

# **A dissociable functional relevance of theta and beta band activity during complex sensorimotor integration**

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## **Abstract**

Sensorimotor integration processes play a central role in daily life and require that different sources of sensory information become integrated. That is, the information related to the object being under control of the agent (i.e., indicator), and the information about the goal of acting. Yet, how this is accomplished on a neurophysiological level is contentious. We focus on the role of theta/beta-band activity and examine which neuroanatomical structures are involved. Healthy participants (N=41) performed three consecutive pursuit tracking EEG experiments in which the source of visual information available for tracking was varied (i.e., that of the indicator and the goal of acting). The initial specification of indicator dynamics is determined through beta band activity in parietal cortices. When information about the goal was not accessible, but operating the indicator was required nevertheless, this incurred increased theta-band activity in the superior frontal cortex signaling a higher need for control. Later, theta and beta-band activity encode distinct sources of information within the ventral processing stream: theta-band activity is affected by the indicator information, while beta-band activity is affected by the information about the action goal. Complex sensorimotor integration is realized through a cascade of theta and beta-band activity in a ventral-stream-parieto-frontal network.

Keywords: sensorimotor integration, cognitive control, theta, beta, parietal cortex, frontal cortex

## **Introduction**

Sensorimotor integration processes play a central role in daily life behavior. Already children's games such as the "Hot Wire" provide impressive testimonials of the complexity of sensorimotor integration processes. From a scientific perspective, the "Hot Wire" game reflects a pursuit tracking task used in cognitive science to study complex sensorimotor control (Pew 1974; Wulf and Schmidt 1997; Hill and Raab 2005; Sekiya 2006; Hill 2009, 2014; Broeker, Ewolds, et al. 2020; Broeker, Haeger, et al. 2020; Parker et al. 2020). In pursuit tracking tasks, an "indicator" (cursor to be operated by a mouse or joystick) must be moved across a trajectory (path), which determines the complexity to operate the indicator. Cognitive mechanisms underlying pursuit tracking processes have been framed by different theories such as the perceptual control theory (PCT; Powers, 1973) according to which motor control is a product of the control of sensory input via negative feedback loops (Marken et al. 2013). The input is compared to a reference variable that is set endogenously and the motor output is adjusted accordingly (Parker et al. 2020). Principles of these concepts are also included in computational accounts on sensorimotor integration (Körding and Wolpert 2004; Franklin and Wolpert 2011) and how such processes contribute to aspects of cognitive control and intentions to act (Christensen and Bicknell 2022). While research on pursuit tracking has a long tradition in cognitive science, and has the advantage of providing continuous data of participants during sensorimotor integration (e.g., Hill and Raab 2005; Raab et al. 2013; Wulf and Schmidt 1997), it has not been much in neuroscience research.

Within cognitive neuroscience, evidence suggests that the intra-parietal sulcus (IPS), the dorsal premotor cortex (PMd) (including regions in the middle frontal gyrus; MFG) and superior-frontal gyrus/sulcus (SFG/SFS) are activated in movement execution (e.g. pointing and coordinated hand–finger movements) using visual input (Filimon et al. 2009; Battaglia-Mayer et al. 2016; Battaglia-Mayer and Caminiti 2019). The relevance of the dorsal frontoparietal network (dFPN) has also been stressed in newer accounts conceptualizing the inter-relation of

feed-forward and feed-backward processes in sensorimotor control in mentioned functional neuroanatomical structures (Ptak et al. 2017). Despite considering forward and backward looping processes in the dFPN, the temporal neural dynamics in connection to functional neuroanatomical structures is not well understood. The perceptual input imposes temporal constraints on motor control and thus on feed-forward and feed-backward mechanisms (Marken et al. 2013). During pursuit tracking there are at least two sources of perceptual information necessary to integrate with motor processes in feedforward or feedback loops: (i) the information being conveyed by the indicator and (ii) the information of the trajectory (path) determining the complexity to operate the indicator. Yet, how these different sources of information map on neurophysiological processes involved in complex intentional sensorimotor integration is unknown. In the current study, we systematically vary the accessibility of information related to the indicator and the trajectory in three consecutive experiments (see methods section): Compared to a baseline task in which indicator and trajectory information were fully accessible (basic paradigm, task 1), we varied the accessibility of the indicator information (estimated-indicator-paradigm, task 2) and the accessibility of the trajectory information (estimated-path-paradigm, task 3) to obtain a fine-grained picture about the neural processes underlying complex sensorimotor integration in experimentally well-controllable conditions.

