Transient Alpha and Beta Synchrony Underlies Preparatory Recruitment of Directional Motor Networks

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Abstract

Modulations in motor cortical beta and alpha activity have been implicated in the preparation, execution, and termination of voluntary movements. The functional role of motor cortex beta activity is yet to be defined, though two opposing theories prevail. The idling cortex theory suggests that large-scale motor networks, in the absence of input, revert to an intrinsic oscillatory state. The alternative theory proposes that beta activity promotes postural tone at the expense of voluntary movement. These theories are primarily based on observations of event-related desynchronization associated with movement onset. Here, we explore the changes in alpha and beta oscillatory activity associated with the specific behavioral patterns during an established directional uncertainty paradigm. We demonstrate that, consistent with current proposals, alpha and beta desynchronization reflects a process of disengagement from existing networks to enable the creation of functional assemblies. We demonstrate that, following desynchronization, a novel signature of transient alpha synchrony underlies the recruitment of functional assemblies required for directional control. Although alpha and beta desynchronization are dependent upon the number of cues presented, they are not predictive of movement preparation. However, the transient alpha synchrony occurs only when participants have sufficient information to prepare for movement and shows a direct relationship with behavioral performance measures.

INTRODUCTION

Neuronal populations have intrinsic oscillatory properties that allow the synchronous activation of multiple networks within the brain. The primary motor cortex exhibits oscillatory activity within beta (≈13–30 Hz) and alpha (≈8–12 Hz) frequency bands (Pfurtscheller, 1998; Baker, Olivier, & Lemon, 1997; Murthy & Fetz, 1992; Pfurtscheller & Aranibar, 1979). Motor-related beta activity is not constrained to the primary motor cortex (M1) and has been measured throughout the motor-related brain network (Klostermann et al., 2007). The cortical origin of the sensorimotor alpha (or mu) and beta rhythms has been proposed to originate from separate sources, with beta generated in M1 (Baker et al., 1997; Murthy & Fetz, 1992) and mu generated in primary somatosensory cortex (S1; Salmelin & Hari, 1994). However, recent studies demonstrate that both alpha and beta rhythms are generated in multiple laminae of M1 (Rönnqvist, McAllister, Woodhall, Stanford, & Hall, 2013; Yamawaki, Stanford, Hall, & Woodhall, 2008), with amplitude dependent on connectivity with S1 and other areas.

Intrinsic beta activity is modulated during the preparation, execution, and termination of voluntary movements (Cheyne, Bells, Ferrari, Gaetz, & Bostan, 2008). Alterations in the modulation of beta have been associated with neuropathologies that exhibit motor abnormality, such as Parkinson’s disease (PD; Hall et al., 2014; Kühn, Kupsch, Schneider, & Brown, 2006; Brown et al., 2004; Brown, 2005) and stroke (Hall, Barnes, Furlong, Seri, & Hillebrand, 2010; Tecchio et al., 2006).

The functional role of beta oscillatory activity is, as yet, unclear. However, evidence from local field potential measures of the basal ganglia of patients with PD suggests a link between exaggerated beta activity and impaired motor function (Weinberger et al., 2006; Brown & Williams, 2005; Kühn et al., 2005). Two theories have been suggested to explain the role of beta activity in motor function. The first, proposed by Pfurtscheller, Stancák, and Neuper (1996), suggests that beta activity is a correlate of idling motor activity. More recently, a second theory has proposed that beta activity promotes postural and tonic activity at the expense of voluntary movements (Pastötter, Hanslmayr, & Bäuml, 2008; Gilbertson et al., 2005). Slowing of voluntary movement during intrinsic elevations in cortical beta activity (Gilbertson et al., 2005) and during 20 Hz entrainment using transcranial alternating current stimulation of motor cortex (Pogosyan, Gaynor, Eusebio, & Brown, 2009) has been cited as further evidence for this theory (Jenkinson & Brown, 2011).

