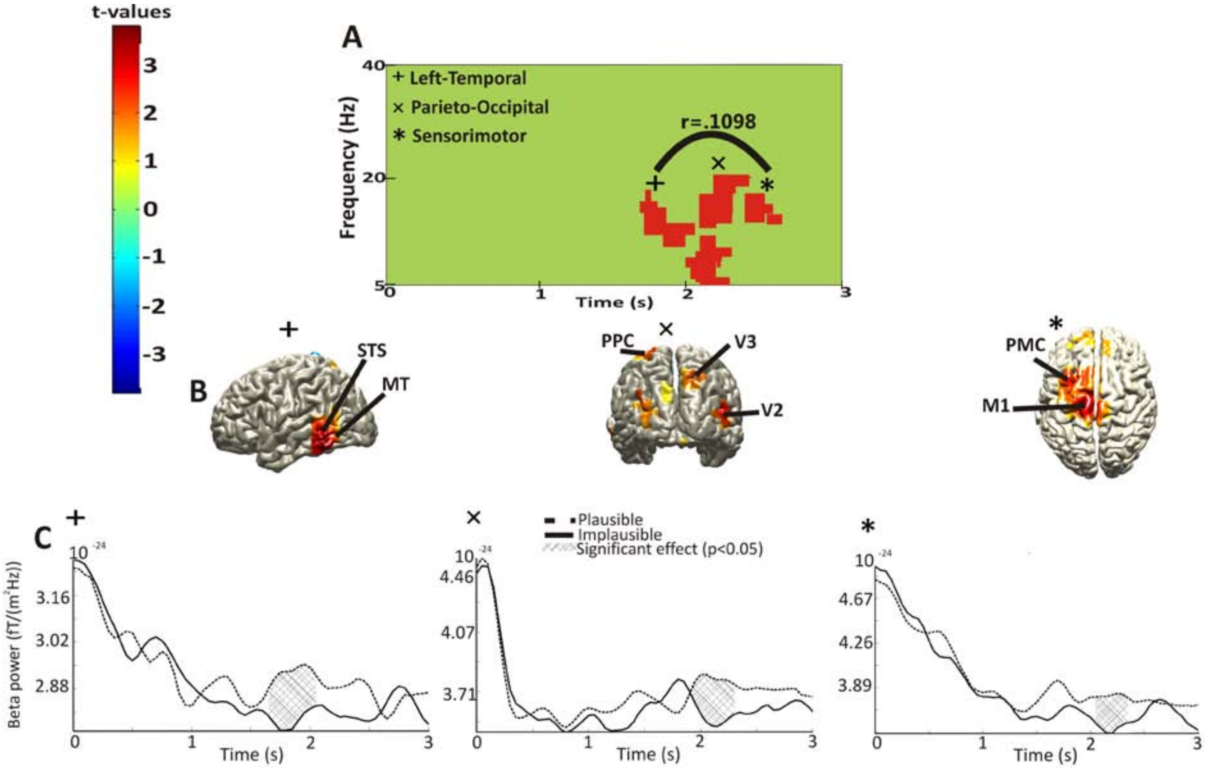

Figure 2. Plausible vs. implausible PLD contrast (modified from [72]). A) Representations of distinct positive spatio-temporal clusters (P < 0.05) found on sensor level for left temporal (+), parieto-occipital (x), and sensorimotor (*) areas. Curve bracket and r-value represents a significant cross-frequency trial-by-trial correlation between left-temporal and sensorimotor areas for the plausible condition. B) Source reconstruction of the significant spatio-temporal clusters found on sensor level. Color maps illustrate t-values. C) Temporal evolution of beta power change for left-temporal (+), parieto-occipital (x), and sensorimotor (*) areas for plausible (--) and implausible (–) PLD movements. Pattern area denotes the highest difference between plausible and implausible movements (P < 0.05). Power is represented on a log scale [72].

beta power was stronger for implausible than for plausible movements (Figure 2C; [72]). In the theory of matching visual input to internal motor repertoires, implausible movements have no stored motor representations and thus should not induce any decrease in sensorimotor beta power, let alone a stronger decrease than that observed for plausible movements.