We used EEG methods for a conceptually meaningful examination of oscillatory activity during sensorimotor integration processes and how changes in the accessibility of indicator and trajectory information modulated oscillatory activity subserving complex sensorimotor integration. Neural oscillatory activity at different frequencies reflects a fundamental principle of information processing in the brain (Varela et al. 2001; Buzsáki et al. 2013) and is also of relevance when it comes to the question of how sensorimotor information is integrated (Engel and Singer 2001; Singer 2011; Beste et al. 2023). Regarding neural oscillatory activity, especially theta and beta band activity have been considered in complex sensorimotor

integration processes (Herrmann et al. 2016; Singh et al. 2020). During pursuit tracking, the trajectory specifies upcoming and potentially varying demands on sensorimotor integration while the agent operates the indicator. Beta band activity has been associated with top-down processing (Fries 2015) possibly reflecting attention to upcoming motor demands (Saleh et al. 2010; Seki and Fetz 2012; Fetz 2013; Khanna and Carmena 2015; Wendiggensen, Adelhöfer, et al. 2022) and may also reflect pre-motor mechanisms guiding motor actions (MacKay 1997) or maintenance of motor representations defining how sensory information has to be mapped onto motor processes (Engel and Fries 2010; Studer et al. 2014; Womelsdorf and Everling 2015; Wendiggensen, Adelhöfer, et al. 2022). It follows that beta band activity can be brought into connection with processes referring to demands imposed on an agent while integrating sensory and motor information a task (e.g., operating the indicator). From that perspective, it is possible that beta band activity is modulated during pursuit tracking, and that variations in the accessibility of information about the trajectory path as well as the indicator modulate beta band activity. Opposed to the trajectory, the indicator is under the direct control of the agent. The agent must control the indicator and to minimize the distance between the position of the indicator and the trajectory. Demands on control capacities of an agent have frequently been associated with theta band activity (Cavanagh and Frank 2014; Cohen 2014; Beste et al. 2023). Prominent conceptions on the role of theta band activity during cognitive control suggest that especially medial frontal theta band activity encodes a surprise signal (Cavanagh and Frank 2014) indicating the need to engage in cognitive control. While the source of this surprise is still a matter of debate (Beste et al. 2023), the conceptual core of this account on theta band activity has relevance in the context of pursuit tracking and operating the indicator. Depending on the accessibility of information about the indicator, it is harder or easier for the agent to operate the indicator: that is, there is more or less need to engage in cognitive control. It follows that whenever information about the indicator is manipulated, there should be modulations of theta band activity. However, computations relevant for feed-forward and feed-back loops not

only depend on the accessibility of the indicator, but also of the target trajectory and theta band activity is also relevant for attentional selection processes (Vanrullen and Dubois 2011; Landau and Fries 2012; Fiebelkorn et al. 2013; Helfrich et al. 2018). Therefore, also theta band activity should be affected by modulations of the indicator as well as the target trajectory during complex sensorimotor integration processes since both aspects carry meaningful information to be grasped by attentional mechanisms. If there are differences in how the accessibility of information related to the path or indicator modulates theta and beta band activity, this would suggest that there are dissociable roles of these frequency bands during complex sensorimotor integration processes as suggested by recent accounts (Beste et al. 2023). New conceptual accounts also bring alpha-band activity into the picture in this regard, since it has been associated with stimulus information and task-demands (Beste et al. 2023). Alpha-band activity potentially reflects controlled access to a domain-general knowledge system (Klimesch 2012) and thus might play a role in the decoding of task demands in complex sensorimotor integration processes.

To investigate neural oscillatory activity at different frequencies associated with complex sensorimotor integration, we perform time-frequency decomposition on the EEG data for our three paradigms and investigate power modulations in the alpha, beta and theta band. To broaden the scope of our work for a larger neuroscientific community, we also analyze the functional neuroanatomical structures associated with these modulations. Therefore, we perform EEG-beamforming (Gross et al. 2001) as this method offers a possibility to investigate the neuronal sources of observed power modulations. EEG-beamforming is a well-implemented and established method in the field (Adelhöfer and Beste 2020; Prochnow et al. 2022; Wendiggensen, Adelhöfer, et al. 2022; Wendiggensen, Ghin, et al. 2022).

As mentioned above, fronto-parietal networks have been implied in complex sensorimotor integration processes. Consequently, we assume that activity modulations of theta and beta band activity are associated with these structures when contrasting the different experimental

variations in the study. However, since features of the visual information are central for movement execution, and it is known that processes in the ventral visual stream contribute to response selection and motor control processes (Kühn et al. 2011; Yu et al. 2022; Eggert et al. 2023) also that pathway likely shows modulations in activity. This is also likely because the ventral visual processing pathway subserves object-centered recognition (Goodale and Milner 1992; Chao and Martin 1999; Goodale et al. 2005; Ayzenberg and Behrmann 2023), which is varied in the experiments (i.e. the accessibility of indicator and trajectory information). Not at least findings that the dorsal visual pathway subserves action control (Gallivan and Goodale 2018) suggest that modulations in the main visual processing pathways may be underlying the dynamics induced in the current study's experiments.

