

Laboratory report

Graduate School of Neural & Behavioural Science
Eberhard Karls Universität Tübingen

The Effect of Theta-Oscillation-Phase on Top-Down & Bottom-Up Attention

Laboratory report

presented by

Tamara Keßler

The study was supervised by

Jan Weber, M.Sc.

Isabel Raposo, M.Sc.

Dr. Dr. Randolph Helfrich

Department for Human Intracranial Cognitive Neurophysiology / Hertie Institute for Clinical Brain Research

Duration of the lab rotation: 29.11.2021 – 18.02.2022

Deadline for submission: 14.03.2022

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Abstract

Contrary to our subjective perception, attention is rhythmically sampled and modulated by oscillatory brain activity, such as theta waves. However, it has not been studied yet if different types of attention, such as bottom-up and top-down attention, exhibit differences in phase-behaviour-dependency. The present project analyses human intracranial EEG data to investigate this topic in a Pop-Out/Search task. While we found robust differences between Pop-Out and Search in their high-gamma activity time course, we were unable to find a significant effect of response time modulation by theta phase. Thus, the role of phase-behaviour-dependency in attention still remains unclear. Future studies might want to take other frequencies ranges into account, or perform analyses on the single-electrode- as well as group-level.

1. Introduction

[William James \(1980\)](#) famously claimed that “Everyone knows what attention is”. It is generally agreed upon that there are (at least) two types of attention: Endogenous “top-down” attention, which can be allocated volitionally, and exogenous “bottom-up” attention, which is automatically captured by external stimuli.

In 2002, [Corbetta and Shulman](#) first introduced the notion of two distinct attentional networks comprising frontal and parietal cortices. They proposed the dorsal attentional network (DAN) to mediate top-down selection of stimuli, while the ventral attentional network (VAN) mediates the bottom-up detection of (unexpected) behaviourally relevant stimuli (see also [Buschmann & Miller, 2007](#); [Vossel, Geng & Fink, 2014](#)). Both of these systems complement each other and are crucial for everyday human behaviour and cognitive processes, such as visual search. Visual search may either require a serial allocation of attention to all potential targets, which is also referred to as “(Inefficient) Search” – or it may be facilitated by the automatic attentional capture of a single salient item, which is also referred to as “efficient search” or “Pop-Out”. Thus, Pop-Out is a type of bottom-up attention, whereas Search would be an example of top-down attention.

In the paradigm that is classically used to investigate differences between Pop-Out and Search, participants are presented with a target stimulus that they are supposed to remember during a retention interval, before trying to find it again in a group of distractors. During Search, the target is not salient, as it only differs from the distractors in one stimulus dimension (i.e., orientation), which is why the remembered target must be compared to every presented item in a serial manner. As a result of that, response times (RTs) scale with the number of distractors. During Pop-Out, however, the target is highly salient as it differs from the distractors in two stimulus dimensions (i.e., orientation and colour) and thus, automatically draws attention to itself without the need to compare the remembered target to every presented item in a serial manner. Consequently, the RTs during Pop-Out are independent of the number of distractors ([Buschmann & Miller, 2007](#); [Slama et al., 2021](#); [Treisman & Gelade, 1980](#); [Ossandón et al., 2012](#)).

Numerous studies have shown that frontal cortex is preferentially employed during inefficient search, while Pop-Out engages parietal cortex and other selective regions across frontal cortex (i.e., lateral frontal cortex, frontal eye fields (FEF), orbitofrontal cortex (OFC)) (see e.g.: [Buschman & Miller, 2007](#); [Li et al., 2010](#); [Slama et al., 2021](#); [Ossandón et al., 2012](#)).

Further, [Buschman and Miller \(2007\)](#) established that bottom-up and top-down attention rely on synchronising neural activity between frontal and parietal areas – however, these two modes of attention prioritise synchrony at different frequency bands. Top-down attention exhibits increased synchrony in lower frequency bands, which may aid integration of information based on long-range coupling between distant areas, whereas bottom-up attention is characterised by increased synchrony in higher frequencies, which may play a role in enhancing stimulus

representations ([Engel, Fries & Singer, 2001](#); [Fries, 2005](#); [Ito, Hearne & Cole, 2020](#)). It should be noted that [Buschman and Miller \(2007\)](#) only took frequency bands in the range of 10 to 80 Hz into consideration and claimed that frequencies below 10 Hz were not meaningful in their paradigm due to their relatively short time epochs. However, several recent studies have provided evidence that dynamics in the theta-band (3 – 8 Hz) play an essential role in mediating top-down attention ([Dugué, Marque & VanRullen, 2015](#); [Fiebelkorn, Saalman & Kastner, 2013](#)). More specifically, it has been shown that behaviour (i.e., the ability to utilise top-down information) fluctuates as a function of theta phase ([Helfrich et al., 2018 & 2019](#); [Fiebelkorn, Pinsk & Kastner, 2018](#)).