Recording from implanted deep brain stimulation electrodes enables measurement of local field potentials and, therefore, oscillatory activity from the subthalamic nucleus (STN) of patients with PD who suffer from increased tonic activity (rigidity) and a slowness of movement (bradykinesia). The observation of exaggerated beta power in the STN of these patients with PD further...
supports the theory that M1 beta promotes tonic activity
(Hammond, Bergman, & Brown, 2007) at the expense of
voluntary movement. Deep brain stimulation to the STN
suppresses beta activity, and the degree of suppression
correlates with the level of improvement in rigidity and
bradykinesia (Bronte-Stewart et al., 2009; Kühn et al.,
2008). This same correlation between the degree of reduced
beta oscillatory activity and improvement in rigidity is ob-
served following effective dopaminergic drug treatment
(Ray et al., 2008; Kühn et al., 2006; Weinberger et al., 2006).

Further studies of both patient and neurotypical pop-
ulations demonstrate beta suppression is a strong predi-
cator of the efficacy of motor preparatory processes, with
greater beta suppression reflected in shorter RTs (Doyle,
Yarrow, & Brown, 2005; Williams et al., 2003). The la-
tency of motor response is well established to covary
with the degree of certainty in the movement direction
(Churchland, Kiani, & Shadlen, 2008; Pellizzer, Hedges,
& Villanueva, 2006; Dorris & Munoz, 1998; Bock &
Arnold, 1992). In this study, we adopted an established
motor–experimental paradigm for varying directional
uncertainty (Tzagarakis, Ince, Leuthold, & Pellizzer,
2010; Pellizzer et al., 2006; Pellizzer & Hedges, 2003) to
measure changes in beta oscillatory power. Previous
studies observe that RTs are significantly lengthened
and beta ERD decreased in proportion to the number
of cues (Tzagarakis et al., 2010). The aim of this study
was to assess alpha and beta oscillatory power during
each phase of the movement. Based on the proposal that
beta promotes tonic activity at the expense of voluntary
movement and that preparatory beta suppression is a
prerequisite for movement onset, we hypothesized that
an increase in directional uncertainty will delay the termi-
nation of tonic activity, inhibit suppression of associated
beta oscillatory activity, and increase RTs correspond-
ingly. Furthermore, based on the assumption that oscil-
latory networks represent transient functional assemblies
created for the purpose of temporally aligning relevant
units to elicit an effective output, we hypothesized that,
following the initial uncoupling from the idling/tonic
network, functional preparation would coincide with a
transient increase in synchronous power. Here, we aimed
to test the theory that the creation of a specific functional
assembly, accompanied by a synchronous event, can only
occur when the function (direction) is known. Therefore,
it will occur in the relevant interval when the required
direction of movement is revealed.

METHODS

Participants

Eighty right-handed volunteers (19 men), with a mean
age of 27 (range 18–71), were recruited. Informed consent
was obtained, and all studies were approved by the local
ethics committee, in accordance with the ethical standards
set by the 1964 Declaration of Helsinki.

Apparatus

Participants were seated at a desk and gripped a custom-
made joystick with their right hand, resting their forearm
on the desk. The joystick was designed to be held between
the thumb and forefinger and was capable of full 360° rota-
tion within the horizontal plane. The motor control task
was displayed on a 21-in., high-definition monitor, placed
at a comfortable height, 90 cm in front of the participant.

