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Single trial beta oscillations index time estimation

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ABSTRACT

Recent work shows that putamen-originating beta power oscillations serve as a carrier for temporal information during tapping tasks, with higher beta power associated with longer temporal reproductions. However, given the nature of tapping tasks, it is difficult to determine whether beta power dynamics observed in these tasks are linked to the generation or execution of motor programs or to the internal representation of time. To assess whether recent findings in animals generalize to human studies we reanalyzed existing EEG data of participants who estimated a 2.5 s time interval with self-paced onset and offset keypresses. The results showed that the trial-to-trial beta power measured after the onset predicts the produced duration, such that higher beta power indexes longer produced durations. Moreover, although beta power measured before the first key-press also influenced the estimated interval, it did so independently from post-first-keypress beta power. These results suggest that initial motor inhibition plays an important role in interval production, and that this inhibition can be interpreted as a biased starting point of the decision processes involved in time estimation.

1. Introduction

Perceiving the passage of time is an ubiquitous experience and a building block for other cognitive processes and behaviors such as controlling movements in time (Allman et al., 2014; van Wassenhove, 2009), both in well-controlled laboratory settings (Van et al., 2014) and in tasks with higher external validity (Matthews and Meck, 2014; Van Rijn, 2014). However, the neural underpinnings of these abilities are not yet well understood. Although it has been convincingly shown that climbing neural activity (CNA, Durstewitz, 2003) is somehow linked to time estimation (e.g., Macar and Vidal, 2004; Wiener et al., 2012; Wittmann, 2013), previous studies have found that EEG-based CNA does not co-vary with trial-to-trial fluctuations in subjective timing (Kononowicz and Van Rijn, 2011; Van Rijn et al., 2011, cf., Wiener et al., 2012) whereas electrophysiological potentials evoked by the end of the interval do covary with the subjective percept Kononowicz and van Rijn (2014a). However, post-interval evoked potentials cannot be used to track or index the dynamics of subjective time (also see Van Wassenhove and Lecoutre (2014)). Typically, dynamics of subjective time has been investigated by tracking slow changes in electric potentials (Macar and Vidal, 2004) or investigated dynamics of neuronal spiking patterns such as interval tuning (Crowe et al., 2014; Merchant et al., 2013), CNA (Merchant et al., 2011) or scalable population codes (Mello et al., 2015). However, the dynamics of neural oscillations has been investigated very rarely (but see Kononowicz (2015), Parker et al. (2014)).

Interestingly, a recent synchronization-continuation tapping studies have shown that putamen-originating beta power was larger for longer durations, suggesting that beta power reflects the to-be-produced duration (Bartolo et al., 2014; Bartolo and Merchant, 2015), and thus indicating that beta power is linked to the development of subjective time or to guidance of internally driven motor sequences. If beta power dynamics is only linked to generation of motor sequences, without having any relationship to interval timing, fluctuations in beta power should not correlate with behavior on a time production task. However, if beta power is linked to internal sense of time it should covary with the length produced interval. Moreover, the nature of tapping tasks makes it impossible to attribute the observed beta power to the onset of a temporal interval, or to the offset of the previous interval, as each response is both offset and onset of an interval. Here we focus on a supra-second time production task in which the onset and the offset of an interval are separately indicated. Additionally, tapping tasks typically use intervals below one second. As timing mechanism were suggested to differ for intervals shorter and longer

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[2] Contributions: designed research, analyzed data, wrote the paper.

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than one second, the aim of this paper is to assess whether the results presented by Bartolo et al. (2014), obtained in a tapping task with subsecond intervals, generalize to longer intervals.

Therefore, to assess whether beta power as well as other frequency bands can track or index the dynamics of subjective time, sufficiently long intervals should be used in a paradigm that allows for distinguishing the onset and offsets of temporal intervals. By assessing the power of different frequency bands of an existing data set (Kononowicz and Van Rijn, 2011) that has been previously used to investigate the relationship between temporal performance and the amplitude of contingent negative variation, we address whether trial-to-trial variability in interval timing is predicted by oscillatory power, both measured before the onset of the trial (see, e.g., De Lange., 2013), and immediately after. This setup allows us to eliminate biases coming from experimentally manipulated durations and instead focus on the naturally occurring fluctuations in timing performance.

2. Method

Detailed information on stimuli, experimental procedures and participants can be found in Kononowicz and Van Rijn (2011). Below we will provide a summary of the information relevant for the analyses reported in this work.

2.1. Stimuli, procedure and data acquisition

We investigate the role of beta power during the self-paced production of intervals of 2.5 s (participants indicated both onset and offset of the interval by a keypress) in a task setup that meets the criteria for an accurate measurement of beta power. First, the length of target interval is long enough to allow post-movement beta power after the initial keypress to fully evolve, and to reach its peak without strong contamination from upcoming movement preparation. Second, because visual feedback was provided after every trial and every trial started with a short waiting period, the experimental setup enforces a minimum inter-trial interval of 2.7 s, allowing beta power associated with the motor response to the offset of the trial to return to "baseline" before the onset of a next trial.

Although the original dataset consists of two separate experiments, these experiments are identical for the purposes of the analyses reported here. We will therefore discuss the original data as one, collapsed, dataset of 32 participants that were tested in a setup as approved by the Ethical Committee Psychology of the University of Groningen. The outline of a task is depicted in Fig. 1. The participants were asked to produce the 2.5 s interval by pressing the spacebar twice using the right hand index finger. Visual feedback was presented after each trial indicating the deviation from the standard duration. During the entire interval a small circle served as a fixation point. Before the first keypress, the circle was shown in light gray on a black background. The first keypress changed the color of the circle to white, as a visual cue that the interval had started. The second keypress removed the circle from the screen, and feedback was presented. The feedback was delivered as a row of five circles, immediately above the location of the fixation point. The middle circle turned green if the time production was between 2.4 and 2.6 s. If time production was between 1.8 and 2.4 s or between 2.6 and 3.2 s, the circle just to the left or right of the middle circle turned green. If the time production was shorter than 1.8 or longer than 3.2 s, the left or right outer circle turned red. Before each trial, participants either saw a short instruction requesting them to blink their eyes, or where just presented a blank screen, depending on the experiment. The time between the instruction to blink and the onset of the interval was at least 1.5 s.