Based on this, the current project analyses behavioural, as well as intracranial EEG data during a Pop-Out/Search paradigm to investigate two main research questions in an exploratory manner:

- 1) Is there a dependency between the phase of the theta oscillation and the overt behaviour (i.e., reaction time) during the response phase?
- 2) Are the differences in the phase-behaviour-dependency when comparing the top-down and bottom-up attentional processes underlying Inefficient Search and Pop-Out, respectively?

It should be noted that due to the time constraints posed by the duration of the laboratory rotation, as well as due to the “rare” nature of the intracranial EEG data, I did not collect any data myself for this project, but re-analysed a subset of an already existing data set (see [Slama et al., 2021](#) for the original study using the full data set). Due to the fact, that we re-analyse a part of the data described in [Slama et al. \(2021\)](#), we expect to reproduce the behavioural findings they described, while our neurophysiological analyses will address a different research question.

2. Materials & Methods

2.1. Participants

This study reanalysed data of a subset of 8 participants from the 22 participants enrolled in [Slama et al.'s \(2021\)](#) study. All participants were pharmaco-resistant epilepsy patients, who were undergoing treatment at the University of California Irvine Medical Center, USA, at the time of the study. The study procedures were approved by the hospital's institutional review board, as well as the Committee for the Protection of Human Subjects at the University of California, Berkeley. All participants had normal or corrected-to-normal vision and no known deficits in visual or colour perception. Each participant gave their written consent prior to study inclusion. Placement of the intracranial electrodes was solely determined by clinical needs.

2.2. Experimental Procedure

Each trial lasts for 4 seconds. Initially, a fixation cross is presented for 500 ms. The target is presented for 1,000 ms, which is followed by a brief delay period 500 ms, during which the target must be retained in working memory. Thereafter, the response phase starts, in which the subject must find the target among a group of distractors during a maximum time window of 2,000 ms. The differences between conditions (Pop-Out vs. Search) were only present during this response phase and were only realised in the colour of the distractors (see [Fig. 1](#)).

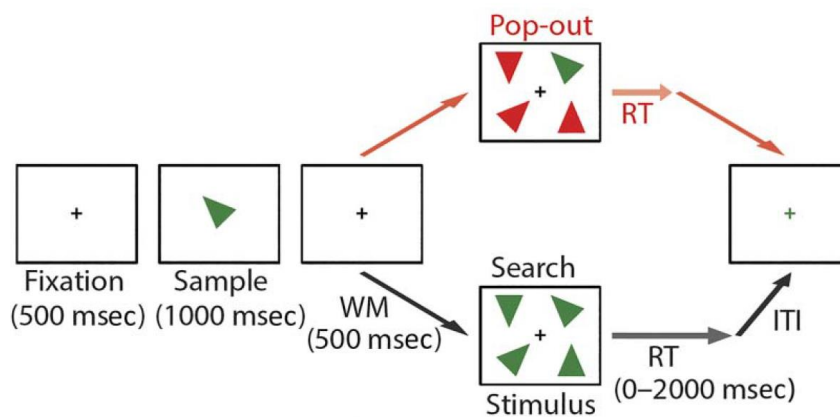


Figure 1: Visualisation of the Pop-Out/Search Task; Adapted from [Slama et al. \(2021\)](#)

2.3. Data Acquisition, Pre-Processing & Data Analysis

Data were recorded at the UC Irvine Medical Center using a Nihon Kohden digital acquisition system with a 128/256-channel amplifier at a digitization rate of 1000/5000 Hz. The sEEG electrodes were manufactured by Integra Life Sciences. The diameter of the electrode contacts was 0.9 mm with an interelectrode distance of 5.0 mm.

The data provided to us were already cleaned and had their anatomy reconstructed based on pre- and post-operative MRI and CT scans (see [Slama et al., 2021](#)). Our further pre-processing and data analyses were done using custom MATLAB scripts (R2021a 64bit, MathWorks) utilising the FieldTrip toolbox ([Oostenveld et al., 2011](#)).