M1 Hand Area Localization

Single-pulse TMS using a Magstim 200² stimulator
(Magstim, Carmarthen, UK) and a standard 70-mm-
diameter figure-of-eight coil held tangentially to the scalp
with the coil handle pointing backward ∼45° laterally. The
EMG activity of the first dorsal interosseous (FDI) muscle in
the right hand was recorded using bipolar, single differen-
tial surface EMG electrodes (DE-2.1; Delsys, Natick, MA).
The surface electrodes comprised two 10-mm silver bar
strips, spaced 10 mm apart, with a 20-Hz to 450-kHz band-
width, 92 µV common mode rejection ratio, and <1015 Ω
input impedance (Delsys 2017, p. 22). The electrodes were
placed over the FDI muscle, and a reference ground elec-
trode was placed over the ulnar process of the right wrist.
The EMG signal was digitized with a sampling rate of 2 kHz
using a Power 1401 digital analogue (Cambridge Electronic
Design, Cambridge, UK) converter and analyzed using Sig-

Motor Control Task

The task used was an instructed-delay reaching task
based on the established paradigm (Tzagarakis et al.,
2010; Pellizzer et al., 2006; Pellizzer & Hedges, 2003), as
seen in Figure 1. The task consisted of 180 trials, each
comprising a center-hold period, a spatial cue presen-
tation (“cue onset”), a target cue presentation (“target
identification”), and a participant response (“movement
onset”). Each trial was initiated by the participant main-
taining a joystick-controlled crosshair within an outline of
a circle in the center of the screen (radius, 0.6° of the visual
angle [VA]) for 2 sec. Participants were instructed to fixate
on the center of the screen throughout the trial. Following
the center-hold period, a spatial cue was presented that
varied randomly in duration between 1 and 1.5 sec. The
spatial cue consisted of one, two, or three possible targets,
presented with the number and positions of targets pseudo-
randomized for each trial. This resulted in three possible
target presentations, each presented 20 times, during the
one-target condition and three possible combinations of
targets, each presented 20 times, during the two-target
condition. Sixty trials in total were presented for each
Each target consisted of an outline of a circle (radius, 0.75° VA) with a center 4° VA away from the center of the screen. Targets were presented at 45°, 165°, and 285° relative to the center of the screen. Following cue onset, one of the targets was highlighted white (target identification). At this point, the participant used the joystick to move the crosshair from the center of the screen toward the highlighted target circle as quickly and accurately as possible. Consequently, directional preparation was possible at cue onset in only the one-target condition, but not in the two-target or three-target conditions, where directional uncertainty continues until target identification.

The RT was defined as the period between a target identification and movement onset. For each of the three target conditions, RT outliers (median RT ± 2 MAD) were removed from the data set. The task was controlled by a custom-made computer program (Microsoft Visual Basic).

**EEG Recording and Analysis**

A five-electrode EEG montage was centered at the location of primary hand area of left M1. Four further electrodes were sited 2 cm anterior, posterior, ventral, and dorsal with respect to the central electrode (Figure 1B). These electrodes were used to confirm the optimal spatial positioning of the M1 electrode. The Ag/AgCl electrodes were coated with conductive Ten20 paste (Weaver and Company, Aurora, CO) for 15 min before being affixed to the scalp to ensure stable polarization potential of the electrodes and reduce impedance. EEG recordings were made using a DC-EEG feedback NEURO PRAX system (neuroConn GmbH, Ilmenau, Germany), referenced online to an electrode placed on the right mastoid process and sampled at 2048 Hz for digital storage.

EEG data from the recording montage were bandpass filtered between 2 and 100 Hz using a Hamming window-synced FIR filter (Oppenheim, Schafer, & Buck, 1999) and notch-filtered at 50 Hz to reduce electrical mains noise. All data were processed using MATLAB and FieldTrip open-source MATLAB toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). Time–frequency analysis was performed using a Morlet wavelet transformation (Tallon-Baudry & Bertrand, 1999; Bertrand & Pantev, 1994). Spectral power in the alpha (8–12 Hz) and beta
A fully counterbalanced repeated-measures design was used. Differences in RTs and beta and alpha amplitude across the three directional uncertainty conditions were analyzed using ANOVAs and paired $t$ tests. The latency of oscillatory power change (event-related desynchronization [ERD]) was identified as the time point at which oscillatory power fell 2.5 SD from the mean baseline power, following the method previously described (McAllister et al., 2013). Change in beta power was analyzed with respect to baseline 500 msec before cue onset, for the initial change following cue onset and target identification. To further determine the relative change in oscillatory power between target identification and movement onset, data were normalized to the point of target identification.

