# NEURAL OSCILLATIONS DISSOCIATE BETWEEN MAINTENANCE AND PROCEDURALIZATION OF NOVEL INSTRUCTIONS

## Oscillations in novel instructions implementation

Silvia Formica, Carlos González-García, Mehdi Senoussi, and Marcel Brass

Department of Experimental Psychology, Ghent University, Belgium

Ghent University
Faculty of Psychology and Educational Sciences
Department of Experimental Psychology
Henri Dunantlaan 2
B-9000 Gent

Corresponding author: Silvia Formica (silvia.formica@ugent.be)

## Abstract

Humans are extremely efficient in rapidly and flexibly converting complex symbolic instructions into novel behaviors. Previous evidence and theoretical models suggest that the implementation of a novel instruction requires the reformatting of its declarative content into an action-oriented code optimized for the execution of the instructed behavior. While neuroimaging research focused on identifying the brain areas involved in such process, its temporal profile and electrophysiological characteristics remain unknown. In the present study, we recorded EEG while we asked participants to either simply maintain declaratively the content of novel S-R mappings for recognition or to proactively prepare for their implementation. By means of time-frequency analyses, we isolated the oscillatory features specifically associated with the proceduralization of the encoded instruction. Before the onset of the implementation target, we observed stronger delta/low-theta activity over frontal electrodes and a significant suppression in mu and beta activity over central electrodes. On the contrary, activity in the alpha band showed no differences between the two tasks. Together, these results support the crucial role attributed to prefrontal regions in orchestrating complex task setting and further extend on it by characterizing the temporal and frequency profile of this process. Moreover, we highlight the critical involvement of motor activity in the proactive preparation for novel instruction implementation.

## Keywords

Instruction implementation; Cognitive control; Motor preparation; Attention; EEG oscillations

## Significance Statement

Humans developed the unique ability of converting novel instructions in effective behavior. This skill is associated with activity in frontoparietal brain regions, whose interplay supports the reformatting of the declarative content of the instruction into an action-guiding representation. However, the time-resolved unfolding of such cognitive processes is still poorly understood. Here, we investigated how oscillatory brain activity differed between simple maintenance and reformatting of novel instructions. In preparation to the target, we observed differences in lower frequencies over frontal regions, and oscillatory features of motor preparation. Together, these results suggest that instruction implementation is mediated by the exertion of top-down cognitive control, reflected in theta dynamics, and motor-related activation.

## 1 Introduction

One peculiar aspect of human cognitive flexibility involves the ability to convert complex symbolic instructions into novel behaviors (Cole et al., 2013). Recent evidence has put forward a two-step heuristic model in which instructions are first encoded and maintained in a declarative format before being transformed into an action plan (i.e., procedural representation) that allows executing the instructed task (Brass et al., 2017). Neuropsychological and behavioral evidence support a dissociation between ‘knowing’ the content of an instruction and ‘doing’ the instructed cognitive or motor action, suggesting that maintaining its declarative content is insufficient to implement the instructed task, and that additional reformatting into a procedural representation is needed for optimal performance (Milner, 1963; Duncan et al., 1996; Wenke et al., 2009; Liefooghe et al., 2012; Bhandari and Duncan, 2014). Such immediate reformatting seems to occur only for small sets of instructions, and only when participants have the intention to implement them (Liefooghe et al., 2012).

A growing number of fMRI studies has focused on revealing which brain regions support the implementation of novel task sets (Hartstra et al., 2011, 2012; Demanet et al., 2016; González-García et al., 2017; Muhle-Karbe et al., 2017; Bourguignon et al., 2018; González-García et al., 2019; Palenciano et al., 2019b, 2019a). These results consistently point towards a crucial role of frontoparietal regions, and in particular of the prefrontal cortex (PFC). Similarly, they provide evidence for distinct neural mechanisms supporting implementing versus memorizing novel instructions (Brass et al., 2017). However, the temporal and spectral characteristics of instruction implementation have received less attention. Crucially, investigating the oscillatory dynamics of instruction implementation allows to pinpoint when the proceduralization of novel instructions starts to diverge from their mere declarative maintenance and will provide specific information about the processes that are involved.

