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Appearance and modulation of a reactive temporal-lobe 8–10-Hz tau-rhythm

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ABSTRACT

Spontaneous 8- to 10-Hz “tau-rhythm” in magnetoencephalographic (MEG) recordings has been reported to originate in the auditory cortex and be suppressed by sound. For unknown reasons however, tau-rhythm is often difficult to detect. In this study, we sought to characterize its emergence and auditory reactivity. Using a 306-channel MEG on 26 right-handed participants, we delivered six-second-long, natural, monaural sounds with pleasant, unpleasant, or neutral emotional valence. In eight participants, a clear, sound-related bilateral suppression of 8–10 Hz tau-rhythm occurred in the temporal areas, close to the source of the 100-ms auditory response. Moreover, these eight “tau subjects” exhibited significantly larger temporal-lobe theta-band (4–8 Hz) power over the entire experimental period compared to the remaining 18 “non-tau subjects”. As it is known that larger theta power is one of signs of drowsiness, this result is consistent with a previously proposed idea that tau-rhythm emerges during drowsiness. Tau-rhythm was furthermore significantly affected by emotional valence in the right hemisphere, where it was respectively suppressed by unpleasant and neutral sounds 8% and 6% more than by pleasant sounds, significantly. Altogether, our results reveal characteristics of tau-rhythm appearance and modulation which have hitherto been difficult to detect non-invasively.

Key words: rhythm; Magnetoencephalography; auditory response; emotion; drowsiness

1. Introduction

Spontaneous brain rhythms are classified according to their frequency band, a tradition set forth by Berger (Chatrian *et al.*, 1974; Buzsaki, 2006). For example, alpha-rhythm is defined as a large amplitude (below 50 μ V) 8–13 Hz rhythm, and is strongest in awake, calm participants with their eyes closed. Alpha-rhythm can be suppressed by visual stimuli, attention, and mental effort (Reviews: Palva and Palva, 2007, Klimesch 2012). Alpha-rhythm has furthermore been shown to originate in parieto-occipital brain regions (“parieto-occipital alpha-rhythm”) and to be modulated by numerous other endogenous brain activities as well (e.g., Hari & Salmelin, 1997). However, there are other brain rhythms in frequency bands similar to the alpha-rhythm which have different topographies and reactivities. Knowledge regarding the source location of these brain rhythms, and the mechanisms underlying their reactivities permits discrimination between them, thereby allowing identification of specific functions. For instance, mu-rhythm, originally described as 7–11 Hz activity seen over the central or centro-parietal regions, features a characteristic arch-shaped wave form with higher frequency components, and is modulated by contralateral movements and by intentions or readiness to move (Gastaut, 1952, Chatrian *et al.*, 1974).

Tau-rhythm is another rhythm that overlaps with the alpha band, albeit one that is mainly recorded by magnetoencephalography (MEG), which can isolate tau-rhythm from parieto-

occipital alpha rhythm via source localization. Tau-rhythm was first reported as a lower alpha band, 8–10 Hz, rhythm that is suppressed by brief auditory stimuli (1-kHz square wave with a 50-ms duration). It was furthermore localized to the auditory cortex, close to the source of the 100-ms auditory response, N100m. Tau-rhythm was also characterized as being insensitive to amplitude modulation due to opening or closing the eyes, and is thus functionally distinguishable from parieto-occipital alpha-rhythm (Tiihonen *et al.*, 1991).

Tau-rhythm was later reported by Lehtelä *et al.* (1997) to be predominant in the right hemisphere, and transiently suppressed by bursts of white noise. Inter-individual variation in tau-rhythm amplitude was also observed in this study, and referencing a sleep study by Lu *et al.*, (1992), was proposed to be caused by differences in vigilance. This observation has been supported by speculation that the parieto-occipital alpha-rhythm is suppressed during light drowsiness (Hari, 2010; Chang *et al.*, 2010), thereby facilitating the emergence of tau-rhythm.

With respect to the function of tau-rhythm, Bastiaansen *et al.* (2001) reported that anticipatory attention in a time estimation task suppressed the temporal lobe 8–10 Hz rhythm when pure tones were utilized as cues. Increased 5–12 Hz rhythm in bilateral temporal regions during retention of a working memory task was found by van Dijk *et al.* (2010), who proposed it to be tau-rhythm, and suggested that it plays a functional role similar to that of the parieto-occipital alpha-rhythm by being involved in allocation of resources in auditory areas. In a

spatial attention experiment, Weisz *et al.* (2011) reported that a tone with 42 Hz amplitude modulation presented to the right ear suppressed 10–12 Hz rhythm in the left superior temporal gyrus. Based on sensor-level signal topography and source location, they argued that this suppression was tau-rhythm, and not an epiphenomenon of visual cortex alpha-rhythm suppression. They further suggested that tau-rhythm is modulated by visual spatial attention and that spatial targets can be distinguished by monitoring tau-rhythm modulation. Further support on the existence of sound-suppressed 10-Hz rhythm in the voxels of primary auditory cortices (based on Automated Anatomical Labeling) has recently been provided by Keitel *et al.* (2016) who used continuous narrated stories as auditory stimuli.