To test the hypothesis that creation of a functional assembly requires and therefore coincides with transient synchrony, we analyzed the change in synchronous power following the initial desynchronization (uncoupling) from the beta. We used a sliding window approach (50 msec) to compute the change in synchronous power between conditions (one, two, and three targets) from the minimum following cue onset to the maximum in the interval up to target identification. We used the same approach to determine the difference in power between the 100-msec pretarget identification and the interval up to movement onset. This approach was used to identify differences in synchronous power when direction was known in the post-cue onset (one-target) or post-target identification (three-target) conditions.

**RESULTS**

**Behavioral Results**

Average RTs are plotted against number of targets in Figure 1C. Results from a one-way ANOVA indicated that RT was significantly affected by number of targets, $F(2, 148) = 488.84, p < .001$, ANOVA, with planned contrasts indicating that RT during one-target presentation ($M = 372.1$ msec, $SD = 56.2$ msec) was significantly less than during two-target presentation ($M = 427.8$ msec, $SD = 55.6$ msec), $t(73) = -21.84, p < .001$, paired $t$ test, and three-target presentation ($M = 449.5$ msec, $SD = 57.5$ msec), $t(73) = -30.3, p < .001$, paired $t$ test. Average RT during two-target presentation was also significantly lower than during three-target presentations, $t(73) = -8.46, p < .001$, paired $t$ test. These findings are in line with those of previous studies using a similar paradigm that found that as directional uncertainty increases, RTs lengthen (Tzagarakis et al., 2010; Pellizzer et al., 2006; Pellizzer & Hedges, 2003).

**Time Series Analysis of Beta ERD**

For each participant, beta-band power was normalized relative to a 1000-msec baseline period, starting 1500 msec before cue onset and averaged across all conditions. On a trial-by-trial basis, the power change from baseline to a 500-msec period after cue onset was computed to determine the initial preparatory beta ERD. For each participant, power change was averaged for the number of targets presented (Figure 2).
A decrease in beta-band power after cue onset was observed in all conditions (one, two, and three targets). The onset latency of this beta desynchronization occurred, on average, 173.8 msec ($SD = 115.3$ msec) after cue onset with no significant difference between target conditions, $F(2, 148) = .689, p = .504$, ANOVA. The amplitude of initial preparatory beta desynchronization was significantly different between conditions, $F(2, 148) = 3.25, p = .041$, showing smaller reduction in power as the number of targets, and therefore, the directional uncertainty increased (Figure 3A). Specifically, during one-target trials, where participants were certain of the direction of movement required, a significantly greater beta desynchronization ($M = 20.25\%$, $SD = 20.47\%$) was observed than with three-target trials ($M = 12.53\%$, $SD = 18.92\%$), where required direction was unknown, $t(73) = -2.47, p = .014$, paired $t$ test (Figure 3B).

Following the initial preparatory desynchronization, the one-target condition exhibited sustained beta suppression, whereas the two-target and three-target conditions showed a partial resynchronization (i.e., an increase in beta power) until the point of target identification (Figure 3C).

Consequently, at the point of target identification, when directional uncertainty was resolved and participants were cued to move, beta power was significantly greater in the three-target condition ($M = 83.14\%$, $SD = 18.97\%$) than the one-target ($M = 75.41\%$, $SD = 16.27\%$) condition, $t(73) = -2.84, p = .005$, paired $t$ test (Figure 3D).

Following target identification, average beta power reduced in all conditions, until the point of movement initiation, termed “response phase ERD” (Figure 4A). The latency of response phase ERD showed no dependence on the number of targets presented, $F(2, 148) = 1.035, p = .358$, ANOVA. In contrast with a previous observation (Tzagarakis et al., 2010), we observed that the amplitude of the response phase ERD was not significantly different between the three different target conditions, $F(2, 148) = .812, p = .445$, ANOVA (Figure 4B). This can be observed from the envelope of beta power when normalized to the 500 msec before target identification (Figure 4C).