Firstly, we resampled the data from 5000 Hz to 500 Hz, before extracting anatomical labels for every electrode based on the [Brainnetome atlas](#). Following that, high-frequency band activity (70 – 150 Hz; in short: HFA) was extracted and a bootstrapped z-scored baseline correction approach was performed. Further, invalid trials were defined and removed. We considered trials, in which no response was given, or whose associated RT was classified as extreme outlier (RT < 5th percentile or > 95th percentile) to be invalid. Lastly, we defined task-active and -inactive electrodes following the approach outlined by [Helfrich et al. \(2018\)](#).

Following the analysis of the behavioural data described by [Slama et al. \(2011\)](#), we computed one-sample t-tests to test the two behavioural measures, RT and accuracy, for condition differences. For the electrophysiological data, we used a permutation approach based on the Kullback-Leibler divergence for significance testing. For the behavioural analyses, we used data from all electrodes, while for the electrophysiological analyses, we focused on the data from task-active electrodes.

3. Results

3.1. Behavioural Data

Participants showed higher accuracy ($t(7) = 4.0922$, $p = 0.0046$) and faster response times ($t(7) = -9.3381$, $p < 0.0001$) during the Pop-Out condition than during Search (Fig. 2).

In the Pop-Out condition, the mean accuracy was 96.63% with a standard deviation of 3.89%. The mean RT (of the participants' median RTs) was 693.1 ms with a standard deviation of 198.6 ms. In the Search condition, the mean accuracy was 84.66% with a standard deviation of 10.03%. Here, the mean RT was 947.1 ms with a standard deviation of 192.3 ms.

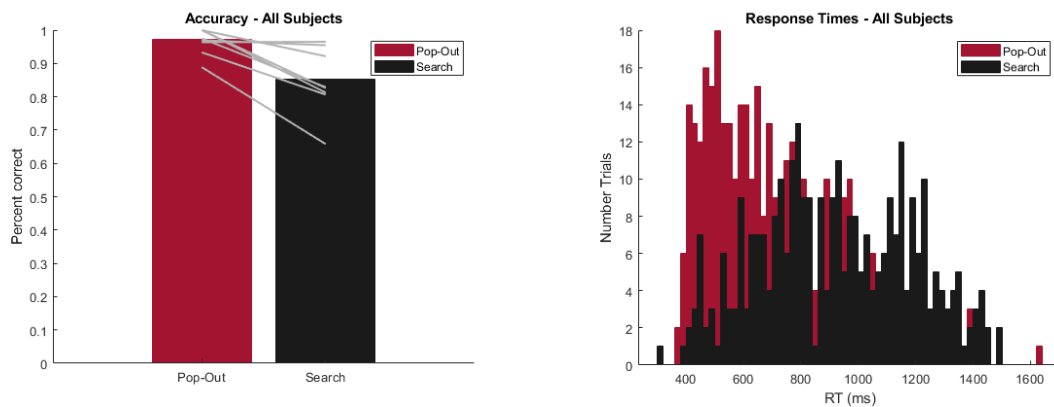


Figure 2: Accuracy and Response Times for the Pop-Out (red) and Search (black) conditions

Left: Ratio of correct responses across the 8 included participants. Performance of the individual participants are indicated by the grey lines.

Right: RT histograms from all correct trials for all 8 participants.

These findings are generally in line with the results by [Slama et al. \(2021\)](#), who reported mean accuracies of 96% (SD = 3.9%) for Pop-Out and 86.8% (SD = 9.6%) for Search ($t(22) = 4.73$, $p < 0.001$) and mean RTs (of the participants' median RTs) of 680.2 ms (SD = 146.5 ms) for Pop-Out and 964.8 ms (SD = 152.2ms) for Search ($t(22) = -14.06$, $p < 0.001$), respectively (Fig. 3).

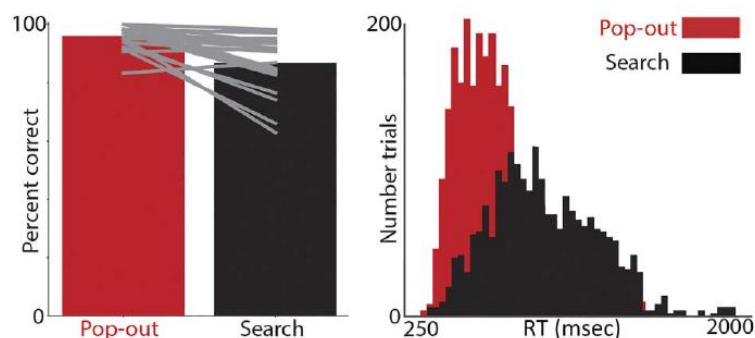


Figure 3: Accuracy and RTs for the Pop-Out (red) and Search (black) conditions; Adapted from [Slama et al. \(2021\)](#)

Left: Ratio of correct responses across the 23 included participants. Performance of the individual participants are indicated by the grey lines.