2.2. Time-frequency analysis

We selected the 20 electrodes (AFz, F3, Fz, F4, FC3, FC1,FCz, FC2, FC4, C3, C1, Cz, C2, C4, CP3, CPz, CP4, P3, Pz, P4) that were used in both original experiments and performed an analysis of oscillatory power by comparing the 3 pseudo-experimental conditions that were previously presented by Kononowicz and Van Rijn (2011), see also Macar (1999): trials in which the response was slightly too

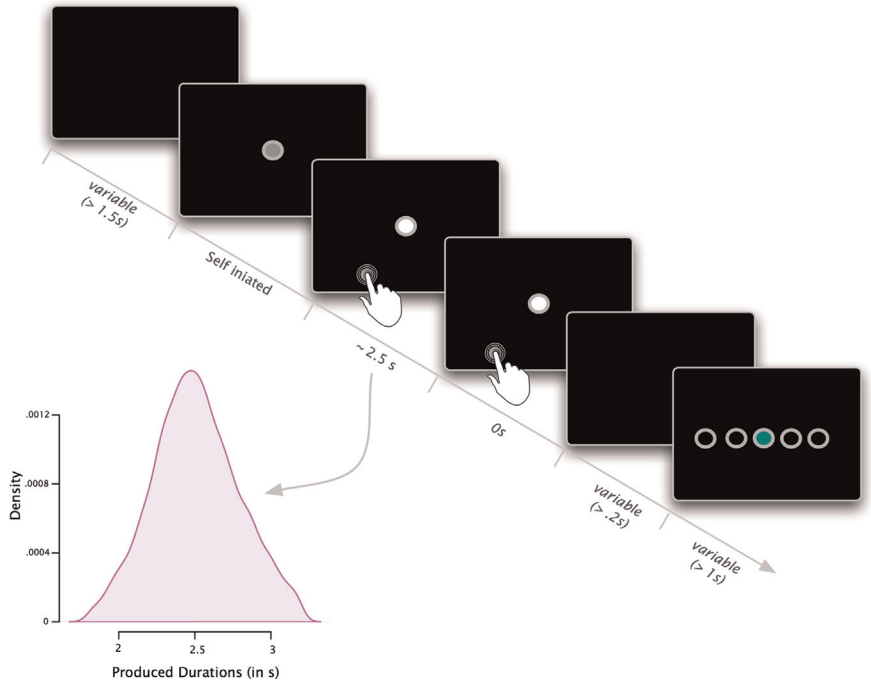

Fig. 1. Time course of an experimental trial. Intervals marked as variable differed slightly between the two experiments. The distribution shown in the lower left corner depicts the probability density function (Sheather and Jones, 1991) of observed time productions ranging from 1.8 to 3.2 for all subjects.

early: Short (2.2–2.4), was Correct (2.4–2.6 s), or was slightly too late: Long (2.6–2.8 s). More extreme responses are typically not analyzed in this paradigm (e.g., Macar et al., 1999) and were therefore not included in the initial time-frequency analyses. However, we will also report on analyses based on the all "green" trials (i.e., responses between 1.8 and 3.2 s). On average 149.7 trials with a response between 2.2 and 2.8 s were analyzed per participant, and 212.5 time production trials ranging from 1.8 to 3.2 s. Time-frequency analysis was performed using FieldTrip (Oostenveld., 2011), an open source Matlab toolbox, using FieldTrip's default FFT methods.

The 1/*f* property was removed from the data time domain prior to the calculation of spectral power by computing the first order derivative as implemented in FieldTrip. Removing the 1/*f* trend ensures that all frequencies of broadband averaged signal contribute equally to beta power estimates and power estimates are dominated by lower frequencies due to the 1/*f* property when absolute baseline normalization is applied (Cohen, 2014). To analyze oscillatory power we used a single Hanning taper with an adaptive time window of 6 cycles per frequency in 15 ms steps for frequencies from 4 to 40 Hz. The amount of spectral smoothing through multi-tapering was set to 1. We used linear baseline subtraction, thus the resulting power changes in the time production interval were expressed as an absolute power change (e.g., Wang et al., 2012) relative to the interval before the first keypress (−0.5 to 0 s) on a trial-to-trial basis. No additional baseline correction was applied for the second keypress locked data.

To quantify the differences between the pseudo-experimental conditions, we run cluster-based permutation analysis, based on two-sided Hotteling's T^2 as provided by FieldTrip (Maris and Oostenveld, 2007) by drawing 1000 sample for the Monte Carlo approximation and using FieldTrip's default 10–10 neighbor template. The randomization method identifies the electrodes whose statistics exceed a critical value ($p < 0.05$). Neighboring electrodes that exceed the critical value are considered to form a cluster. The cluster level statistic is defined as the sum of values of a given statistical test in a given cluster, and is compared to a null distribution that is created by randomizing the data between conditions across multiple subjects. The *p* value is estimated based on the proportion of the randomizations exceeding the observed maximum cluster-level test statistic.