Specifically, we reasoned that both declarative maintenance and proactive proceduralization of novel instructions likely engage processes of attentional selection. Such top-down mechanisms are associated with modulations of posterior alpha band (8 – 14 Hz) oscillations (Sauseng et al., 2005; Jensen and Mazaheri, 2010; Bonnefond and Jensen, 2012; Mok et al., 2016; Poch et al., 2017). On the contrary, we expected some oscillatory features to be specifically associated with proceduralization. First, the proactive reformatting of the instruction into a proceduralized action-bound representation should involve the allocation of cognitive control, reflected in stronger theta synchronization over mid-frontal scalp electrodes mediating long-range binding (Cohen and Donner, 2013; Itthipuripat et al., 2013; Cavanagh and Frank, 2014; Verbeke and Verguts, 2019). Moreover, this reformatting is expected to induce the preparation of the instructed motor plan, and therefore a desynchronization of beta (20 – 30 Hz) and mu (8 – 12 Hz) frequency bands over central electrodes, revealing motor activation (Pineda, 2005; Cheyne, 2013; Tzagarakis et al., 2015; Schneider et al., 2017b; Rhodes et al., 2018). Moreover, since these features are sensitive to the set size, we were additionally interested in investigating whether they would be modulated by the number of instructions to be proceduralized (Onton et al., 2005; Schneider et al., 2017a; Poch et al., 2018).

To test our hypotheses, we recorded EEG activity while participants performed a Memorization task, which encouraged a declarative maintenance of novel Stimulus–Response (S-R) mappings for recognition, and an Implementation task, intended to prompt their proactive reformatting for execution. After the presentation of four mappings, a retro-cue selected a subset of them as potential targets for the subsequent recognition or execution task. We reasoned that brain activity during the Cue-Target interval (CTI) would reflect a two-steps action (Myers et al., 2017): attention would first be internally oriented towards the selected items, and then the prioritized representations would be reformatted into a behavior-optimized state. In the context of instruction implementation, the task-optimized representation is a procedural, action-bound code of the S-R mapping, whereas successful maintenance is optimally achieved by means of a declarative representation of stimulus and response that does not entail any action plan.

## 2 Materials and Methods

### *2.1 Participants*

Thirty-nine participants took part in the experiment ($M_{age}$ = 21.74, *SD* = 4.50, 33 females) and received 30 euros as compensation. Sample size was not computed a priori but, based on previous research, we aimed for a sample size of at least thirty. All participants had normal or corrected-to-normal vision and thirty-three reported to be right-handed. Data from two participants were discarded due to low task performance (individual mean accuracy exceeded by 2.5 standard deviations the group mean accuracy in one of the two tasks and/or accuracy in response to catch trials in one of the tasks was below 60%); data from two additional participants were discarded following visual inspection because of excessive noise in the EEG recordings, resulting in a final sample size of thirty-five participants. All participants gave their informed consent prior to the beginning of the experiment, in accordance with the Declaration of Helsinki, and the protocols were consistent with the general ethical protocol of the Faculty.

### *2.2 Materials*

The same set of stimuli was used as in previous studies on instruction implementation (González-García et al., 2020; Formica et al., submitted). It consisted of 1550 pictures, grouped in two macro categories: animate non-human animals and inanimate objects (vehicles and musical instruments) (Griffin et al., 2007; Konkle et al., 2010; Brady et al., 2013; Brodeur et al., 2014). All images had their background removed, were centered in a 200x200 pixels square and were converted to grayscale. Stimuli presentation and response collection were performed using Psychopy toolbox (Pierce, 2007).