Collectively, these studies support the existence of tau-rhythm as a unique rhythm that is distinct from parieto-occipital alpha rhythm, and one which exhibits particular sensitivity to auditory stimuli. Incidentally, parieto-occipital alpha rhythm has been reported to be modulated by auditory stimuli in accordance with their emotional valence (Onoda *et al.*, 2007; Başar *et al.*, 2012; Uusberg *et al.*, 2013; Weinreich *et al.*, 2016). Considering tau-rhythm's reported sensitivity to auditory stimuli, it seems likely that tau-rhythm would also be sensitive to the emotional valence of the auditory stimuli. Indeed, it is even conceivable that the results from the aforementioned reports regarding parieto-occipital alpha rhythm were influenced by tau-rhythm modulation. However, due to the difficulty in distinguishing tau-rhythm from parieto-occipital

alpha rhythm, reports regarding it remain sparse, and characterization of its responsiveness to emotional auditory stimuli remains unclarified.

One possible reason for tau-rhythm's elusiveness in MEG may be due to differences in subject brain structure. As is well known, MEG is sensitive to neuronal equivalent currents that are directed tangential to the scalp surface. Therefore, the amplitude of tau-rhythm can range several fold depending on the current direction of the source. Alternatively, tau-rhythm may be masked by other stronger rhythms such as parieto-occipital alpha-rhythm. As mentioned earlier, parieto-occipital alpha-rhythm has been speculated to decrease in times of drowsiness. Thus, variability in subject status (i.e. level of drowsiness) may affect the degree to which tau-rhythm is masked by parieto-occipital alpha-rhythm. If so, then clarifying the level of drowsiness within subjects via a known index may be important for identifying those subjects in which tau-rhythm is measurable. One candidate that has been proposed as an index of drowsiness is, temporal theta-rhythm (Maynard & Hughes, 1984; Hughes, 2001, Chang, 2010), which can be measured and compared between subjects in the manner discussed by Lehtelä *et al.* (1997).

With the present study we thus identified subjects with distinguishable tau-rhythm using MEG while taking into consideration the characteristics of parieto-occipital alpha-rhythm and temporal theta-rhythm (as an index of drowsiness). After identifying subjects with distinguishable tau-rhythm, we furthermore investigated whether tau-rhythm modulated

according to the emotional valence of auditory stimuli. The results provide further MEG evidence regarding reactive temporal tau-rhythm and its functional characteristics in endogenous brain activity.

2. Materials and methods

2. 1. Subjects

This study targeted 29 healthy subjects, three of whom were excluded: two due to excessive eye blinking, and one due to questionable source location for the N100m auditory response. Thus, the final analysis comprised data from 26 subjects (14 females, 12 males; mean $\pm$ SD age, 28.6 ± 6.6 yrs; age range, 21–47 yrs; all right-handed), data from 15 of whom was collected and presented in a previous study regarding slow evoked responses to emotional sounds (Yokosawa, *et al.*, 2013). Written informed consent was obtained from each subject prior to the MEG experiments, which were approved by the Ethics Committee of the Hospital District of Helsinki and Uusimaa.

2. 2. Stimuli

The stimuli and their presentation were as previously described (Yokosawa, *et al.*, 2013). Briefly, we selected eight “pleasant & low arousal sounds” (P sounds; e.g., music, birdsong,

etc.), eight “neutral sounds” (N sounds; e.g., typewriter, wind, etc.), and eight “unpleasant & high arousal sounds” (U sounds; e.g., scream, car crash, etc.) from the International Affective Digitized Sounds database (2nd Edition; IADS-2, University of Florida) to use as auditory stimuli. Each stimulus was modified to have a duration of 6 s and onset/offset envelopes no shorter than 10 ms. The stimuli were also all normalized to have uniform maximum sound pressure. A 100 ms cue-tone with a 10 ms onset/offset envelope was presented 2 s before each stimuli, at pitches of 500 Hz, 1 kHz, or 2 kHz, corresponding to stimuli of a particular valence (P/N/U). Cue pitch assignment was counterbalanced across subjects. The time from cue onset until stimulus onset (0–2 s) was referred to as the anticipation period. The time from stimulus onset until the end of the epoch (2–8 s) was referred to as the listening period. The interval between epochs was 12 s. All auditory cues and stimuli were presented via a flat panel loudspeaker (Panphonics Oy, Finland) located in front of the subject in the magnetically shielded room..

The experiment was divided into two approximately 20 min sessions, each comprising 20 P, N, and U cue-stimuli presented in random order, for a total of 40 epochs per stimulus valence type per subject. Each session also included one to six oddball epochs comprising a 40-ms burst of white noise at an arbitrary time point of the cue-stimulus epoch. The subjects’ task was to count the number of oddball epochs in each session and report the total number to the

experimenter upon completion of the experiment. The oddball epochs were excluded from the analyses.

Before the main experiment, the participants took part in a 6-min training session to learn the relationship between the cue-tones and the valence of the upcoming emotional auditory stimulus. For further details regarding the stimuli, Pleasure-Arousal scales, sound contents, sound pressure envelopes, and experimental procedures, please see our previous report (Yokosawa, *et al.*, 2013).