## **Materials and Methods**

### *Participants*

A sample of 41 healthy young adult participants (28 females) between 18 and 30 years of age was recruited for this study (mean age =  $25.56 \pm 2.99$  years). Previous studies using a continuous pursuit-tracking paradigm in an EEG setup showed reliable effects with smaller samples or samples of comparable size (Hill 2009, 2014). Therefore, we assume the study to be sufficiently powered. All participants had normal or corrected-to-normal vision and were free of any medication. The participants provided written informed consent before any of the study procedures was commenced and received a compensation of 30 Euros. The study was approved by the IRB of the TU Dresden (EK 390082019).

### *Tasks*

Participants completed three variations of the manual tracking task in which the participants were asked to track the trajectory of a line shown on 24 inches display (1920 x 1080 pixels and a refresh rate of 60 Hz) using a joystick (Thrustmaster T16000M). The experiment was

programmed using PsychoPy2 (Peirce et al. 2019) and the task has been validated previously (Böttcher et al. 2023). In all versions of the task, the tracking trajectory was built by a concatenation of two sine and cosine terms, respectively and as described before (Böttcher et al. 2023).

$$f(x) = \sum_{i=1}^3 a_i \cdot \sin(i \cdot x) + b_i \cdot \cos(i \cdot x)$$

For the first segment of the trajectory (i.e., random trajectory segment), coefficients  $a$  and  $b$  were randomly generated numbers between -1 and 1 to ensure the trajectory stretches precisely to the top or the bottom of the screen. The second segment, i.e., constant trajectory segment, was kept constant across all trials and participants, with values for  $a$  and  $b$ :  $a_1 = 0.23$ ,  $a_2 = -0.01$ ,  $a_3 = -0.81$  and  $b_1 = 0.44$ ,  $b_2 = -0.33$ ,  $b_3 = -0.05$ . During the experiment, a red filled circle (i.e., target indicating the trajectory, 48 pixels diameter/1.44° visual angle) moved across the screen. The participant's viewing distance was 60cm. The target's velocity was kept constant along the trajectory path. Participants controlled a crosshair (i.e., indicator/cursor) of equal size as the target and were instructed to keep the indicator on the target as best as possible. The participants were able to control the indicator's vertical and horizontal movement. Joystick deflection resulted in proportional movement of the indicator on the screen, i.e., maximum joystick deflection moved the indicator to the screen's edge and no deflection moved it to the screen center. The target always started from the center of the screen and then randomly moved to either the left or right edge of the screen at one out of three possible velocities. The direction of target movement and velocities was counterbalanced. Overall, there were 54 trials in the first two tasks and 60 trials in the third task, which lead to a task duration of about 20 minutes. The respective trial duration was dependent on the length of the random trajectory segment and ranged approximately around 10 s. To minimize preparatory effects the time interval between the trials varied randomly (mean = 1.5 seconds). A 30-second pause was available every 25



trials. No feedback on tracking performance was provided to the participants. Before starting the respective task, six practice trials were performed by the participants.

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Insert Figure 1 about here  
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In the basic paradigm (task 1) participants were instructed to track the fully visible target on the trajectory path with the visible indicator/cursor using the joystick (see Figure 1A).

In a first variation of the task, the estimated-indicator-paradigm (task 2), the trials started with a visible indicator and a visible target moving on the random trajectory. After start of the constant trajectory segment, at a randomly chosen time point from 0-30 % of the segment, the indicator was occluded for 2 seconds, resulting in only the target moving along the trajectory being visible. Participants were instructed to follow the visible target also when the indicator was invisible. All other aspects (e.g. trial number) were identical to the basic task (i.e. task 1).

In a second variation of the task, the estimated-path-paradigm (task 3), it was not the cursor, but the target moving on the trajectory which was occluded. This resulted in only the indicator being visible, with no visible target moving along the trajectory. Participants were asked to follow the trajectory also when there was no visible target moving along it. The occlusion always started at the first frame of the constant trajectory and also here, the target moving on the trajectory was visible at the beginning of each trial (see Figure 1C). To facilitate the tracking without a visible trajectory indicator (i.e., target), every 10<sup>th</sup> trial was a ‘maintenance’ trial which was identical to trials in the basic paradigm (i.e., indicator/cursor and trajectory/target were visible throughout the trial). The overall trial number for task 3 was therefore 60 trials, including 54 variation trials and 6 maintenance trials. The order of task 1 and 2 was counterbalanced across subjects. Task 3 was always performed after the first two tasks, to give participants experience following the visible target on the trajectory before having to follow the trajectory without visible target in task 3.