Right: RT histograms from all correct trials for all 23 participants.

3.2. Neurophysiological Results

The definition of task-active electrodes yielded a total of $N = 213$ active electrodes, while the remaining 386 electrodes were classified as task-inactive (see Fig. 4; for numbers on the single subject level, see Table S1).

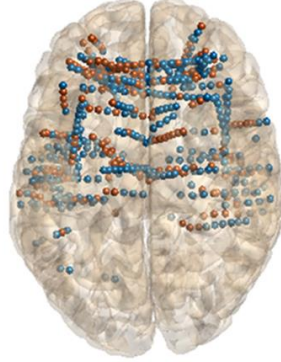


Figure 4: Spatial distribution of all subjects' task-active (orange; $N = 213$) and -inactive (blue; $N = 386$) electrodes across the brain ($N(\text{all}) = 599$)

The visual inspection of the task-active electrodes' high-gamma activity grand average revealed condition differences in the HFA time course. While the HFA levels stay comparable throughout the sample and delay phase, there are robust differences during the response phase: While the high-gamma activity during Pop-Out trials can be described as phasic (i.e., it both increases and decreases quickly), the activity stays at an elevated level for much longer during Search trials (see Fig. 5).

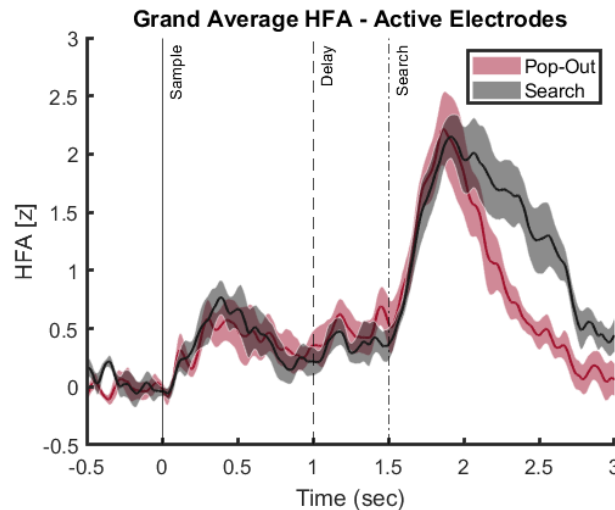


Figure 5: Task-active electrodes' grand average of HFA, contrasting Pop-Out (red) and Visual Search (black) conditions

The analysis of the dependency between theta phase and behaviour yielded significant results at some of the task-active electrodes. For example, in case of subject IR44 one of their nine active electrodes exhibited significant modulations effects of RT through theta phase ($p = 0.003$).

Here, we found two types of modulation effects: Firstly, a significant reduction in mean RT around the $+\frac{1}{2}\pi$ phase of the theta oscillation and secondly, a significant increase in mean RT around the $-\frac{1}{2}\pi$ phase. More specifically, the detected reduction effects were strongest for a frequency of 4 Hz, while the augmentation effects peaked at 7 Hz (see Fig. 6).