### *2.3 Experimental design*

Participants performed two tasks (from now on we will refer to them as “Implementation task” and “Memorization task”) during one single session, and the order of the two tasks was counterbalanced between participants. The structure of the trials for the two tasks was identical up to the presentation of the target (Figure 1). Each trial started with a red fixation cross presented for 2000ms (± 100ms) signaling the inter-trial interval and allowing participants to blink if needed, followed by a white fixation cross for 250ms. Next, the encoding screen containing four S-R mappings (arranged in two rows) appeared for 5 seconds. Mappings consisted of a new image associated with a bimanual response: “index” referred to both index fingers (keys r and i) and “middle” referred to both middle fingers (keys e and o). These responses were used instead of the more traditional left and right options to avoid automatic motor activations elicited by the mere presentation of lateralized response words (Bundt et al., 2015). Out of the four presented mappings, two contained images of animals and two images of inanimate objects. After a 750ms delay, the retro-cue appeared and remained on the screen for 250ms. This consisted of a square presented centrally, with one, two or four (i.e., neutral retro-cue) colored corner(s). Importantly, when the retro-cue selected two mappings, these were always on the same side of the screen. Participants were instructed that the retro-cue signaled which mapping(s) could be probed, with 100% validity (except in the case of catch trials, see below). The subsequent cue-target interval (CTI) had a jittered duration, lasting on average 1750ms (± 100ms). Finally, participants were presented with the target screen, which differed depending on the task. In the Implementation task, the image of one of the cued mappings was presented centrally and participants were required to press the associated pair of keys (both index or both middle fingers). In the Memorization task, one mapping (i.e., image and associated response) was presented centrally. Participants had to report whether the presented mapping matched one of those selected by the retro-cue, by pressing with both fingers of one hand for “yes” or both fingers of the other hand for “no”. The sides for “yes” and “no” were randomly assigned on a trial basis to ensure that participants could not prepare any response during the CTI. Labels with “yes” and “no” appeared at the bottom of the target screen together with the mapping. In 50% of the trials, the target screen showed the same mapping as in the encoding (“yes” response). In the other 50% of trials, the image was presented associated with a different response with respect to encoding (“no” response). Crucially, despite the similarities in trial structure, the Memorization task relied on the declarative maintenance of the mappings as no response could be prepared, whereas the Implementation task encouraged a proactive preparation of the selected mappings for the execution of the required action plan. Both tasks included catch trials ( ~25% for each task), in which the target screen displayed a different image than the four displayed in the encoding screen. In this case, participants were required to press the spacebar. This was done to discourage participants to adopt specific strategies, such as memorizing only the mappings associated with one response option. Since we were interested in the brain activity before the onset of the target, EEG recordings from catch trials were analyzed together with regular trials. For each task, participants completed 5 experimental blocks, for a total of 180 trials (60 per load, Figure 1).

Each of the two tasks was preceded by a practice session. This consisted of mini-blocks of 12 trials, including all possible load conditions (i.e. number of mappings selected by the retro-cue) and at least one catch trial. The only difference with the main task was the presence of feedback at the end of each trial, signaling the accuracy of the response or encouraging participants to respond faster in case no response was registered within the maximum response time of 3 seconds. Performance was assessed at the end of each mini-block: if accuracy was above 80%, practice was concluded, otherwise a new mini-block started, up to a maximum of 3 blocks. S-R mappings used during the practice were never presented again during the main task. The total duration of the experiment, including cap preparation and cleaning, practices, main tasks and breaks was approximately 150 minutes.

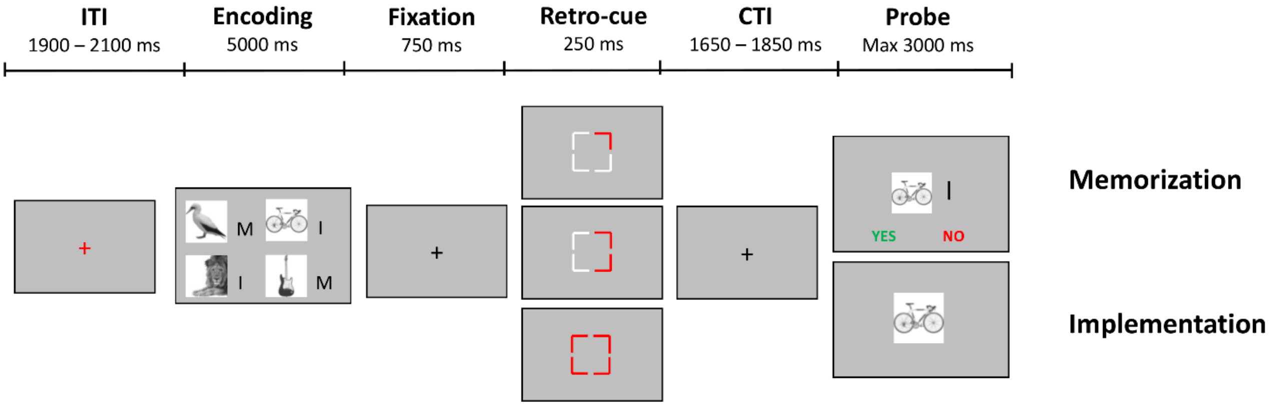

**Figure1: Behavioral paradigm.** Participants had to first encode four S-R mappings, for subsequent recognition (Memorization task) or for a choice-reaction task (Implementation task). During the retention interval, a valid Retro-Cue selected one, two or all four mappings as relevant for the upcoming probe. Participants performed the two tasks separately in a block design.