2. 3. Recordings

MEG signals were recorded with a 306-channel whole-scalp neuromagnetometer (VectorView™, Elekta Neuromag Oy, Helsinki, Finland) at the MEG Core, Aalto NeuroImaging, Aalto University, Espoo, Finland. The passband was from DC to 200 Hz, and the signals were sampled at 600 Hz. Additionally, an electro-oculogram (EOG) was recorded to monitor eyeblinks. Of the MEG signals recorded, those from 102 pairs of orthogonally oriented planar gradiometers were used in our analyses.

2. 4. Analysis

Prior to the analyses, the MEG signals obtained in the two sessions were concatenated off-line after conversion of the data into the same reference head position using Maxfilter software. Epochs in which MEG or EOG signals exceeded threshold values were presumed to contain

excessive ambient noise, or eye blink artifacts, and were excluded from the analysis. Because MEG signal and noise strength differed depending on individual subjects and ambient conditions, rejection thresholds ranged from 200–500 fT/cm, and were determined on an individual basis via visual inspection of raw data.

Subjects with tau-rhythm

We first investigated whether tau-rhythm was discernable in each subject. Tau-rhythm can be characterized by amplitude suppression during sound presentation, and by its source proximity to the N100m response location. Therefore, in each subject we first inspected sensor-level topographical maps of 8–10-Hz rhythmic activity during the test sounds. We then subsequently identified the sensor locations that were most sensitive to the N100m response for the cue-tone onset. Subjects whose 8–10 Hz rhythmic activity overlapped with the sensor locations for their cue-tone onset N100m response were deemed to exhibit tau-rhythm. The detailed procedure for this analysis was as follows.

All raw signals recorded by each of the 102 pairs of gradiometers were averaged over all epochs for each stimulus valence type. Then, the sensors with the largest cue-tone onset N100m responses were identified in each hemisphere of each subject and labelled, “N100m sensitive sensors”.

The raw MEG signals of the 102 pairs of gradiometers were band-pass filtered at 8–10 Hz, and activity envelopes extracted via Hilbert transform. The envelopes, which represent the time courses of tau-rhythm amplitude, were averaged across all epochs for each stimulus valence type. Next, the root-mean-squares of the envelopes of the gradiometer pairs were calculated, and an average envelope calculated for each pair. The resulting 8–10 Hz activity envelopes were averaged over two time windows: 3–8 s (within the listening period); and a one second period between epochs, typically from 10–11 s in which the activity sufficiently recovered (hereafter, silent period). Using the difference in 8–10 Hz activity between the listening period and the silent period at each sensor, scalp topographies of each subject were made. The sensors with the strongest 8–10 Hz activity modulation were labelled, “tau-rhythm sensitive sensors”. The subjects in whom “tau-rhythm sensitive sensors” overlapped with “N100m sensitive sensors” were considered “tau subjects”.

Modulation by emotional valence

The 8–10 Hz activity envelopes obtained from the N100m sensitive sensors were statistically analyzed in tau subjects. The envelopes were averaged separately across epochs for each stimulus valence type (P/N/U), and averaged over the anticipation period (0.2–2 s) and the listening period (2.2–8 s). Note that the first 200 ms of each period were purposely excluded due to the presence of strong transient responses. The mean activity for the two time windows

was normalized by mean activity over the time from -1–0 s prior to cue-tone presentation (hereafter, baseline period). The normalized activity was compared in each hemisphere in each time period separately by one-way repeated-measures analysis of variance (ANOVA), with valence type as the main factor and tau-rhythm activity as the dependent variable. In the case of a significant main effect, post-hoc pairwise comparisons were conducted using Bonferroni's correction. The statistical significance threshold was set at $p < 0.05$.

Evaluation of possible alpha-rhythm contamination

Parieto-occipital alpha rhythm is usually much larger in amplitude than tau-rhythm and could potentially have contaminated the 8–10 Hz signals detected by N100m sensitive sensors in the temporal-lobe regions. To evaluate possible alpha-rhythm contamination in each of the tau subjects, the characteristics of the parieto-occipital alpha-rhythm at the sensor most sensitive to the alpha-rhythm in the parieto-occipital region was investigated in a manner similar to that for the tau-rhythm.

First, the raw signals from the 102 gradiometer pairs for each of the tau subjects were fourier-transformed (FFT) in successive 6.8 s time windows with 3.4 s overlaps, and then averaged across the time windows in the frequency domain. From this, the frequency within the alpha-rhythm band (8–13 Hz) with the highest spectral density in each subject was identified. Next, the root-mean-squares of the FFT spectral densities from each gradiometer pair were calculated

and averaged together for each tau subject separately. These results were furthermore filtered within subjects within a 2 Hz band centered on the subject's peak alpha-rhythm frequency. Based on these data, the posterior-occipital sensor with the highest spectral density was identified and labelled as the, "alpha-sensitive sensor".