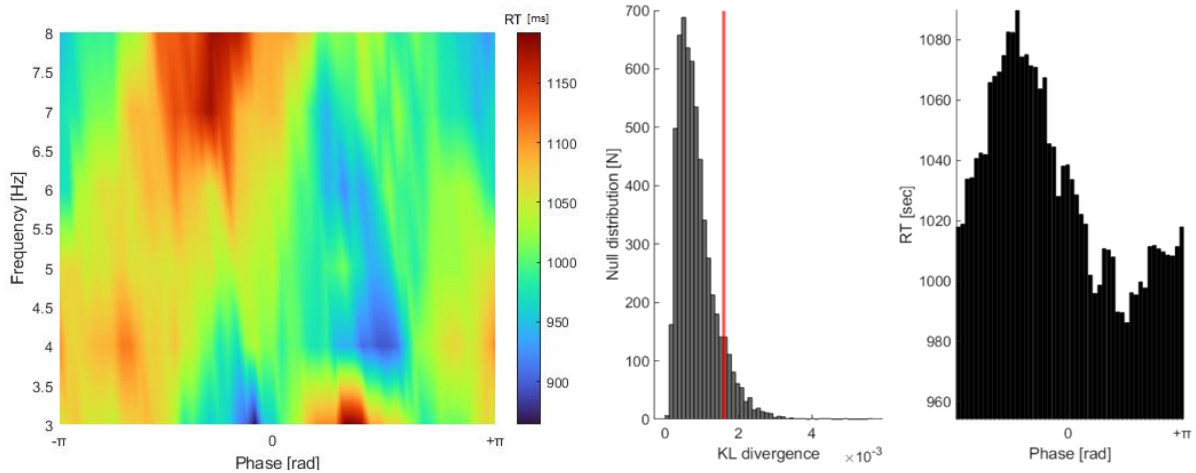


Figure 6: Phase-Behaviour-Dependency between Theta Oscillation and RT for subject IR44, electrode ROF7

Left: Phase-RT-dependency across the Theta frequency range (3 – 8 Hz)

Right: Phase-RT-dependency averaged over Theta range & its Kullback-Leibler divergence (red) plotted against surrogate distribution

Here it must be noted that while we did find significant modulation effects of theta phase on RT at the single electrode level, for the majority of task-active electrodes results remained insignificant: Across all subjects, only 15 out of the 213 total active electrodes yielded significant results ($p < 0.05$; see supplementary table S2). The overall median of z-normalised Kullback-Leibler divergence scores was below 0 for every frequency, further visualising the insignificant results (see Fig. 7).

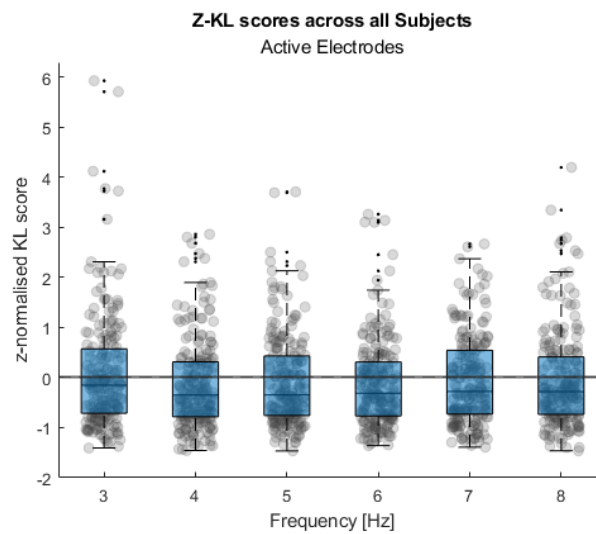


Figure 7: z-normalised Kullback-Leibler divergence as a function of frequency for every task-active electrode across subjects

Lastly, we computed the percentage of RT variance that was explained by theta phase. On average, theta activity measured at task-active electrodes could account for 5.42% of RT average, while at task-inactive electrodes 4.51% of the behavioural variance were accounted for. In contrast to that, the permutation distribution explained 0.13% of RT variance (see supplementary [table S3](#) for values on the single-subject level).

4. Discussion

The present project investigated behavioural and electrophysiological differences in bottom-up and top-attention in a Pop-Out/Search paradigm and examined if a phase-behaviour-dependency existed between the phase of the theta oscillation and response times.

We were able to robustly reproduce the behavioural findings described by [Slama et al. \(2021\)](#) of significantly reduced RTs and increased accuracy for Pop-Out trials, compared to Search trials. However, we were unable to find a significant phase-behaviour-dependency effect for the theta range on a larger scale.

We detected condition differences in the HFA time course. After peaking during the response phase, the high gamma activity during the Pop-Out condition falls quickly back to its baseline level, while the activity during the Search condition stays at an elevated level for longer. This is in line with the longer RTs we found for Search compared to Pop-Out. Further, it has been established that HFA scales proportionally with RT and that HFA can be interpreted as a proxy of cognitive engagement in task processing (see e.g., [Lachaux et al., 2012](#)). Therefore, the extended period of increased HFA levels during Search may reflect the increased cognitive resources needed to retain the target item in working memory and comparing it in a serial manner to all presented items.

Previous studies have shown that coupling of HFA amplitude and theta phase could be used to reliably predict response times on a trial-by-trial basis ([Voytek et al., 2015](#); [Parvizi & Kastner, 2018](#)). This, in conjunction with studies establishing the rhythmic nature of the neural mechanisms underlying sustained attention and their modulation by theta phase ([Fiebelkorn, Pinsk & Kastner, 2018](#); [Helfrich et al., 2018](#)), led us to expect to find a similar phase-behaviour-dependency in our paradigm.