### *2.4 EEG Recordings and pre-processing*

Electrophysiological data were recorded using a BioSemi ActiveTwo system (BioSemi, Amsterdam, Netherlands) with 64 Ag–AgCl electrodes arranged in the standard international 10–20 electrode mapping (Klem et al., 1999), with a posterior CMS-DRL electrode pair. Two reference electrodes were positioned at the left and right mastoids. Eye movements were registered with a pair of electrodes above and below the left eye and two additional electrodes at the outer canthi of both eyes. EEG signals were recorded at a 1024 Hz sampling rate.

EEG data were preprocessed using the Fieldtrip toolbox (Oostenveld et al., 2010), running in MATLAB (MATLAB R2017b, The MathWorks, Inc., Natick, Massachusetts, United States). First, the data were downsampled to 512 Hz and re-referenced to the average of the mastoids. Then, a 0.5 – 45 Hz band-pass FIR filter was applied to the data, together with a Notch filter at 50 Hz and its harmonics. Data were epoched relative to the onset of the retro-cue (from -1000 to 2500 ms) and demeaned to the average of the whole epoch, to improve independent component analysis (ICA) (Groppe et al., 2009). Only trials in which the participant performed the correct response were retained for subsequent analyses. Trials exhibiting movement artifacts or excessive noise were removed following visual inspection of the data. Next, eye movements artifacts were removed by means of ICA, using the EEGLAB (Delorme and Makeig, 2004) runica algorithm as implemented in Fieldtrip. Components to discard were selected based on their topography, the correlation between their time course and the horizontal and vertical electrooculography, and their power spectrum. For most participants, two components were removed (capturing blinks and horizontal eye movements, respectively); in six participants blinks were reflected in two components, leading to the removal of three IC, and in two participants only one component was removed. Finally, data were visually inspected again to ensure successful cleaning and one (N = 6), two (N = 2) or three (N = 1) excluded channels were interpolated by means of spherical spline interpolation (Perrin et al., 1989). This cleaning procedure resulted in an average of 151.09 trials for the Implementation task (*SD* = 12.29, 83.94%) and 143.06 trials for the Memorization task (*SD* = 14.07, 79.48%). For each load condition, an average of 81.7% of trials were retained (Implementation, Load 1: 52.14 (*SD* = 3.64) trials, Load 2: 50.26 (*SD* = 5.19) trials, Load 4: 48.68 trials (*SD* = 5.74); Memorization, Load 1: 49.88 trials (*SD* = 4.84), Load 2: 47.86 trials (*SD* = 5.86), Load 4: 45.31 trials (*SD* = 5.94).

### *2.5 Spectral Analysis*

For each Task x Load condition (Memorization-Load 1, Memorization-Load 2, Memorization-Load 4 and Implementation-Load 1, Implementation-Load 2, Implementation-Load 4), time-frequency analysis was performed separately using complex Morlet wavelet convolution, to estimate spectral power from 1 to 45 Hz in steps of 1 Hz. The number of cycles in the wavelet was frequency-specific, ranging from 2 at 1 Hz and linearly spaced up to 7 cycles at 45 Hz, to achieve a good trade-off between temporal and frequency precision (Cohen, 2014). This analysis resulted in one time-frequency spectrogram for each channel, condition and participant. Condition-specific decibel normalization was then applied, using the time window between -600 and -300ms before the onset of the retro-cue as baseline. To avoid data contamination due to the smearing in time of the processing of the target, all statistical analyses are performed on the time window from 0 to 1800ms with respect to retro-cue onset, therefore leaving 100ms gap between the end of our analyses window and the earliest jittered target onset.