Finally, using methodology identical to that used for calculating tau-band envelopes, the activity envelope in the alpha-rhythm band was calculated for each subject at the alpha-sensitive sensor. Then the modulation of alpha activity at the alpha-sensitive sensors by auditory stimuli and their emotional valence was investigated identically to the method described for tau activity in the section, "Modulation by emotional valence." We considered a lack of overlap in the pattern of activity between alpha and tau-rhythms for each valence type as a sign that parieto-occipital alpha-rhythm had not contaminated temporal tau-rhythm.

Effect of drowsiness

As an index of drowsiness, the level of temporal theta rhythm was computed for each participant. First, the MEG signals recorded by the 102 gradiometer pairs in each subject were Fourier-transformed. Then, mean amplitude within the theta band (4–8 Hz) was calculated from the frequency distributions. Subsequently, the mean amplitude was averaged over 13 homologous sensor units in each hemisphere over temporal regions. Since the theta spectral densities were not always normally distributed, Mann Whitney's U test (IBM SPSS Statistics

20) was performed to compare the spectral density of the theta-band over the course of the experiment between tau subjects and non-tau subjects. The statistical significance threshold was set at $p < 0.05$.

3. Results

Subjects with tau-rhythm

Figure 1 (upper panel) shows oscillations recorded in seven successive epochs (-1 to 11 s) from a temporal sensor in a single subject (corresponding to that shown in the bottom left corner in Fig. 2) that were filtered at the tau-band from 8 to 10 Hz. These traces reveal that even at the single epoch level, tau-band amplitude is suppressed in response to auditory stimuli (i.e. during the listening period). In the same subject, the mean envelope of tau-band activity across all 120 epochs is shown for each gradiometer pair in the lower panel of Fig. 1, with the mean across all sensors represented by the thick black line. Suppression of tau-band activity is apparent soon after the cue-tone, and continues throughout the listening period (2 to 8 s).

Figure 2 shows the tau-band topographical maps calculated for eight subjects that met our criteria for identification as tau-sensitive subjects. As the maps reveal for each of these subjects, tau suppression was largest bilaterally in temporal areas that encompassed the N100m sensitive sensors. The tau subjects consisted of 3 females and 5 males (mean $\pm$ SD age, 27.6 ± 9.0 yrs). The remaining subjects (hereafter non-tau subjects) consisted of 11 females and 7 males (mean

$\pm$ SD age, 29.0 ± 5.4 yrs). There were no significant differences between tau and non-tau subjects with respect to sex or age.

Modulation by emotional valence

Figure 3 shows the mean time courses of the baseline-normalized tau-envelopes for each valence type for the left and right hemisphere (a and b, respectively) in tau subjects. Suppression of tau activity is clearly apparent bilaterally for all valence types after cue-tone presentation and throughout the listening period. The one-way ANOVAs comparing baseline-normalized tau activity between valence types in each hemisphere in each time period (see Figure 4) revealed that there was a main effect of category only in the right hemisphere in the listening period ($p = 0.004$, $F = 8.235$, effect size: $\eta^2 = 0.137$), and post-hoc pairwise comparisons using Bonferroni's correction showed that sounds with neutral or unpleasant valence suppressed tau activity significantly more than those with a pleasant valence ($p = 0.009$ and 0.05 , respectively). No main effects were observed in either hemisphere in the anticipation period, nor in the left hemisphere in the listening period.

Evaluation of possible alpha-rhythm contamination

The position of the parieto-occipital alpha-sensitive sensor for each tau subject is marked by a blue circle on the topographical maps shown in Fig. 2. In two subjects the parieto-occipital

alpha-sensitive sensor was not the most but rather the second most sensitive to alpha-rhythm. These sensors are denoted by the dotted blue circles. The mean time courses for the baseline-normalized alpha-band envelopes based on the alpha-sensitive sensors for each valence type are shown in Figure 3. Suppression of alpha activity was observed after cue-tone onset but not during the listening period, a pattern of activity that contrasted with the time courses of tau-rhythms. Results from one-way ANOVAs revealed no significant main effect of valence type during either the anticipation period nor listening period.

Effect of drowsiness

The mean amplitude of the theta-band over the course of the experiment was 21% larger for tau subjects ($n = 8$) than for non-tau subjects ($n = 16$) (Mann Whitney's U test: $p=0.026$, effect size: $r = 0.44$).

4. Discussion

We studied the reactivity of magnetoencephalographic 8–10-Hz tau brain rhythms to brief non-emotional cue-tones and to subsequent long-duration auditory stimuli that had either neutral, pleasant or unpleasant emotional valence. Tiihonen *et al.* (1991) reported that 8–10 Hz tau-rhythm is suppressed by auditory stimuli and that the sources are located close to N100m sources. Using these features of tau-rhythm as selection criteria, we focused our analyses on

eight tau-rhythm subjects who exhibited bilateral suppression of 8–10-Hz activity over temporal areas during presentation of the auditory stimuli (Figs. 1, 2), with the greatest tau-rhythm suppression occurring in the vicinity of the N100m sensitive sensors. Importantly, although the sources of the tau-rhythm were not expressly calculated, the fact that the MEG signals were recorded by gradiometers strongly implies that the sources of the suppressed 8–10 Hz rhythm were located in direct vicinity to the sensors at which the suppressed rhythm was recorded.