Both cluster analysis and linear mixed model analyses were computed for 200 ms time windows with steps of 100 ms from 0 to 1.6 s after the first keypress. The 1.6 s time point was chosen to reduce the impact of motor preparatory processes as no trials were included in these analyses with estimations shorter than 2.2 s. All analyzes were performed on a frequency range associated with beta power in earlier work (15–30 Hz, e.g., Haegens et al., 2011;

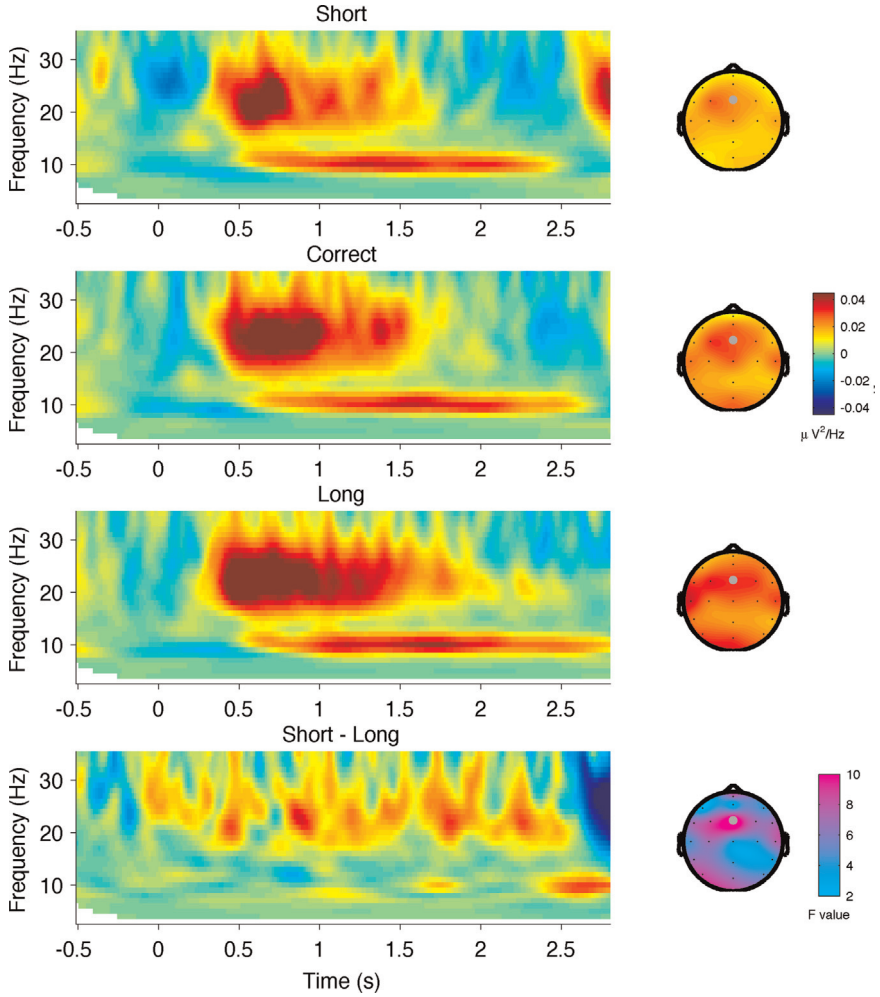

Fig. 2. Time-frequency decomposition of the first keypress-locked data measured at FCz for the pseudo-experimental Short (2.2–2.4 s), Correct (2.4–2.6 s), and Long (2.6–2.8 s) conditions with corresponding topographies. Topographical plots are based on a 15 to 30 Hz frequency band and focus on the time windows that showed significant differences in the cluster based analysis. The bottom-most spectrogram depicts the power differences for Long minus Short categories. The spectrograms and three top-most topoplots depict power in uV^2/Hz, as depicted in the legend to the right of the second topoplot. The topoplot at the bottom depicts the results of cluster based permutation test in *F*-values. *F*-values for all significant time windows were averaged. For more details, see the main text.

Jenkinson and Brown, 2011). As depicted in Fig. 2, post-first-keypress oscillatory beta power falls within the selected frequency range. To ensure that any effects observed for beta power are not an artifact of a general modulation of oscillatory power, we also assessed the power per pseudo-experimental condition in theta (4–7 Hz) and alpha (8–14 Hz) bands. For display purposes the data for beta band frequency was smoothed using an eight-element kernel, but all reported analyses are based on raw, unsmoothed data.

3. Results

As expected in an interval timing experiment in which feedback is provided, participants accurately reproduced 2.5 s intervals as depicted in the density plot inset shown in Fig. 1. Detailed information on behavioral performance can be found in Kononowicz and Van Rijn (2011). The three top-most rows of Fig. 2 depict the time-frequency averages based on the signal recorded at FCz, and averaged over participants for the three pseudo-experimental conditions. The two most salient oscillatory events visible for all three pseudo-experimental groups during the time production interval are an early increase in beta power (around .6 s after onset), and a later increase in alpha power (Fig.4, starting around .5 s after onset and continuing until the 1.5 s of the interval, after which it starts to decrease). The topoplots shown next to the time-frequency plots depict the average beta power for the measured electrodes between 0 and 1.8 s after first keypress, indicating that for all three conditions the strongest beta power can be found at left centro-frontal electrodes. The increase in beta power after a keypress has been interpreted to reflect idling processes in the sensorimotor cortex, as after an initial peak it slowly decreases until the next response is given (e.g., Pfurtscheller., 2003). In line with this explanation, the top-panel of Fig. 3 shows that beta power reaches its peak about half a second after the first keypress and then starts to desynchronize until the participant presses the key to end the interval (see the bottom-panel of Fig. 3). Interestingly, closer inspection of Fig. 3 further shows that already around the peak of beta power, differences between the conditions become visible.