### *2.6 Statistical Analyses*

For behavioral data, reaction times (RTs) and error rates (ER) were separately entered in 2 (Task: Memorization vs Implementation) x 3 (Load: 1, 2, 4) repeated measure ANOVAs, performed in JASP (Jasp Team, 2019)

To evaluate the statistical significance of differences between two EEG time-courses or time-frequency spectra, we adopted a cluster-based permutation approach (Maris and Oostenveld, 2007), which is appropriate to assess the reliability of neural patterns over neighboring data points. Moreover, this approach is robust against the multiple-comparison problem, as the significance of clusters found in the observed group-level data is estimated against a distribution of clusters obtained by randomly permuting the data at the participant level. First, we performed a two-sided t-test (α = 0.05) between the two conditions to be compared. Then, we considered as cluster a group of adjacent data points with same sign significance and as cluster-size the sum of all t-values in the cluster. Next, we used 10000 permutations of participant-level data to estimate a distribution of cluster sizes under the null hypothesis that there are no differences between conditions. The *P*-value for each cluster in the observed group-level data corresponds to the proportion of permutations in which the largest cluster size was larger than the size of the considered observed cluster. Again, we used a significance alpha level of 0.05, therefore only observed clusters whose size was larger than the size of the largest cluster in at least 95% of permutations are reported.

When needed, averaged Task- and Load-specific power values were extracted from time window and frequency ranges of interest (see below) and entered in repeated measures ANOVAs, performed in JASP (Jasp team, 2019).

### *2.7 Contralateral alpha suppression*

Consistent findings reported alpha desynchronization over posterior regions contralateral to the attended spatial location, indicating top-down anticipatory mechanisms of orienting attention in the perceptual or internal space (Sauseng et al., 2005; Thut et al., 2006; Rihs et al., 2007; van Dijk et al., 2008; Rihs et al., 2009; Jensen and Mazaheri, 2010; Gould et al., 2011; Rohenkohl and Nobre, 2011; Bonnefond and Jensen, 2012; Capilla et al., 2014; Myers et al., 2015; Wallis et al., 2015; Mok et al., 2016).

To estimate the suppression of alpha contralateral to the cued hemifield, we used the time-frequency spectra corresponding to Load 1 and Load 2, separately for the two tasks. Trials with neutral retro-cues were excluded from this analysis because they did not elicit attentional orienting towards one of the two visual hemifields. Based on previous literature, two pairs of electrodes were selected in right (P8, PO8) and left (P7, PO7) posterior parietal regions (Gould et al., 2011; Schneider et al., 2017b; de Vries et al., 2019b; van Ede et al., 2019). Power spectra were extracted from these electrode pairs, averaged in the alpha frequency range (8 – 14 Hz), and collapsed between retro-cues pointing to the left and right hemifield, in order to extract one power time series for the contralateral hemisphere and one for the ipsilateral hemisphere. The two time series were compared by means of cluster-based permutation testing, separately for the two tasks (see Statistics section). Additionally, the cluster-based permutation approach was also used to compare the contralateral alpha suppression between the two tasks. Namely, for each task the ipsilateral power time series was subtracted to the contralateral one, separately for each participant, and the resulting difference waves were compared. This analysis was performed to test whether the deployment of alpha to orient attention towards relevant mental representations was analogous in both tasks.

### *2.8 Load-dependent alpha increase*

Posterior alpha power has been observed to increase with the number of items relevant after attentional selection in a WM task (Jensen, 2002), also following retrospective selection (Manza et al., 2014; Poch et al., 2017, 2018). To investigate the increase in alpha power relative to the number of retained items, we extracted the average power for the frequencies ranging from 8 to 14 Hz, separately for each condition and task, from the electrode pair Pz and POz (Jensen, 2002). Since the cluster-based permutation approach adopted above is not suited for factorial designs and we expected this to be a sustained effect, we averaged the power values across the whole time window from 0 to 1800ms with respect to the onset of the retro-cue. This operation led to one averaged alpha power value for each Task-Load combination per participant, that were entered in a 2 (Task) x 3 (Load) repeated measure ANOVA.

### *2.9 Mid-frontal theta in Implementation*

To investigate the differences in oscillations between the the two tasks, we averaged the time-frequency spectrogram (2 – 30 Hz) from mid-frontal electrodes Fz and AFz, separately for each task (Onton et al., 2005; Popov et al., 2018; Cooper et al., 2019). We adopted again the described cluster-based permutation approach to find significant clusters of different activation. Since in this case we did not average across a specific frequency range, clusters were created on the basis of adjacency of data points on both the time and the frequency dimensions. Finally, to further investigate the load-specific dynamics in low frequencies, we extracted the averaged power in the frequency range 2 – 5 Hz ('low theta') and 6 – 8 Hz ('high theta') in the time window of the observed significant cluster (600 – 1200ms), separately for each Load condition and Task. We entered these values in a 2 (Task) x 3 (Load) x 2 (Theta range) repeated measure ANOVA.