**Time Series Analysis of Alpha ERD**

Time series analysis within the alpha frequency range (8–12 Hz) revealed a decrease in power in all conditions following initial cue onset (Figure 5A). Alpha power showed significantly greater desynchronization following one-target (high directional certainty) preparation...
(M = 20.18%, SD = 21.43%), compared with two-target (M = 10.14%, SD = 29.55%) preparation, t(73) = −2.17, p = .031, paired t test, and three-target (M = 12.63%, SD = 24.6%) preparation, t(148) = −2.13, p = .034, paired t test.

Following initial alpha response-phase ERD, a transient increase in alpha synchrony was observed in the one-target condition (M = 2.93%, SD = 13.04%), t(73) = 1.936, p = .057, paired t test, but not the two-target (M = −2.33%,
than in the three-target condition (\(M = 72.44\) msec, \(SD = 242.7\) msec, \(t(73) = -1.373, p = .174\), paired \(t\) test, or three-target (\(M = -.75\% , SD = 14.93\% \), \(t(73) = -.418, p = .677\), paired \(t\) test, conditions (Figure 5B). Conversely, following target identification, a significant transient increase in alpha synchrony was observed in the two-target (\(M = 6.32\% , SD = 17.34\% \), \(t(73) = 3.134, p = .002\), paired \(t\) test, and three-target (\(M = 5.2\% , SD = 14.71\% \), \(t(73) = 3.059, p = .005\), paired \(t\) test, conditions, but not the one-target condition (\(M = -.89\% , SD = 12.38\% \), \(t(73) = -.617, p = .539\), paired \(t\) test (Figure 5D). This condition-dependent alpha synchrony is clearly visible in the envelope of alpha power (Figure 5A and C).

**RT and Transient Alpha Synchrony**

To further investigate the relationship between transient alpha synchrony and RT, we analyzed the latency of peak alpha synchronization following target identification in the two- and three-target conditions. We found that peak alpha synchrony occurred significantly earlier in the two-target condition (\(M = 203.4\) msec, \(SD = 75.56\) msec) than in the three-target condition (\(M = 242.7\) msec, \(SD = 72.44\) msec), \(F(2, 148) = 5.525, p = .021\), ANOVA, corresponding to the shorter RT in the two-target condition.

**DISCUSSION**

This study suggests that the profile of synchronous power change in the alpha and beta frequency range is directly associated with the recruitment of appropriate networks in preparation for movement.

As expected, RT was directly dependent on the ability of participants to predict the direction of required movement based on the stimulus information. This is consistent with previous reports (Tzagarakis et al., 2010; Churchland et al., 2008; Pellizzer et al., 2006; Dorris & Munoz, 1998; Bock & Arnold, 1992) and confirms that participants engaged with the experiment as required.

Consistent with general observations in a variety of experiments involving movement paradigms (Cheyne, 2013; Jurkiewicz, Gaetz, Bostan, & Cheyne, 2006; Pfurtscheller & Lopes da Silva, 1999; Pfurtscheller et al., 1996; Pfurtscheller & Aranibar, 1979), a significant decrease in both alpha and beta synchronous power was observed following the presentation of the initial onset cue in all conditions. We propose that this desynchrony reflects a process of disengagement from on-going network activity to allow the assignment of appropriate motor units to generate a required output. Of note, the amplitude of both alpha and beta ERD is directly dependent on the number of targets presented. This suggests that, where information is present that allows for the identification of the appropriate response, those neural populations are enabled to be disengaged in preparation for recruitment to an output assembly. Taken together, these observations of disengagement from an active network support the theory of beta and, indeed, alpha oscillations in the promotion of postural tone at the expense of voluntary movement (Pastötter et al., 2008; Gilbertson et al., 2005). However, the observation of partial resynchronization of the beta rhythm in the two- and three-target conditions is also consistent with an inhibition of movement in the absence of a motor plan. Following initial ERD, we demonstrate that the on-going profile of beta power is predictive of the participant’s preparatory state. In the one-target condition, beta suppression is sustained up to the point of target identification, whereas the two-target and three-target conditions exhibit a partial resynchronization of beta power until the required target direction is indicated. Given that temporary reassignment to a postural network is unlikely, with the impending need to move, resynchronization is likely to reflect the temporal realignment of potential units with the functional networks required to generate motor output after target identification. Although speculative, this suggests that beta synchrony in motor cortex reflects and serves a dual purpose, including the maintenance of postural tone (Pastötter et al., 2008; Gilbertson et al., 2005) and providing a temporal pacer to maximize effective motor responses.