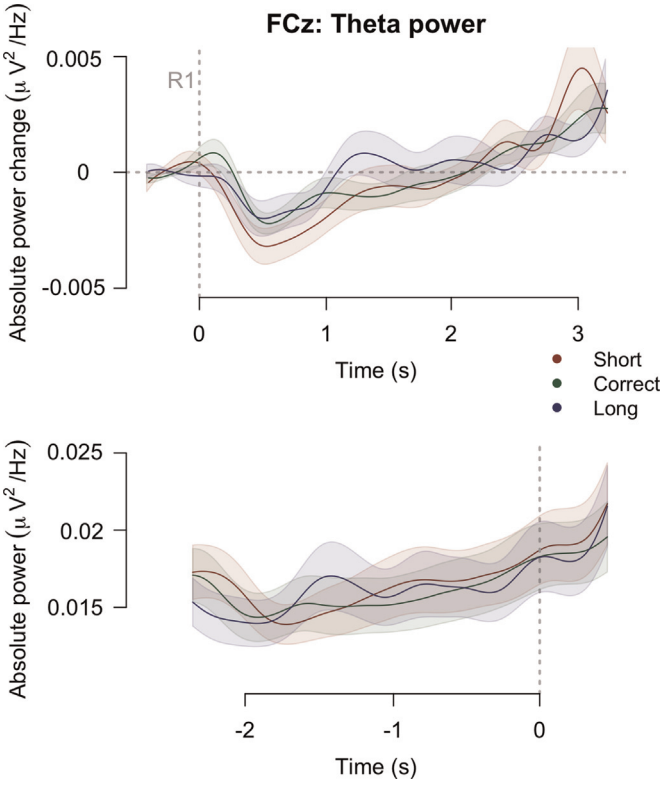

Fig. 4. Time course of theta power at FCz. The upper and lower graphs depict first keypress-locked and second keypress-locked data, respectively. The areas around the curves indicate one standard error of the mean.

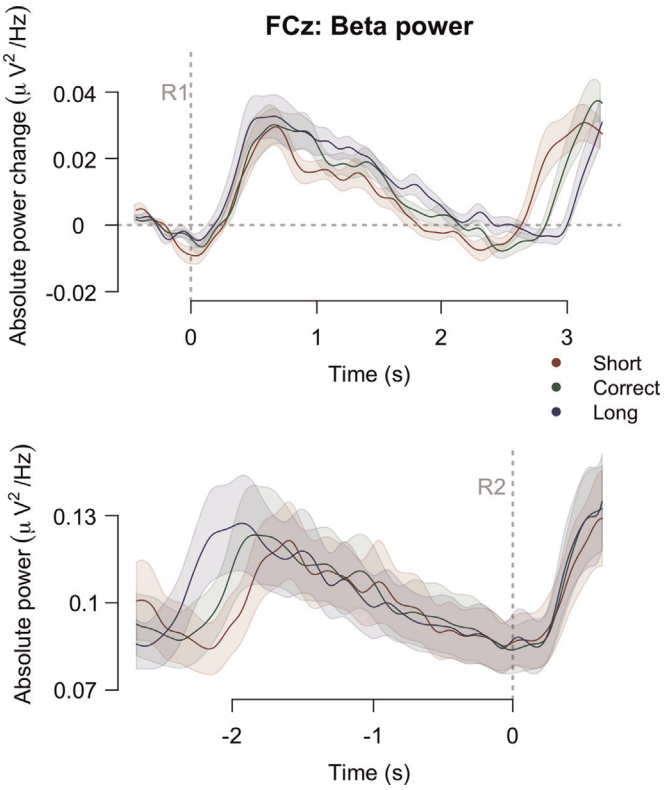

Fig. 3. Time course of beta power at FCz. The upper and lower graphs depict first keypress-locked and second keypress-locked data, respectively. The areas around the curves indicate one standard error of the mean.

We first investigated differences in oscillatory power among the pseudo-experimental conditions over all electrodes and time points ranging from 0 to 1.6 s after the first keypress using a sliding window of 200 ms in 100 ms steps. Hereto, we ran a cluster-based permutation analysis, averaging over frequencies bands between 4 and 7 Hz for theta band, 8 and 14 Hz for alpha band, and 15 and 30 Hz for beta band, separately for the three conditions. We did not find any significant effects for theta and alpha bands (all clusters for all time windows $p < 0.1$), but we found a significant effect of beta power in the following time windows: 0.4–0.6 s, $p = 0.017$; 0.5–0.7 s, $p = 0.019$; 0.8–1 s, $p = 0.035$; 0.9–1.1 s, $p < 0.001$; 1–1.2 s, $p = 0.002$; 1.1–1.3 s, $p = 0.006$; 1.2–1.4 s, $p = 0.002$; 1.3–1.5 s, $p = 0.007$; 1.4–1.6 s, $p = 0.020$. The most significant cluster ranging from 0.9 to 1.1 s is shown in the bottom right of Fig. 2. This significant cluster consists of all analyzed electrodes with a maximum at FCz. Subtracting the power observed at FCz in the Short from the Long condition provides the difference time-frequency plot shown in the bottom panel of Fig. 2. The dominance of green and blue colors in the beta range starting at about 0.4 s and continuing for at least the whole duration of the Short condition illustrates that beta power is higher in the Long condition. Fig. 3, in which the average beta power at FCz is plotted over the time course of a trial for the three pseudo-experimental conditions, supports this interpretation, as in the top, onset-locked panel the beta power is higher for the Long condition than for the Short condition, with the Correct condition in between. The bottom, offset-response-locked panel of

Fig. 3 shows that this difference is driven by the initial increase in beta power, as no differences between the three pseudo-experiment conditions can be observed in the last second before the offset-response ($p > 0.1$), nor does this Figure suggest any differences in the speed of desynchronization as the slopes are very similar.