In contrast to tau-rhythms, parieto-occipital alpha-rhythms were not suppressed during presentation of the auditory stimuli (2–8 s in Fig. 3 (c)). These results demonstrate that tau-modulation is not an epiphenomenon of parieto-occipital alpha-rhythm (i.e. that parieto-occipital alpha-rhythm did not contaminate tau-rhythm. Both tau-rhythm and parieto-occipital alpha-rhythm were suppressed by the cue-tones (Fig. 3 (a) – (c)), and remained suppressed for up to two seconds, much longer than the cue-tone duration of 0.1 s. However, the suppression of parieto-occipital alpha-rhythm was comparatively not as sharp, and we suspect was caused more by anticipation of the upcoming test sounds.

Our results furthermore revealed that tau-rhythm is suppressed by auditory stimuli in accordance with their emotional valence (P/U/N; Fig. 4), with suppression strongest against unpleasant sounds, especially in the right hemisphere. There are two possible explanations for this laterality. One explanation is based on the “right hemispheric hypothesis”. This hypothesis

assumes right-hemisphere dominance for processing emotions, regardless of emotional valence. It was reported, for instance, that emotional prosodies more strongly activated the right auditory association area than the left area (Ethofer *et al.*, 2006). The other explanation is based on the right-hemispheric dominance of tau-rhythm reported by Lehtelä *et al.* (1997). They reported that tau-rhythm in the right hemisphere had a larger amplitude in the absence of sound, and was suppressed more during auditory stimulation than tau-rhythm in the left hemisphere. However, in our study, a significant difference between amplitudes of tau-rhythm in the right and left hemispheres was not observed in either the baseline period nor in listening period. Since no other previous works have shown right-hemispheric dominance of tau-rhythm, we think that the right hemispheric hypothesis regarding emotional processing is the more likely explanation for the right-hemispheric difference observed according to emotional valence during the listening period in the present study. Meanwhile, although no significant difference between emotional valence types was observed during the anticipation period, our previous work suggested that early processing of emotion can occur during this period (Yokosawa, *et al.*, 2013). We therefore suspect that emotional processing was likewise occurring during the anticipation period of the present study. Further study with a larger sample size could perhaps reveal these subtle effects.

Tau subjects comprised only a third of the total number of subjects in the present study. It has been suggested that tau-rhythm can emerge during drowsiness (Lu *et al.*, 1992). To investigate

this idea, we measured temporal theta-rhythm (an index of drowsiness) in all subjects, and found that it was significantly larger in the tau subjects than in the non-tau subjects. Larger theta-rhythm is associated with increased drowsiness (Maynard & Hughes, 1984; Hughes, 2001, Chang, 2010) and therefore our results suggest that the tau subjects were drowsy during the experiment. Our results thus imply that a certain level of drowsiness is needed for proper detection of tau-rhythm. Correspondingly, it may be important for future studies examining the reactivity of tau-rhythm to auditory stimuli to consider the circadian rhythms of subjects, and correspondingly control the timing of the experiments.

One limitation of this work is that real sounds, e.g., music, wind and voice, were utilized as auditory stimuli in the experiment. They may be inefficient for suppressing tau-rhythm compared to offensive sounds that were used in previous works, e.g., square waves (Tiihonen *et al.*, 1991) or noise bursts (Lehtelä *et al.*, 1997). Moreover, real sounds have individual acoustic properties (e.g., temporal profiles or frequency structures) which may modulate tau-rhythm in different ways. As such, real sounds might induce comparatively more complex cognitive reactions, thereby obscuring the simple reactivity of tau-rhythm. Apart from drowsiness, this could also have contributed to the fact that suppression of tau-rhythm was observed only in one third of the participants. Another limitation of this work is that it could not determine whether tau-rhythm reacted directly or indirectly emotional processing. For instance, the stronger tau-

rhythm suppression for unpleasant sounds may have been due to stronger attention towards the content of the unpleasant sound (Fig. 4). If so, the suppression following the cue-tone (0–2 s in Fig. 3 (a) and (b)), which lasted until stimulus onset, may also have been caused by attention towards the upcoming test sounds, not by slow recovery time.

Overall, our results are in line with the idea proposed by Lu *et al.* (1992) that tau-rhythm emerges during drowsiness. The obtained tau-rhythm originated in the temporal lobes, close to the N100m sources, and the amplitude was modulated depending on the emotional valence of the stimuli. If tau-rhythm has auditory functionality similar to that of alpha-rhythm in visual perception processing, then reliable non-invasive detection of tau-rhythm is desirable for investigating endogenous brain reactivity to sound. Moreover, akin to the manner alpha-rhythm is used in the visual domain, it may also be possible to use tau-rhythm in future investigations of memory or cognitive impairment. To investigate such higher functions of tau-rhythm further, some methods to control subject drowsiness and enhance tau-rhythm modulation are desired.