### *Estimation of tracking performance*

Tracking performance was calculated as mean Euclidian distance between target and indicator across all frames per trial, resulting in one distance value per trial. Trials with a mean tracking performance of three standard deviations above or under the mean per subject were labeled as outliers and excluded from the analysis of behavioral and the EEG data.

### *EEG recordings and pre-processing*

The EEG data were continuously recorded with a sampling frequency of 500 Hz using Brain Products Inc. amplifiers and 60 equidistantly positioned Ag-AgCl electrodes with a reference electrode placed at position Fpz. During the recording it was ensured that electrode impedances were below 10 k $\Omega$ . Offline EEG pre-processing was performed in EEGLab (Delorme and Makeig 2004). We used an automated processing pipeline to ensure that the data from the different experiments were processed with the same standards. After FIR high-pass filtering at 0.5 Hz, line noise at 50 Hz was filtered using the *pop\_cleanline* plugin for EEGLab. Then, flat channels (i.e. channels with at least 5 seconds of flat line) and channels with a channel correlation of less than 0.85 were removed and a low-pass filter (Hamming windowed FIR filter) at 40 Hz was applied. Discarded bad channels were interpolated afterwards using a spherical method. For the subsequent independent component analysis (ICA, infomax algorithm), the EEG data of all three experiments were concatenated and detrended. Moreover, artefacts were removed using a joint probability method (as implemented in *pop\_jointprob*; (Delorme and Makeig 2004)). By means of the "IClabel algorithm" all ICs not reflecting brain activity were identified. Components not reflecting brain activity with at least 50% probability were then discarded. The topographies of the first five remaining components were then checked visually, and artifactual components were excluded. All remaining components were applied to the data of each task respectively and the EEG was reconstructed through back-

projection of the IC data. Subsequently, the EEG data were parallelized with the behavioural data of each task version. That is, only trials were used for the EEG data analysis that were also included in the behavioral data analysis. For each task version, the data was then segmented according to the different conditions in the tasks taking the entire trial length into account (i.e., 13 seconds). For task 1 (basic paradigm), we divided the data into random and constant trajectory segments, each three seconds long. For task 2 (estimated-indicator-paradigm), we segmented the data into occluded and non-occluded parts, each two seconds long. For task 3 (estimated-path-paradigm), we segmented the data into occluded and non-occluded parts, each three seconds long. Only the constant segment for task 1, and the “occluded segments” for task 2 and 3 were used for the further analysis. Another artifact rejection step was applied in the segmented data using a joint probability method (Delorme and Makeig 2004) thus yielding the single-trial data used for the further analyses steps.

#### *Time-frequency decomposition and beamforming*

For each task version, the time-frequency analysis was performed on the single-trial data in the Fieldtrip Toolbox (Oostenveld et al. 2011). Before applying Morlet wavelets for the time frequency analysis, a baseline correction was applied in the time period 750ms before the trial start. Within this time interval, only the fixation cross is presented. Using a Morlet parameter of 5, the time-frequency analysis was performed in the theta (4-7 Hz), alpha (8-12 Hz) and beta (13-30 Hz) frequency band. To investigate significant differences in the power of the three frequency bands between the three different tasks, we used cluster-based permutation tests (2,000 Monte-Carlo iterations and a cluster alpha level of 0.05). Both task variations, i.e. the estimated-indicator-paradigm and the estimated-path-paradigm, were contrasted with the basic paradigm (task 1) and both task variations were also contrasted with each other. Only frequency bands where comparisons between the tasks were significant in the cluster-test at sensor-level were used for the subsequent beamforming analysis, which was conducted using the dynamic

imaging of coherent sources (DICS) beamformer (Gross et al. 2001). During DICS beamforming, we first determined the cross-spectral density matrix for each task using a Fast Fourier Transformation (FFT) on the alpha (8-12 Hz), beta (13-30 Hz) and theta (4-7 Hz) frequency bands. The common spatial filter was calculated for each task, using the DICS beamformer. Beamforming was performed with the MNI-based forward model template with 5mm spatial resolution, as implemented in the Fieldtrip toolbox. The contrasts between the tasks were calculated as the source power difference divided by the sum of the two contrasted tasks (X and Y), thereby normalizing the difference using the following ratio:

$$r = \frac{power_{task X} - power_{task Y}}{power_{task X} + power_{task Y}}$$

Based on the assumption of an equal noise distribution in the contrasted tasks, this procedure reduces biases due to noise in the data and avoids that effects are driven by outliers (Mückschel et al. 2016). We utilized the "Density-Based Spatial Clustering of Applications with Noise" (DBSCAN) algorithm (Ester et al. 1996) to identify alpha-, beta- and theta-band activity clusters in order to identify functional neuroanatomical regions that showed differences in activity between the contrasted tasks. This was done to guarantee that source activity was only assessed for well-defined functional neuroanatomical regions (Adelhöfer et al. 2020). The radius for the search (i.e. epsilon parameter), which had to be established for the algorithm, was 1.5 times the length of each voxel's edge. Depending on the contrast's direction, we utilized the most positive or negative 1% of the power distribution of all voxels within neuroanatomical regions labelled on the Automatic Anatomical Labeling (AAL) atlas for the DBSCAN. The clusters found by the algorithm were evaluated visually and defined based on the number of voxels and anatomical labels.

## Results

### *Behavioral data*

The t-test comparing the mean tracking error (across subjects for all trials) for task 1 (basic paradigm; mean error =  $92.09 \pm 9.89$  pixels) vs. task 2 (estimated-indicator-paradigm; mean error =  $103.62 \pm 11.39$  pixels) revealed a significantly larger tracking error for task 2 with  $t(40) = -7.86, p < .001, d_z = -1.23$ . Furthermore, the t-test comparing task 1 and task 3 regarding the mean tracking error showed a significantly larger tracking error for task 3 (estimated-path-paradigm; mean error =  $102.71 \pm 9.85$  pixels) compared to task 1;  $t(40) = -9.26, p < .001, d_z = -1.45$ . There was no significant difference between the mean tracking error for task 2 and task 3,  $t(40) = 0.60, p = .55$ .

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Insert Figure 2 about here  
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### *Time-frequency decomposition and EEG beamforming analyses*

The cluster-based permutation test at sensor-level revealed significant differences between the visible trajectory segment in the basic paradigm (task 1) compared to the occluded indicator segment in the estimated-indicator-paradigm (task 2) for the theta frequency band. The test revealed one positive (i.e., theta power during visible indicator > occluded indicator) cluster in the time interval 0.47-2 s after occlusion onset ( $p < .05$ ). On the source level, the DICS beamforming for this contrast revealed theta activity modulations in inferior occipital and temporal areas (BA 20, BA37).

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Insert Figure 3 about here  
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Comparing the visible trajectory interval in the basic paradigm (task 1) to the invisible trajectory interval in the estimated-path-paradigm (task 3), the cluster-based permutation test detected

significant differences in the theta and beta band. For the theta band, the test revealed one positive and one negative cluster on the sensor level with  $p < .05$  in the time window 0.06-2.05 s after the occlusion onset. Here, a positive cluster indicates higher theta power in the visible trajectory interval, whereas a negative cluster shows higher theta power during the occluded trajectory interval. On the source-level, DICS beamforming for the negative cluster (visible < occluded trajectory) revealed theta activity modulations in superior frontal areas (BA8) (Figure 4B). For the positive cluster (visible > occluded trajectory), theta activity modulations were detected in inferior temporal areas (BA20) and in a cluster containing precentral, postcentral and superior frontal areas (BA6, BA3). For the beta band, the test on sensor-level revealed two significant positive (visible > occluded trajectory) clusters in the time interval 0.8-3 s after occlusion onset with  $p < .05$ . Reconstructing source-level activity for this contrast, the DICS beamforming showed beta band activity modulations in inferior temporal areas including the fusiform gyrus (BA36, BA37) (Figure 4A).

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Insert Figure 4 about here  
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On the sensor-level, the cluster-based permutation test detected significant power differences between the occluded indicator (in the estimated-indicator-paradigm, i.e. task 2) and occluded trajectory condition (in the estimated-path-paradigm, i.e. task 3) for both the beta and theta band. For the theta frequency band, the test detected one negative cluster, indicating more theta power during the occluded trajectory condition compared to the occluded indicator condition, in the time interval of 0.13-0.89 s after occlusion onset, with  $p < .05$ . Reconstructing the source-level activity for this contrast, the DICS beamforming revealed theta modulations in inferior occipital areas including the fusiform gyrus (BA36, BA37) and in superior occipital areas including the cuneus (BA18). For the beta band, the cluster-test on sensor-level revealed two significant positive clusters in the time window 0.22-1.74 s after occlusion onset with  $p < .05$ ,

indicating more beta power in the occluded indicator condition. On the source-level, beta-band modulations were detected in superior occipital areas including the angular gyrus (BA40).