While we found a modulation effect of RT by theta phase for a few single electrodes across our participants, the majority of task-active electrodes showed no significant effect (15 significant / 213 total task-active electrodes). We believe that this lack of significant effect sizes may either be due to the statistical approach we chose or due to differences in the attentional mechanisms involved in the paradigms of our project and previous studies.

On the one hand, [Helfrich et al. \(2018\)](#), for example, employed an Egly-Driver task in their study to investigate the effect of theta phase on stimulus detection rates. This type of task is typically used to study visual attention and it relies only to a very limited

extend on sustained working memory. On the other hand, while our Pop-Out/Search task is also based on visual attention, it also requires a sustained working memory representation of the target – especially during the serial comparison of all presented items in the Search condition. It is conceivable that these different attentional mechanisms underlying the two paradigms, may be the basis for the lack of phase-behaviour-dependency in our paradigm. It seems possible that there is some underlying phase-behaviour-dependency in this paradigm – but maybe in another frequency range (e.g.: in the delta-range, see [Helfrich et al., \(2017\)\)](#).

Further, it should be mentioned that some of the significant effects described by [Helfrich et al. \(2018\)](#) only arose at the group-level, while the results at the single-electrode-level only showed small trends. Therefore, it seems plausible that we may have missed some larger scale significant effects in our data due to us not conducting any group-level analyses.

Another factor that may have resulted in us overlooking potential effects, is the sparse spatial sampling of intracranial EEG. Since electrode placement is dictated by individual clinical needs, electrode locations differ between subjects and there is no global coverage of the whole brain ([Parvizi & Kastner, 2018](#)). Thus, it is possible that there may be localised clusters that exhibit significant modulation effects, which we could not detect because our sample might have lacked (a sufficient number of) electrodes in these locations.

To conclude, the role of theta-phase-behaviour-dependency in attention is still unclear. While previous studies have found convincing evidence for a modulation of attention by theta phase, our project did not find similar effects on a larger scale. However, it is possible that these effects still exist, but that our analyses or data were not able to pick up on them.

Acknowledgements

Throughout the duration of my laboratory rotation, I have received a great deal of support and academic guidance.

First and foremost, I would like to thank my primary supervisors, Jan Weber and Isabel Raposo. Without their assistance, knowledge, enthusiasm, and dedicated involvement in every step throughout the process, this project would have never been accomplished.

Secondly, I wish to express my gratitude to my senior supervisor, Dr. Dr. Randolph Helfrich, for providing the data and his expertise, which was invaluable in deepening my own understanding of approaches to data analysis and electrophysiology.

Further, I would like to thank my colleagues Dr. Frank van Schalkwijk, Dr. Michael Hahn, Dr. Janna Lendner and Markus Kopf for welcoming me in the lab, all the stimulating discussions and valuable input during our lunch breaks, lab dinner nights and team meetings.

Lastly, I would also like to extend my special thanks to my friend Hannah Terborg (Aalto University, Finland) for providing me with valuable feedback on my written report.

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Appendix: Supplementary Tables

	IR39	IR41	IR43	IR44	IR57	IR63	IR66	IR72
Active / All Elecs	9 / 60	44 / 83	21 / 81	9 / 41	37 / 93	28 / 59	23 / 67	42 / 115

Table S1: Number of task-active electrodes in ratio to number of all electrodes per subject

	IR39	IR41	IR43	IR44	IR57	IR63	IR66	IR72
Sig. elecs / Active elecs	0 / 9	3 / 44	2 / 21	1 / 9	1 / 37	2 / 28	3 / 23	3 / 42

Table S2: Number of significant electrodes in ratio to subject's total number of active electrode ($\alpha = 0.05$); Calculated via permutation approach

	IR39	IR41	IR43	IR44	IR57	IR63	IR66	IR72
Active	8.13%	3.09%	6.83%	6.71%	3.79%	4.60%	5.46%	4.77%
Inactive	4.36%	4.17%	4.44%	4.04%	3.30%	8.32%	3.89%	3.57%
Perm.	0.10%	0.09%	0.22%	0.12%	0.06%	0.29%	0.09%	0.09%

Table S3: Percentage of RT variance explained by theta phase for every subject; Calculated for task-active and -inactive electrodes, as well as for the permutation distribution