5. Conclusion

“Tau-rhythm”, a characteristic spontaneous brain rhythm that is suppressed by auditory stimuli, was detectable in the temporal brain regions of one third of tested subjects, likely due to drowsiness. Our results indicate that the amplitude of tau-rhythm can be modulated by endogenous brain activity, e.g., emotion, and furthermore reveal the characteristics of its

appearance and modulation which have hitherto been difficult to detect non-invasively.

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Contributors

KY elaborated the study design, participated to the whole research, and prepared the manuscript and figures. YM participated to the experiment and contributed to the analysis. HS contributed to the analysis. All authors have read and approved the final version of the manuscript.

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Conflict of interest

The authors have no conflicts of interest to declare.

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FIGURE CAPTIONS

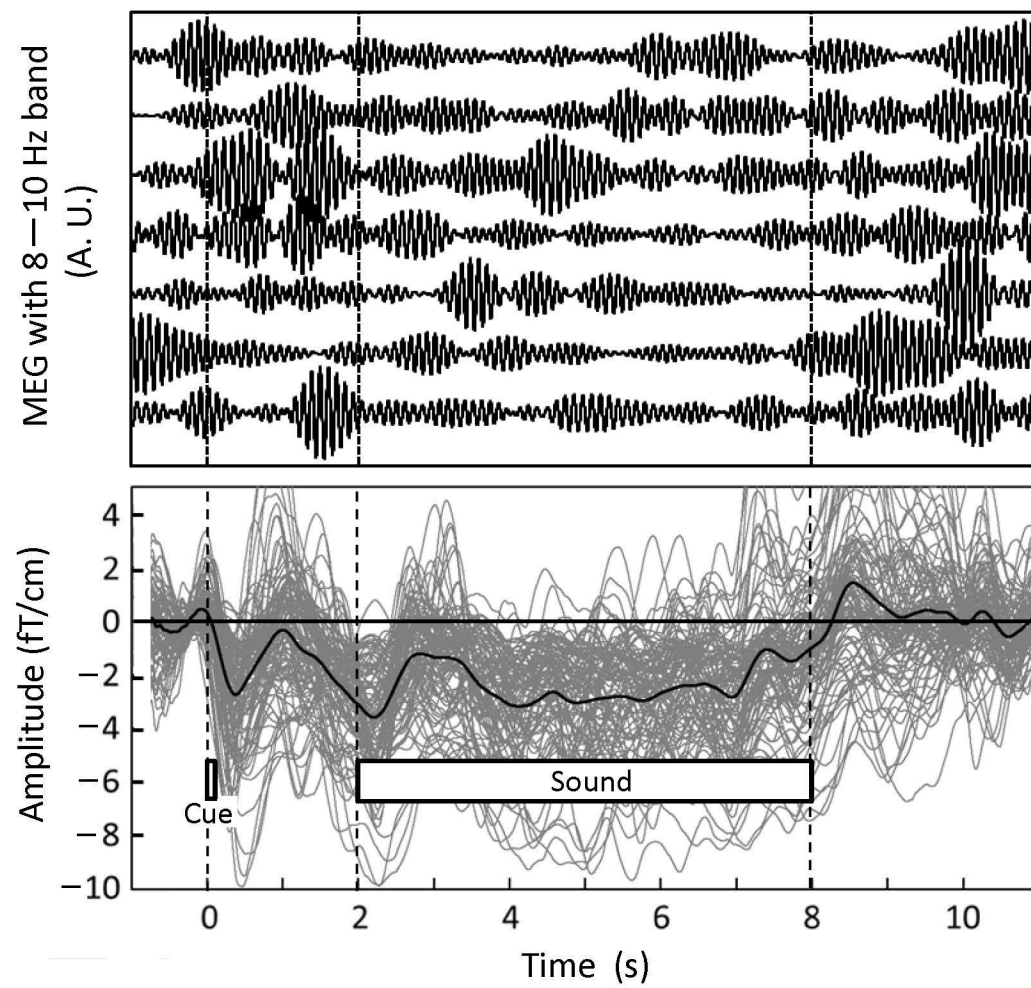
Figure 1. Suppression of 8–10 Hz band rhythm during the presentation auditory stimuli. (Upper column) Several epochs of non-averaged MEG signals recorded by the left N100m sensitive sensor of a subject and filtered with an 8–10 Hz band. (Lower column) Amplitude of 8–10 Hz rhythm averaged over responses to all epochs recorded in the same subject. Butterfly plot of responses at all 102 sensor positions (gray lines) and their average (black line) as deviations from the averaged amplitude within 10–11 s are shown. The deviations demonstrate event-related suppression in response to the auditory stimuli.

Figure 2. Contour maps of amplitude modulation obtained by the vector-sum of orthogonal gradiometers. Blue lines indicate amplitude suppression in response to auditory stimuli (3–8 s) compared to silence. The eight tau subjects showed clear event-related suppression around bilateral temporal regions when hearing test sounds, with greatest suppression occurring near the most N100m sensitive sensors. Red circles denote the N100m sensitive sensors used in our analyses. Blue circles denote sensors that were most sensitive to alpha-rhythm located in the parieto-occipital region.