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Insert Figure 5 about here  
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## **Discussion**

The current study aimed at elucidating the neurophysiological principles underlying complex sensorimotor integration processes with focus on theta and beta band activity. More particular, goal of this study was to provide insights whether different sources of sensory information relevant during complex sensorimotor integration (operationalized using pursuit tracking) have dissociable and overlapping effects on activity in theta and beta band activity. In the first task, the basic paradigm, the participants had to perform continuous action monitoring. In the second task, the estimated-indicator-paradigm, participants still had to continuously track the trajectory with the indicator, while estimating the indicator's position during the occlusion intervals. In the third task, the estimated-path-paradigm, participants had to continuously track the trajectory with the now visible indicator, with increased sensorimotor demands during the occlusion intervals, since there was no visual information about the trajectory.

Behaviorally, tracking performance was best in the basic paradigm (task 1) in which full information about the indicator and the trajectory was evident. In task 2 (estimated-indicator-paradigm) and task 3 (estimated-path-paradigm), where the trajectory and the indicator information were discarded for the second part of each trial, tracking performance was worse. Task 2 and 3 did not differ from each other suggesting that information about the indicator and the trajectory is equally important for complex sensorimotor integration processes. However, this notwithstanding, the neurophysiological data analysis revealed indicator and trajectory information are processed differently during sensorimotor integration processes.

When contrasting the basic paradigm (task 1) and the estimated-indicator-paradigm (task 2), it is shown that theta band activity was higher when indicator information was fully accessible (task 1), compared to when it was not accessible (task 2). Occlusion of the indicator led to activity modulations in the left inferior and temporal gyrus (BA22, BA37) as well as the inferior occipital cortex (BA19). These brain regions belong to the ventral visual processing pathway subserving object-centered recognition (Goodale and Milner 1992; Chao and Martin 1999; Goodale et al. 2005; Ayzenberg and Behrmann 2023). The reduction of theta-band activity in the ventral stream associated object-centered recognition likely results in declines in behavioral task performance as evidenced by the diminished behavioral performance in task 2 (estimated indicator) as compared to task 1 (basic paradigm). Of note, ventral stream activity has recently been shown to contribute to goal-directed action selection, because it provides the information about which visual features are relevant to include in response selection operations and motor control (Kühn et al. 2011; Eggert et al. 2023). Interestingly, not only theta band activity, but also beta band activity was associated with modulation in the ventral stream pathway. However, this was only the case when contrasting the basic paradigm (task 1) and the estimated-path-paradigm (task 3) – that it is when accessibility of path information was manipulated. It is shown that whenever sensory information about the trajectory is not available, beta band activity becomes downregulated. Evidence suggests that the efficacy of the sampling of sensory information depends on beta activity (Lalo et al. 2007) and that beta band activity is central for sensory gating (Seki and Fetz 2012; Khanna and Carmena 2015), necessary to maintain the status quo of the sensorimotor system (Engel and Fries 2010). Of note, recent findings have suggested that the integration of sensory information and motor processes is a function of beta band activity (Pastötter et al. 2021; Beste et al. 2023). However, brain regions associated with beta band activity were more located downstream the ventral pathway (i.e., in the anterior temporal lobe) than the brain regions associated with modulations of theta band activity (cf. contrast between basic paradigm (task 1) and estimated-indicator-paradigm (task



2)). Interestingly, evidence suggest that the anterior portion of the temporal lobe processes object representations abstracted away from pure perceptual properties (Kriegeskorte et al. 2008; Peelen and Caramazza 2012). Even more important, the anterior temporal lobe supports visual processing when this is taxed by challenging conditions such as insufficient input (Chiou and Lambon Ralph 2016). Exactly this is the case when information about the trajectory is not available, but pursuit tracking has to be performed nevertheless. Apparently, theta and beta band activity encode distinct sources of information within the ventral processing stream important for complex sensorimotor integration: theta band activity is more affected by manipulating accessibility to information about the indicator, while beta band activity is more affected by manipulating accessibility to information about the trajectory. Opposed to the indicator, the trajectory information is not under the control of the agent, but represents a given framework in which sensorimotor integration processes take place. The monitoring of this is central to estimate and maintain the status quo of the sensorimotor system while performing an action. Since the latter is a function of the beta band (Engel and Fries 2010) it is plausible that especially beta band activity and less so theta band activity is modulated by degrading trajectory information.