To quantify the observation that initial beta power increases with estimated duration, we calculated normalized maximum power from 0 to 1.6 s after the first keypress using sliding window of 200 ms in 100 ms steps, for all trials with productions between 1.8 and 3.2 s (the "green" feedback trials). Trials in which theta, alpha, or beta power deviated more than 4 z-scores were removed from further analysis (3.6%). As suggested by Cohen and Cavanagh (2011), single trial power should be predictive of behavioral performance. To this end, we used linear-mixed effects models (e.g., Pinheiro and Bates, 2000; Gelman and Hill, 2007; see Bagiella et al. (2000) for arguments in favor of these methods in psychophysiology, and Kononowicz and Van Rijn (2011), Van Rijn (2014), Boehm et al. (2014) for earlier applications of this technique) to assess whether oscillatory power as measured on individual trials can predict the estimated duration associated with that trial. (Note that duration is entered as continuous variable in these analyses, not categorized in three pseudo-experimental conditions.) These regression models include a component for subject-based error variance and allow for testing the effect of multiple continuous experimental manipulations while taking the (repeated measures) structure of the design into account. Moreover, and especially relevant to EEG studies, these methods do not require an equal number of observations in each cell of the design. Multicollinearity has been assessed using variance inflation factor (VIF). None of the VIF values exceeded 1.1, indicating that multicollinearity is unlikely to have had a major influence on the results. Note that Rogerson (2001) recommended maximum VIF value of 5. F and p values were calculated based on a Type 3 ANOVA with Satterthwaite approximation of degrees of freedom, using *lmerTest* package. We focused on the FCz electrode, as that electrode showed the highest values for the cluster statistics, had the overall highest beta power, and also was the electrode of interest in the previous reports (Macar et al., 1999; Kononowicz and Van Rijn, 2011). To ensure that any observed effect can be attributed to modulations of beta power, and not just to a general modulation of power, we also determined alpha and theta power and included those in the analyses as predictors of estimated duration. The time courses of theta and alpha power averaged over the selected frequency band are presented in Figs. 4 and 5.

We first focused on the subset of trials that were categorized as one of the three pseudo-experimental conditions. Time productions were entered as dependent variable whereas normalized theta, alpha, and beta power were entered as predictors. We allowed for random intercepts for subjects. Fig. 6, top panel, depicts the estimated means and 95% confidence intervals for the three frequency bands, taken from a model in which all three frequency bands are entered as predictors. Each of these models was run separately for all 200 ms windows. As can be seen in Fig. 6, top panel, theta and alpha power does not correlate with the length of produced interval in any of the analyzed time windows. However, the effect of beta power can be found as early as 0.2 to 0.6 s after the first keypress as indicated by the diamond data points depicting estimates from mixed model fit for two windows: 0.2–0.4 s, $\beta=6.1$, $F(4812)=2.5$, $p=0.011$; 0.3–0.5 s, $\beta=5.5$, $F(4596)=2.6$, $p=0.009$; 0.4–0.6 s, $\beta=5.5$, $F(4042)=2.8$, $p=0.006$. These estimates shows that for every unit increase of absolute power, the produced interval is estimated to be ~6 ms longer.

Beta power was also predictive of time productions later in the interval: 0.7–0.9 s, $\beta=4.8$, $F(4028)=2.4$, $p=0.016$; 0.8–1 s, $\beta=6.4$, $F(4363)=3.3$, $p=0.001$; 0.9–1.1 s, $\beta=4.4$, $F(4528)=2.0$, $p=0.043$;

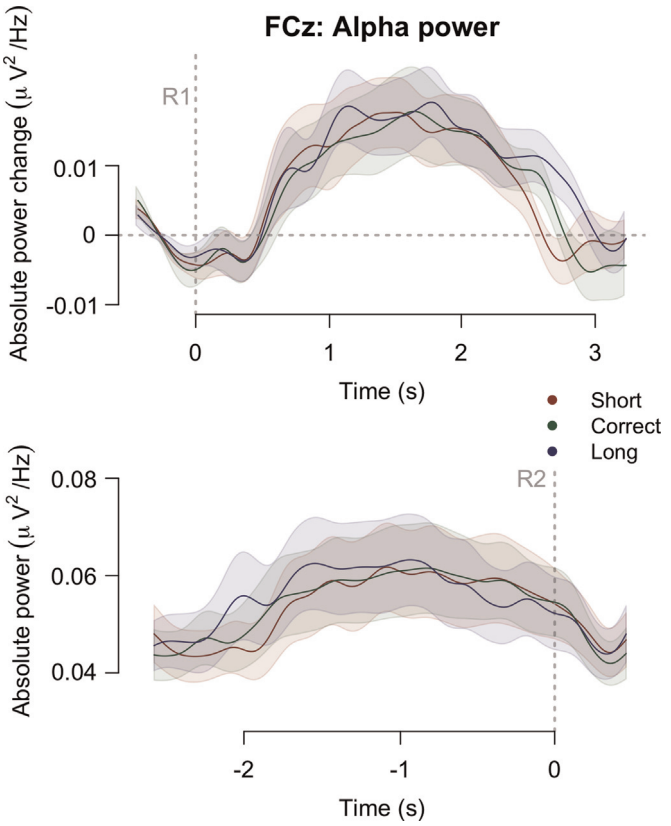

Fig. 5. Time course of alpha power at FCz. The upper and lower graphs depict first keypress-locked and second keypress-locked data, respectively. The areas around the curves indicate one standard error of the mean.

1.1–1.3 s, $\beta=7.4$, $F(4715)=3.5$, $p<0.001$; 1.2–1.4 s, $\beta=6.4$, $F(4707)=2.9$, $p=0.003$; 1.3–1.5 s, $\beta=4.2$, $F(4735)=2.0$, $p=0.044$; 1.4–1.6 s, $\beta=4.8$, $F(4773)=2.2$, $p=0.026$; 1.6–1.8;s, $\beta=5.5$, $F(4773)=2.4$, $p=0.019$, which is also depicted in Fig. 6, top row.