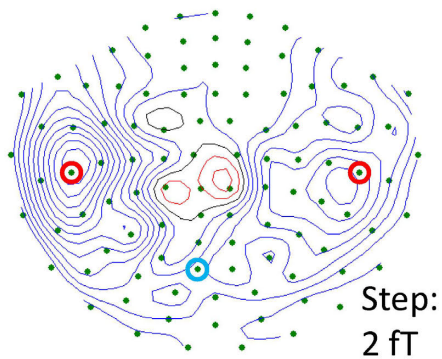
Figure 3. Amplitude modulation of rhythms in response to auditory stimuli according to their emotional valence type (P/N/U). The 8–10 Hz rhythms were recorded by the most

N100m sensitive sensors located in temporal regions of the eight tau subjects (see Fig. 2) (Left: (a) and Right: (b)); the 8–13 Hz rhythm were recorded by the most sensitive sensors to parieto-occipital alpha-rhythm (c). All amplitudes were normalized by the averaged values within $-1-0$ s. Event-related suppression during the listening period (2–8 s) is evident only for tau-rhythm in (a) and (b).

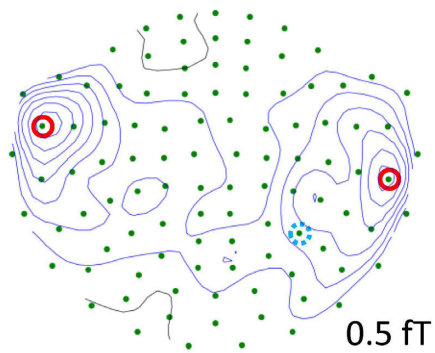
Figure 4. Group level analysis of amplitude modulations of 8–10 Hz rhythm according to the emotional valence of the auditory stimuli. There was a significant main effect of emotional valence in the right hemisphere as per ANOVA ($p=0.004$), with post-hoc comparisons (Bonferroni corrected) further revealing significant differences of $P > U$ ($p = 0.05$) and $P > N$ ($p = 0.009$) ($n=8$, error bar: S.D.).