The precise roles of the beta rhythm notwithstanding these data support the independence of the alpha and beta rhythms, which subserve separate functional processes (see van Wijk, Beek, & Daffertshofer, 2012, for a review). Importantly, we identify a novel oscillatory feature in this experiment that corresponds to the participants’ ability to engage a specific motor network. Following the initial alpha and beta ERD, a transient “burst” of alpha is observed in the one-target condition, but not in the two-target or three-target conditions. We propose that this signature reflects the recruitment of units to the functional assembly required to generate the motor output. This is supported by the observation that following target identification a transient burst of alpha is observed in the two-target and three-target conditions, but not in the one-target condition. These signatures are temporally consistent with the participants’ ability to assign the appropriate network based on information about the required movement. This feature dependency is borne-out behaviorally, as the alpha burst occurs significantly earlier in the two-target condition than the three-target condition, corresponding to the significant difference in RT between those conditions. This feature is consistent with electrophysiological recordings, which have shown alpha oscillations reflect feedback inhibition in the cortex (Michalareas et al., 2016; Bastos et al., 2015), with feedback inhibition suggested to tune directional pyramidal cells in the motor cortex (Isomura, Harukuni, Takekawa, Aizawa, & Fukai, 2009; Merchant, Naselaris, & Georgopoulos, 2008; Georgopoulos & Stefanis, 2007). We posit, given the occurrence of the transient alpha signal only when sufficient information is available to form a motor plan, that it reflects the recruitment in readiness of units required to execute the movement. This may include pyramidal tract neurons,
but they are unlikely to be the sole generator given the relative minority of these cells (Keller, 1993). The switching of beta and alpha here, given the relatively low spatial resolution of the measurement, is consistent with gating by inhibition hypothesis (Jensen & Mazaheri, 2010). In particular, when considered alongside the observation of increased alpha in M1, following removal of connectivity with S1 (Rönnqvist et al., 2013), it is possible that increased alpha reflects active inhibition of somatosensory input to facilitate formation of a motor plan based on current information. Indeed, the inhibitory basis of these signals is supported by several studies that demonstrate the role of GABAergic modulation in generation of the beta (Muthukumaraswamy et al., 2013; Hall et al., 2010, 2011; Jensen et al., 2005) and alpha (Rönnqvist et al., 2013) rhythms.

In contrast with previous observations (Tzagarakis et al., 2010), we observed no significant difference between conditions in either the latency or the amplitude of the response-phase ERD. Importantly, the differences in response-phase ERD amplitude can be accounted for directly by the oscillatory power at the point of target identification, which is predicted by the number of targets. Further change in synchronous power is removed by normalization to that point. We propose that, although beta desynchronization is an important process in the generation of movement, the critical distinction in this experiment lies in the preparatory, rather than response, phase.

In summary, we demonstrate that both alpha and beta desynchronization reflects a process of disengagement from existing networks to enable the creation of functional assemblies. We also demonstrate a novel signature of transient alpha synchrony, which is predictive of RT and thus likely associated with the recruitment of a functional assembly required to generate the motor output.

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