Additionally, we also performed an analysis on all trials to which the participants received "green" feedback, that is, with time productions from 1.8 to 3.2 s. The estimates of the full model are shown in the middle panel of Fig. 6. The effect of beta power was found in several time windows: 0.6–0.8 s, $\beta=6.2$, $F(6689)=2.1$, $p=0.034$; 0.7–0.9 s, $\beta=8.2$, $F(6688)=2.8$, $p=0.005$; 0.8–1 s, $\beta=8.0$, $F(6738)=2.8$, $p=0.006$; 0.9–1.1 s, $\beta=6.9$, $F(6753)=2.2$, $p=0.027$; 1–1.2 s, $\beta=7.8$, $F(6756)=2.5$, $p=0.012$; 1.1–1.3 s, $\beta=2.8$, $F(6765)=4.1$, $p<0.001$; 1.2–1.4 s, $\beta=10.9$, $F(6763)=3.5$, $p<0.001$; 1.3–1.5 s, $\beta=7.9$, $F(6752)=2.6$, $p=0.009$; 1.4–1.6 s, $\beta=8.6$, $F(6762)=2.8$, $p=0.005$; 1.5–1.7 s, $\beta=10.8$, $F(6772)=3.4$, $p<0.001$; 1.6–1.8 s, $\beta=12.8$, $F(6760)=3.8$, $p<0.001$. These estimates shows that for every unit increase of standardized beta (i.e., z-score), the produced interval is estimated to be ~10 ms longer.

Contrary to the analysis for 2.2–2.8 time productions we found effects of theta power in the following time windows: 0.6–0.8 s, $\beta=-3.6$, $F(6755)=-1.9$, $p=0.046$; 0.7–0.9 s, $\beta=-4.7$, $F(6768)=-2.7$, $p=0.008$; 0.8–0.1 s, $\beta=-4.8$, $F(6755)=-2.8$, $p=0.006$; 0.9–1.1 s, $\beta=-4.6$, $F(6752)=-2.6$, $p=0.008$; 1–1.2 s, $\beta=-3.8$, $F(6747)=-2.3$, $p=0.023$; 1.1–1.3 s, $\beta=-4.6$, $F(6754)=-2.8$, $p=0.005$; 1.2–1.4 s, $\beta=-5.9$, $F(6752)=-3.6$, $p<0.001$; 1.3–1.5 s, $\beta=-6.2$, $F(6743)=-3.9$, $p<0.001$; 1.4–1.6 s, $\beta=-5.9$, $F(6762)=-3.6$, $p<0.001$; 1.5–1.7 s, $\beta=-5.6$, $F(6777)=-3.4$, $p<0.001$; 1.6–1.8 s, $\beta=-6.5$, $F(6767)=-3.9$, $p<0.001$; as depicted in Fig. 6.

For the full range of "green" responses, the analysis shows that for every unit increase of standardized beta, the produced interval is estimated to be ~12 ms longer, and every unit increase of theta

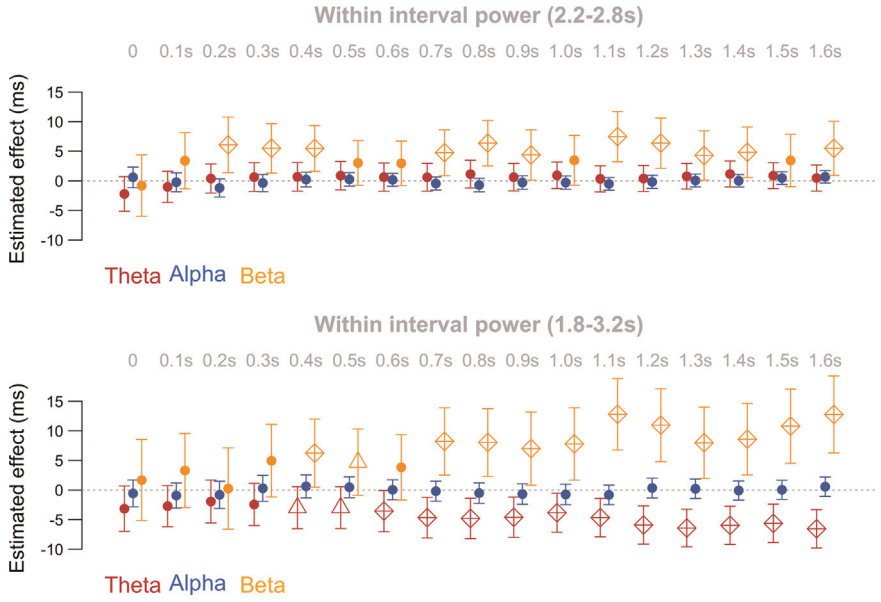

Fig. 6. The estimated effects and associated 95% confidence intervals derived from the linear mixed model fitted to theta, alpha, and beta power data. The upper panel is based on time productions ranging from 2.2 to 2.8 s, the standard pseudo-experimental groups. The bottom panel shows the estimated effects for the extended range of time productions, ranging from 1.8 to 3.2 s. The time label indicates onset of a time window (200 ms) in which a given model was fitted.

reduces the estimated duration with ~15 ms.

These changes in beta power after the first keypress can reflect induced or phasic oscillatory changes. However, pre-movement, preparatory beta power has been shown to index fluctuations in decision biases (De Lange et al., 2013), and thus any preparatory beta effects could influence the observed post-keypress effects. On the other hand, the beta power measured before the subject-paced onset could influence subsequent behavior independently from the motor-response evoked beta, mimicking the correlations between pre-stimulus oscillatory activity and stimulus processing (Busch and VanRullen, 2010; for reviews see, Deco and Romo (2008), Engel et al. (2001)). Therefore, we also measured standardized beta power over the 0.5 s interval prior to the first keypress for all "green" trials (i.e., productions larger than 1.8 and smaller than 3.2 s) and subjected this data to similar linear mixed effect analyses. (Similar analyses of the restricted dataset showed numerically similar effect sizes, but these failed to reach significance.) Fig. 7 shows the parameters of linear mixed model, again indicating a stronger effect of beta power than of theta or alpha. Indeed, formal model comparisons, by means of Akaike Information Criterion (AIC, see for example Wagenmakers and Farrell, 2004), showed that the comparison of a model including pre-interval beta to a model that only including an intercept confirmed that inclusion of pre-interval beta power is justified ($\Delta AIC=2$, $\chi^2_{(1)}=4.7$, $p=0.031$; and including theta and alpha was not warranted, $ps>0.3$, c.f., Anliker, 1963; Ng et al., 2011). The effect of beta on produced duration was significant ($\beta=20.0$, $F(1,2261)=2.3$; $p=0.019$). Interestingly, when both pre-interval, or pre-first-keypress beta and post-first-keypress beta power is entered in an analysis, both predictors contribute to the model in case of all time windows ranging from 0.4 to 1.8 s after first keypress. (all $p<0.05$) and the correlation between both fixed effects is low (all VIF < 1.5) indicating that both components reflect independent aspects of the interval timing task.