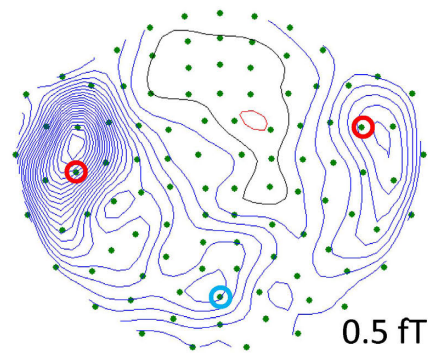
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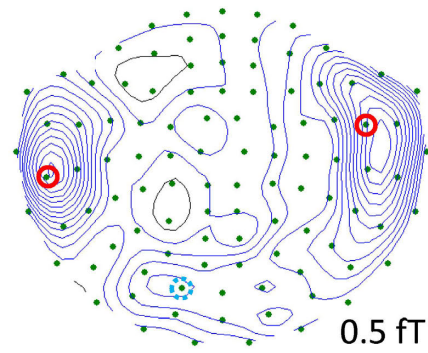
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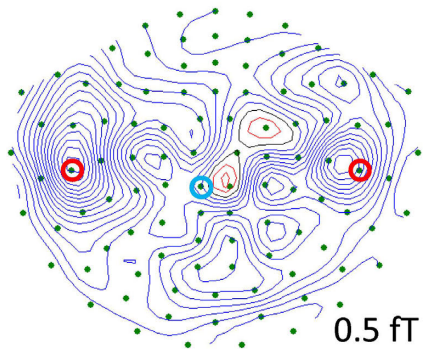
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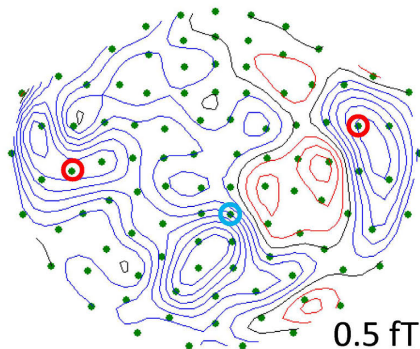
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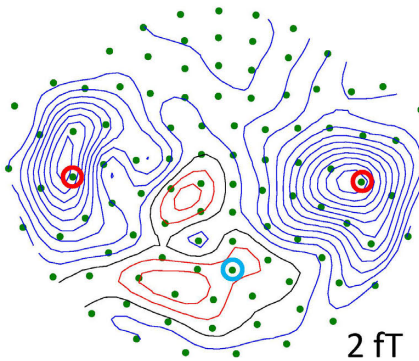
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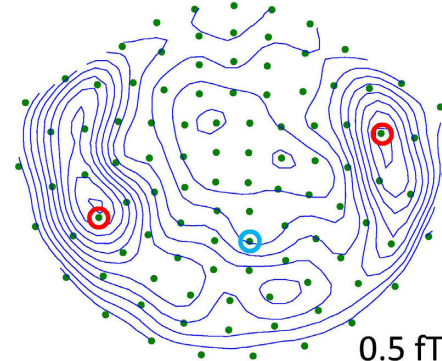
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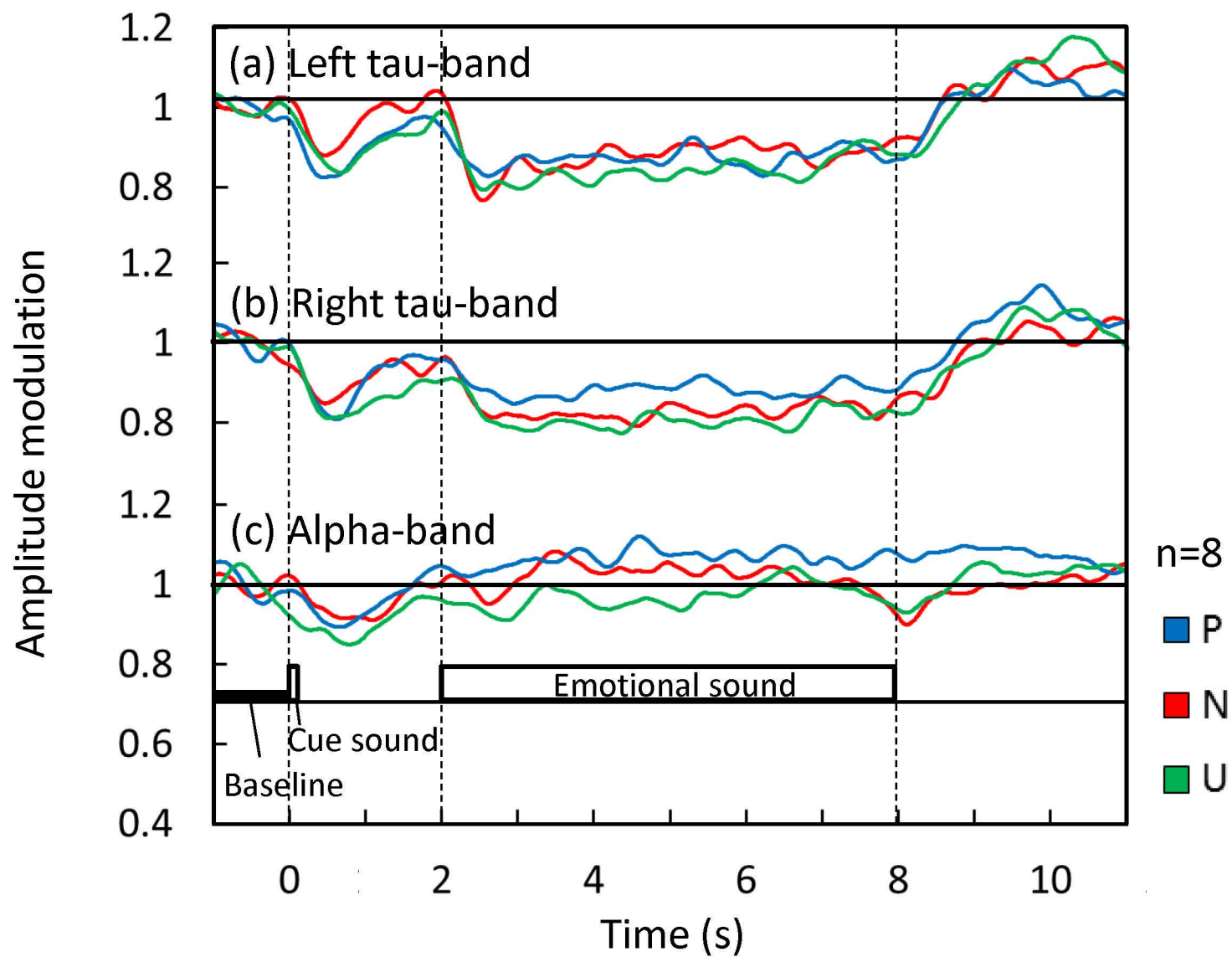


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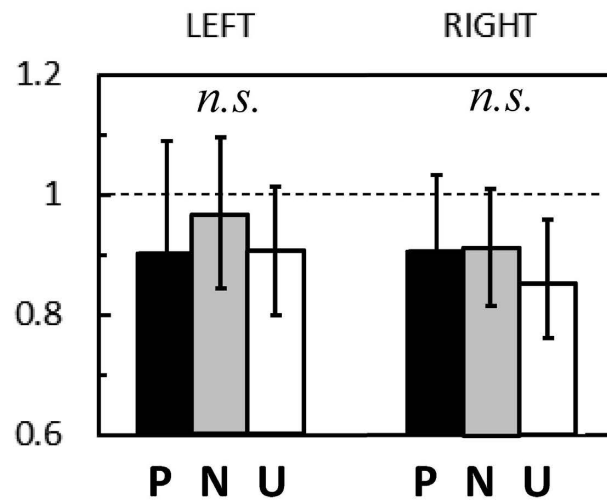


Sub. 8





Anticipation (0.2—2.0 s)



Hearing (2.2—8.0 s)