This finding thus argues, that a decrease of sensorimotor beta power reflects more than a mere match of visual input to the internally stored motor repertoire in sensorimotor cortex. Rather, the results by Pavlidou and colleagues argue that a decrease of beta power might reflect the process of attempted matching. Thus, the strength of beta decrease might depend on the stimulus, as well as, the task. In the case of professional dancers observing dance movements without a specific task [65] sensorimotor beta power might decrease because the visual input is continuously matched to the internal, learned patterns of dance movements as it recognizes and evaluates the observed dance movements. To non-dancers, on the other hand, the dance movements do not incorporate any meaning as no stored representations of these movements exist. Therefore, sensorimotor cortex is not necessary for the visual perception of the observed dance movements and gets decoupled from the process. This is reflected in hardly any changes in sensorimotor beta power for non-dancers. In the study by Pavlidou and colleagues [72], implausible movements needed to be distinguished from plausible movements. This task might induce a constant matching of all stimuli to the internally stored representations of normal movements to decide whether the stimulus is plausible or not. This is reflected in the constant decrease of sensorimotor beta power for plausible *and* implausible movements (Figure 2C; [72]). Since implausible and plausible movements are similar, but no matching representations for implausible movements exist, the attempted matching process might recruit more resources of potential matches, resulting in a stronger decrease of beta power (Figure 2C; [72]).

This hypothesis implies that the degree of sensorimotor beta decrease for plausible movements can be modulated by task difficulty, i.e. by the degree of similarity of the to-be-distinguished stimulus, while such a modulation should not be possible for plausible movements. This prediction, however, needs further investigation.

Interactions between visual and sensorimotor areas

In the previous chapter, we have reviewed evidence that beta power in sensorimotor areas can be modulated by visual input. It is well-established that visual input to the cortex is first processed in visual cortex before potentially reaching processing stages in other areas. An open question thus is, by which mechanisms visual input in the case of movement recognition is transferred from visual to sensorimotor areas. While beta-band activity has been repeatedly shown to play an important role in the dynamic formation of large-scale networks [74-76] few studies have investigated the role of beta power for the coupling of visual and motor areas.

Pavlidou and colleagues studied whether spectral power might be a source of inter-areal communication. They found a significant cross-frequency trial-by-trial power correlation between visual alpha/gamma and sensorimotor beta power when participants where differentiating between plausible and scrambled movements [71]. In addition, a significant cross-frequency trial-by-trial power correlation was also observed between visual beta and sensorimotor beta power during the differentiation between plausible and implausible movements (Figure 2A; [72]). Both studies suggest that sensorimotor beta band activity may supply a mechanism to couple visual and sensorimotor areas into a functional network during the recognition of familiar biological movements [77].

In addition, similar to the above, studies of motor imagery of hand movements have also detected changes in beta power in sensorimotor areas [62,78], as well as persistent cross-frequency correlations between beta power in sensorimotor and gamma power in posterior cortices [78]. Notably, both processes involve a similar network involvement, highlighting the importance of beta in long-range communication between visual and sensorimotor areas, suggesting that beta is functionally and causally linked to motor behavior.

Summary and outlook

In this review, we have surveyed studies investigating the role of beta oscillations in movement execution, movement imagery and movement observation. These studies demonstrate a functional role of beta oscillations in sensorimotor areas which goes beyond the classical role of motor execution and preparation. We discussed evidence that modulations of sensorimotor beta oscillations during movement perception might reflect attempted matching of visual input to internal templates of movement stored in an individual motor repertoire. In addition, we reviewed studies arguing for the importance of beta oscillations in long-range communications. Beta oscillations have been shown to link visual and sensorimotor areas allowing the transmission of information between them, and effectively combining them in a highly functional network [71,72,78]

Previous non-invasive brain stimulation studies have emphasized the importance of visual and sensorimotor areas for biological movement perception: By applying transcranial magnetic stimulation (TMS) on visual [79,80] or sensorimotor [80] areas these studies have demonstrated a significant impairment in the processing of biological movements. These studies, however, could not shed light on the role of beta oscillations for the processing of biological movements. To further establish a causal link between sensorimotor beta oscillations and visual movement perception, future studies might use methods of brain stimulation, such as transcranial alternating current stimulation, which allows neuronal modulation in a specific frequency. While modulating beta oscillations during biological movement perception, future studies can investigate the effects not only on perception but also on the interactions between visual and sensorimotor areas.

Moving forward it will be interesting to examine how diseases, which are known to affect sensorimotor beta activity, affect movement recognition. As discussed above, it is well known that PD is associated with abnormal beta activity [14,49,81]. It might be interesting to study whether these patients perceive movement stimuli differently than healthy subjects. Furthermore, it has been shown that movement stimuli trigger motor improvement in patients with PD [82]. Less is known however, how sensorimotor beta band activity is modulated in PD patients by such movement stimuli. How will this improve - if at all - the interactions between visual and sensorimotor areas in these patients, and will cross-frequency correlations play a role in the transmission of information across multiple cortices, as shown in healthy subjects [71, 72]? Future studies can shed light to these questions to further enhance the importance of beta in long-range communication and its functional role in biological movement perception.

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