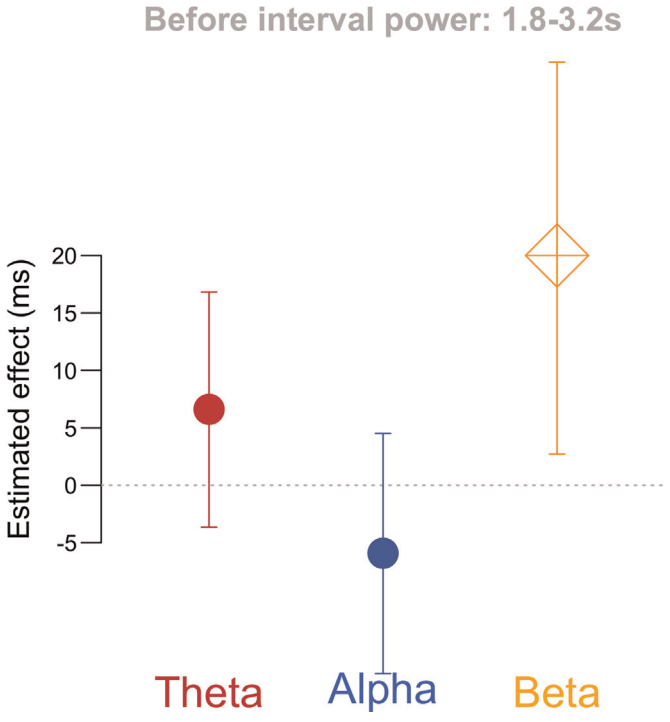

Fig. 7. The estimated effects and associated 95% confidence intervals derived from the linear mixed model fitted to theta, alpha, and beta power data as measured before the keypress starting the interval, based on the trials with time productions ranging from 1.8 to 3.2 s.

4. Discussion

According to Bartolo et al's recent study (2014; also see Bartolo and Merchant (2015)) in monkeys, beta power originating from the putamen may index temporal durations, such that bigger beta power coincides with longer durations between consecutive taps. Here we tested whether this effect extends to interval timing in humans in a reproduction paradigm while controlling for a number of potential artifacts and explicitly tested whether both pre-first-keypress and post-first-keypress beta power contribute to this effect. In line with the earlier results, we showed that trial-to-trial beta power positively correlates with the length of produced duration in a 2.5 s time production study, generalizing the original findings of Bartolo et al. (2014) by extending it to longer durations.

Thus, beta power at the onset of an interval is a reliable index of trial-to-trial fluctuations in produced duration, allowing us to predict how long the estimate of an interval will be about two seconds before participants actually end the production.

Of course, as participants had to initiate a time interval by pressing a key, the increase in beta power reflects a post movement synchronisation, which has been associated with a mechanism of active motor inhibition (Joundi et al., 2012, Pfurtscheller et al., 2003; Pogosyan et al., 2009; for a review see Kilavik et al. (2013) in the supplementary motor area and motor cortex (Jurkiewicz et al., 2006; Koelewijn et al., 2008). After this increase in inhibition at the interval onset, the process of recovery, expressed as a gradual desynchronisation of beta power, continues until the interval is terminated. However, the analyses reported here show that the intensity of the initial post-movement synchronization has a long lasting effect, as the estimated power of the synchronization determines when a response is given about two seconds later. Obviously, instead of the power after onset, these effects on estimated duration might also be caused by different desynchronization speeds, but the second keypress-locked data did not show any differences in the gradual beta desynchronisation. Thus, these results suggests that the length of the produced duration changes as a function of the amount of initial inhibition set at the trial onset, a finding supported by the interpretation that post-movement beta power indexes an amount of inhibition (Pfurtscheller et al., 2003) or balance between excitation and inhibition (Jensen et al., 2005; Kaminski et al., 2012). The notion that post-movement beta power at the trial onset is related to inhibition is supported by Parkinson studies. Praamstra and Pope (2007) described a reduction in post movement beta synchronisation in Parkinson patients who experience motor and perceptual timing difficulties, both caused by an aggravated dopaminergic system (Jahanshahi et al., 2010). Moreover, the hypothesis of motor inhibition for timing is congruent with observation that monkeys in the synchronization-continuations task time the pauses and not the kinematics of their movements (Donnet et al., 2012).

Apart from beta modulation at the interval onset, we also found that beta power as measured before the onset of the interval predicts the produced duration (cf., De Lange et al., 2013; Mazaheri et al., 2009). This suggests that a to be estimated duration is partly determined by the brain state before the interval initiation. Obviously, as participants could initiate the onset of trial, it might be that these tonic effects are partly based on participant-induced preparation effects. However, these results do add to the general notion that trial-to-trial fluctuation in the amount of beta power can influence timing behavior, presumably by pre-setting the level of inhibition or by affecting the starting point or other parameters of the decision process.