Opposed to beta band activity, theta band activity is more broadly affected by the experimental manipulation of different sources of sensory information in this study. This is exemplified by the fact that changes in the availability of the indicator (see above) and the trajectory information have an impact on theta band activity (cf. contrast between basic paradigm (task 1) and estimated-path-paradigm (task 3)). When the trajectory information was inaccessible, activity modulations were evident not only in the anterior temporal cortex, but also in the anterior part of the superior frontal gyrus (SFG; BA8), as well as in posterior superior frontal cortices including the motor cortex, pre-motor cortex and the supplemental motor area (BA6). Of particular relevance is that the modulation of theta band activity was strong in the anterior part of the superior frontal gyrus (SFG; BA8). Here, the contrast (task 1 minus task 3)

was negative indicating that theta band activity was stronger in the anterior SFG when trajectory information was not accessible (estimated-path-paradigm, task 3), compared to when it was accessible (basic paradigm, task 1). In the other frontal brain regions, the contrast was still positive indicating that theta band activity was not as strongly modulated as it was the case in the anterior SFG. Of note, the effect in the anterior SFG reflected an initial, burst-like increase in theta band activity (i.e., within the first 500ms). Such short-lasting increases in theta band activity likely reflect the emergence of a “surprise signal” conception of theta band activity (Cavanagh and Frank 2014; Beste et al. 2023). The computation of a surprise signal needs a goal-state to perform a comparison between the desired and the achieved outcome of an intended action. Exactly this information is, however, not available once the trajectory is not visible. When information about the trajectory was not accessible, but when tracking (i.e., operating the indicator) was required nevertheless, intentionally operating the indicator is initially more demanding and the increased theta band activity likely signals a higher need for control to perform intentional tracking in the absence of a goal-state (i.e., the trajectory). Subsequently (from 500ms onwards), however, theta band activity was not increased (in estimated-path-paradigm (task 3) compared to basic paradigm (task 1)) when information about the trajectory was still not accessible. Rather, theta band activity was smaller in task 3 (estimated path) as compared to task 1 (basic paradigm) and associated with inferior temporal as well as superior frontal cortices including the motor cortex, pre-motor cortex and the supplemental motor area. These structures have previously been associated with processes important for the integration of visual input with motor commands (Filimon et al. 2009; Battaglia-Mayer et al. 2016; Mückschel et al. 2017; Battaglia-Mayer and Caminiti 2019; Eggert et al. 2023). According to an account framing the role of superior frontal cortices including the motor cortex, pre-motor cortex and the supplemental motor area (Ptak et al. 2017), movements are specified in terms of spatiotemporal and kinematic properties defining a desired state and the associated motor command. The reduction of theta band activity in the regions thus indicates

that these processes become inefficient, which is corroborated by the behavioral data clearly showing reduced tracking performance in task 3 (estimated-path-paradigm) as compared to task 1 (basic paradigm). The results suggest that it is the sensory information of the goal of acting (i.e., trajectory) that depends on beta band activity. Theta band activity encodes information which can refer to the trajectory information and the indicator information. Currently, it can only be speculated why this may be the case. However, biophysical properties of the theta signal are well-suited to enable information integration (Buzsáki and Draguhn 2004; Buzsáki 2006; Cavanagh and Frank 2014). Moreover, theta band activity has been shown to carry distinct fractions of information which has to be merged during sensorimotor integration processes (Mückschel et al. 2017; Pscherer et al. 2020, 2022; Takacs et al. 2020). Theta-band activity has also been associated with internally-oriented cognition (Wolff et al. 2019; Hua et al. 2022) such as working memory processes (Beste et al. 2023). Following this account, the necessary retrieval of path information during the estimated-path-paradigm (task 3) might involve theta band activity. These properties of theta band activity may explain why theta band activity is involved in the processing of information related to the indicator and the trajectory in the current study – both aspects need be integrated with each other.

While these results already show that both theta and beta band activity are related to different sources of information used during complex sensorimotor transformation processes, the distinctiveness in the role of theta and beta band activity becomes particularly clear when contrasting the estimated-indicator-paradigm (task 2) and the estimated-path-paradigm (task 3): Specifically in the initial time period after degrading indicator or trajectory information (i.e., within the first 500ms), theta band and beta band activities were modulated in opposite directions. This clearly distinguishes the comparison of task 2 and task 3 from the comparisons of both task variations (i.e. task 2 and 3) with the basic paradigm, where modulations were mostly seen in later time periods. While theta band activity is higher in periods of inaccessible trajectory than indicator information in occipito-parietal cortices, beta band activity in inferior