The data reported here were originally reported in a paper that focused on the role of the contingent negative variation (CNV) in time estimation. It has been proposed that the amplitude of the CNV reflects accrual of subjective temporal information (Macar et al., 1999; Wittman, 2013). However, recent empirical work has questioned this assumption (e.g., Kononowicz and Van Rijn, 2011, Van Rijn, 2014, Ng et al., 2011). In our earlier work (Kononowicz and Van Rijn, 2011), we did not find any evidence for a relation between the estimated duration and the CNV amplitude, but we did find habituation effects in the CNV – a finding at odds with an accumulation account. However, the reanalysis of this data set, together with the results of Bartolo et al. (2014), demonstrate that beta power at trial onset index timing performance, suggesting that timing mechanisms (e.g., motor inhibition) typically not considered in the theories of interval timing may be important in time production. Interestingly, recent work has linked the notion of inhibition, beta power, and dopamine level in the nigrostratal pathway, proposing that the dopamine level can be traced by beta power fluctuations (Jenkinson and Brown, 2011, also see Meyniel and Pessiglione, 2014). Within this framework, larger beta power is caused by a low level of dopamine: An increase in beta power is signaling the maintenance of a status quo in the sensorimotor system (Engel and Fries, 2010) whereas a decrease of beta power in the cortical-basal ganglia system increases the likelihood for a new action (Jenkinson and Brown, 2011). It also has been shown that dopamine impacts interval timing in humans (e.g., Rammsayer, 1997, 1999) and animals (e.g., Meck, 1986, 2006, also see Narayanan et al., 2012), and it has been argued that dopamine might play an indirect role in the built-up of temporal expectancies (Matthews et al., 2014). More specifically, it has been shown that the administration of dopamine agonizts speeds-up, and antagonists slows down, the internal passage of time (Meck, 1996). Since dopamine agonizts would result in reduced beta-band synchronization, and antagonists would result in increased beta-band synchronization, and thus in shorter and longer estimates, the framework proposed by Jenkinson and Brown (2011) is consistent with the effects of neuropharmacological manipulations on time estimation. However, as the time production task used in this experiment requires both the timing component and motor actions, it is difficult to dissociate both components, if that is at all possible given the interactions of the cognitive and motor circuits in the corticostriatal loop (Frank, 2011). For example, Coull et al., (2012) have shown that in a time estimation task dopamine modulates the nigrostriatal dopaminergic "motor" pathway including the putamen and SMA, even if the task is purely perceptual (also see Arnal and Giraud (2012), Fujioka et al. (2012), Teki (2014) for the role of beta power in predictive timing). In the light of these considerations, the observed beta power, evoked by activity in corticostriatal circuits, is likely caused by a process central to the estimation of time.

Alternatively, instead of describing time production as a release from a state of inhibition over time, one might also consider that the beta power indexes parameters of an evidence accumulation process that is underlying interval timing (e.g., Balci and Simen, 2014; Luzardo et al., 2011; Simen et al., 2013; Van Rijn et al., 2011). According to accumulation-to-bound models, a decision is reached by accrual of sensory evidence over time. Interestingly, beta band power has already been associated with a build up of activity reflecting integrated sensory evidence (e.g., Donner et al., 2009; Gould et al., 2012; Haegens et al., 2011; Tzagarakis et al.,2010; Wyard et al., 2012). The time it takes to reach a bound can be influenced by either the accumulation rate, by changes in the starting point, or by fluctuations in a decision threshold. However, as the beta power at the onset of the trial predicts duration, and the second keypress-locked data did not show any differences in the ramping beta desynchronization, these data align best with the suggestion that the beta power at the onset of a trial could influence the starting point of an accumulation process that has to decide on when to end the interval. Interestingly, the fact that only the initial beta power influences time production could suggest that interval termination is a ballistic process (Schurger et al., 2012; see also Taatgen et al. (2007), Van Rijn and Taatgen (2008), Taatgen and Van Rijn (2011), for similar explanations in terms of classical information processing models), where a parameter at the interval onset influences a cascade of neural events leading to the final outcome. Of course, this parameter could be linked to motor inhibition (Pfurtscheller et al., 2003) or to an initial urgency to respond (Cisek et al., 2009) that is going to increase over time and will serve as a multiplication factor for incoming evidence. Note that according to the urgency gating idea, ramping activity is not accumulating any kind of quantity, but is reflecting an increase in urgency (Boehm et al., 2015).

Theta power is assumed to play an important role in interval

timing (see, for example, Gu et al., 2015). It is therefore not unexpected to also find modulations in theta power at the interval onset (i.e., a negative correlation between theta power and time productions). Although the effect of theta power is opposite to the beta power effect, the observed effects are not contradicting the interpretations of beta power. For example, Cravo et al., 2011 did find that fronto-central theta power increases under conditions of larger motor preparation and temporal anticipation, regulated through the mechanism of cortical excitability (Cravo et al., 2011). Similarly, in time production tasks, bigger theta power could reflect an enhanced anticipatory state at the interval onset. Moreover, modulations of theta power have been associated with a reduction of response threshold (Cavanagh et al., 2011), but also with other features of drift diffusion models (Van Vugt et al., 2012), which aligns with the accumulation model-based interpretations of the beta power effects. Of course, the notion of excitability and cortical inhibition and response thresholds are closely intertwined and theta and beta power may index modulations of cortical inhibition or properties of diffusion process (Simen et al., 2011). Interestingly, Cravo et al. (2011), also see Arnal et al. (2014) found that the coupling between theta phase and beta power contributes to a mechanism controlling excitability levels according to temporal expectation, providing further support for the notion that theta and beta band power might be signatures of temporal performance. In addition, preliminary analyses also showed signatures of an effect in the gamma band, as in Bartolo et al. (2014). As pointed out by an anonymous reviewer (see also Oswal et al., (2013), these effects could be due to participants holding the button depressed for a longer period of time in the trials categorized as long. As gamma and beta power seem to index independent components (Muthukumaraswamy, 2014), it is unlikely that differences in the way the key was pressed are driving the result. As no information on the duration of the keypress was recorded, we have refrained from inferences on the basis of these effects, but future studies could measure the response duration or force to elucidate the role of gamma effects in interval timing.

The observed relationship between beta power, both before and after the keypress triggering the start of the trial, and the produced duration provides strong evidence in favor of the notion that the amount of beta power at the onset of a trial is an important marker for the duration of a subsequent time production, allowing us to predict at the onset of a trial when the participant will end that trial about two seconds in the future.

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