parietal cortices was higher when the indicator was inaccessible, not the trajectory information. Since theta band activity modulations were observed early after the trajectory information was discarded from the screen, the increase in theta band activity may reflect the coding of a surprise signal. However, since a similar dynamic was not observed when discarding the indicator information, a surprise signal account cannot explain the finding. Moreover, the surprise signal account frames frontal theta band activity and not theta band activity in lower-level cortical structures (Cavanagh and Frank 2014). Theta band activity in such lower-level structures (e.g. the occipito-parietal regions) likely reflects attentional sampling processes (Vanrullen and Dubois 2011; Landau and Fries 2012; Fiebelkorn et al. 2013; Helfrich et al. 2018). The finding that theta band activity was increased in the absence of trajectory information (i.e., information about the goal of acting) may be interpreted that participants may increase their attentional sampling for potentially upcoming trajectory information. The increase of beta band activity when the information of the indicator was discarded was associated with right parietal cortices. Opposed to the trajectory, the indicator is under direct control of the agent and has to be moved to the trajectory. This involves processing of spatial information and how to move the indicator. Both functions, the processing of spatial information and how to operate an object are functions of the dorsal visual processing stream (Milner and Goodale 2006). Especially parietal association cortices have been put into connection with a role of beta in peripheral sensory sampling (Witham and Baker 2007; Khanna and Carmena 2015) and are well-known to pre-specify motor programs (Cisek and Kalaska 2002; Jaffard et al. 2008; Beste et al. 2009; Bernier et al. 2012; Sulpizio et al. 2017).

There are some limitations that should be considered when interpreting results from EEG beamforming analysis. The spatial resolution of the obtained brain areas depends on the grid that was used for the analysis and the results are sensitive to noise in the sensor data as well as to the preprocessing pipeline applied to the initial data. However, EEG beamforming is an established method that provides reliable results (Adelhöfer and Beste 2020; Prochnow et

al. 2022; Wendiggensen, Adelhöfer, et al. 2022; Wendiggensen, Ghin, et al. 2022). Furthermore, future studies should also consider the potential role of prestimulus activity for the observed oscillatory patterns during pursuit-tracking with different sensorimotor demands. Prestimulus/pretrial activity has been shown to contribute to trial activity in multiple, non-additive ways (Huang et al. 2017; Wainio-Theberge et al. 2021; Wendiggensen, Ghin, et al. 2022). Moreover, future studies should further assess individual variability of tracking performance to achieve a broader picture of the processes reflected in the behavioral tracking data.

In summary, the study provided insights how different sources of sensory information during goal-directed acting become integrated on a neurophysiological level. This was accomplished through comparing three consecutive pursuit tracking experiments in which the source of visual information available for tracking was varied (i.e., that of the indicator and the goal of acting). The initial specification of indicator dynamics is determined through beta band activity in parietal cortices. When information about the goal was not inaccessible, but operating the indicator was required nevertheless, this incurred increased theta band activity in the superior frontal cortex signaling a higher need for control. Later, theta and beta band activity encode distinct sources of information within the ventral processing stream: theta band activity is affected by the indicator information, while beta band activity is affected by the information about the action goal. Complex sensorimotor integration is realized through a cascade of theta and beta band activity in a ventral-stream-parieto-frontal network.

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## Figure Legends

### *Figure 1.*

Overview of exemplary trials for all tasks. The target was displayed as red circle, the indicator was a white crosshair. After the initial start vector, the target moved along the trajectory that was concatenated of a random and constant segment. The dashed line was not visible to the participants, only the target moving along it. Grey-shaded areas indicate time windows of occlusion. (A) Basic paradigm (task 1). Both indicator and trajectory are visible throughout the whole trial. Participants have to follow the target on the random and constant segment. (B) Estimated-indicator-paradigm (task 2). Participants have to follow the target on random and constant trajectory. The indicator is occluded for 2 seconds during the constant trajectory segment. The target is visible throughout the whole trial. (C) Estimated-path-paradigm (task 3). Participants have to follow the target on random and constant trajectory. The trajectory is occluded for 3 seconds during the constant trajectory segment. The indicator is visible throughout the whole trial.

### *Figure 2.*

Density and distribution of mean tracking error per subject for all three tasks.

### *Figure 3.*

Results of the time-frequency and beamforming analysis for the contrast Task 1 - Task 2. Frequency power differences for significant electrodes in the cluster-based permutation test on the left. The topography for the theta power difference in the top-right corner. Extracted source-level cluster for this contrast are displayed on the right.

*Figure 4.*

Results of the time-frequency and beamforming analysis for the contrast Task 1 - Task 3. Frequency power differences for significant electrodes in the cluster-based permutation test on the left. The topography for the respective power difference in the top-right corner. Extracted source-level cluster for this contrast are displayed on the right. (A) Results for the beta frequency band. (B) Results for the theta frequency band.

*Figure 5.*

Results of the time-frequency and beamforming analysis for the contrast Task 2 - Task 3. Frequency power differences for significant electrodes in the cluster-based permutation test on the left. The topography for the respective power difference in the top-right corner. Extracted source-level cluster for this contrast are displayed on the right. (A) Results for the beta frequency band. (B) Results for the theta frequency band.