### *2.10 Motor-related mu and beta suppression in Implementation*

We hypothesized Implementation to be associated with proactive motor preparation of potential responses, in comparison with the Memorization task. To test for this, we first adopted a cluster-based permutation approach, to look for significant clusters of difference in power across a broad group of electrodes over motor and pre-motor cortices (FC1, FC2, FCz, FC3, FC4, C3, CP3, C1, CP1, Cz, CPz, C2, CP2, C4, CP4) (McFarland et al., 2000; Marchesotti et al., 2016). It is worth pointing out that we averaged activity in a large cluster of non-lateralized channels. Responses were bimanual in the Implementation task, while they were lateralized in the Memorization task. Nevertheless, we think the difference in response lateralization between tasks does not represent a confound for our hypothesis, since we aimed at investigating pre-movement preparatory oscillatory activity, rather than the effector-specific M1 activation (Pfurtscheller and Neuper, 1997; Neuper and Pfurtscheller, 2001; Pfurtscheller et al., 2006). To further investigate the effect of the number of proceduralized mappings on motor preparation, we extracted the average mu (8 – 12 Hz) and beta (20 – 30 Hz)[1] power in the time window 700 – 1600ms after retro-cue onset separately for each Task and Load condition, and entered these values in two separate repeated-measures ANOVAs with factors Task (Implementation vs Memorization) x Load (1, 2, 4).

## 3. Results

### 3.1 Behavioral results

Concerning behavioral performance, we expected the retro-cue to have a beneficial effect on reaction times and error rates in both tasks (Souza and Oberauer, 2016). Repeated

---

[1] There is quite a significant variability in the literature concerning the limits of each frequency band. Beta is usually identified as ranging from 13/15 Hz to 30 Hz. Here, we chose to focus on “high beta” (20 – 30 Hz), to avoid contamination from the activity of neighboring frequencies (i.e., alpha band) and because of the characteristics of the significant cluster.

measures ANOVA on RTs confirmed a significant main effect of Load[2] ($F_{1.44,\ 49.06}$ = 104.65, $p < 0.001$, $\eta^2_p = 0.76$): RTs increased with the number of mappings selected by the retro-cue (Load 1: *M* = 978ms, *SD* = 196, Load 2: *M* = 1168ms, *SD* = 150, Load 4: *M* = 1266ms, *SD* = 142). The main effect of Task was also significant ($F_{1,\ 34}$ = 237.20, $p <$ 0.001, $\eta^2_p = 0.87$), with slower RTs in Memorization (*M* = 1355ms, *SD* = 185) than Implementation (*M* = 907ms, *SD* = 160). The interaction between the two factors also resulted to be significant ($F_{1.32,\ 44.88}$ = 4.42, $p = 0.031$, $\eta^2_p = 0.11$). More specifically, the effect of Load was larger in the Implementation task ($F_{1.44,\ 49.06}$ = 93.20, $p < 0.001$) compared to the Memorization task ($F_{1.44,\ 49.06}$ = 45.50, $p < 0.001$) (Figure 2a).

Error rates showed a significant main effect of Task ($F_{1,\ 34}$ = 11.08, $p = 0.002$, $\eta^2_p = 0.25$) and of Load ($F_{1.67,\ 57.91}$ = 25.65, $p < 0.001$, $\eta^2_p = 0.43$). Participants were significantly more accurate in the Implementation task (*M* = 0.14, *SD* = 0.09) compared to the Memorization task (*M* = 0.19, *SD* = 0.10), and were more accurate when less items were selected by the retro-cue (Load 1: *M* = 0.12, *SD* = 0.07, Load 2: *M* = 0.17, *SD* = 0.10, Load 4: *M* = 0.20, *SD* = 0.12). The interaction between the two factors was not significant ($p = 0.266$) (Figure 2b).

Regarding catch trials, participants could successfully detect a new image in both the Memorization task (error rate in catch trials: *M* = 0.13, *SD* = 0.08) and the Implementation task (*M* = 0.09, *SD* = 0.07). Nevertheless, they were significantly less accurate ($t_{34}$ = 3.16, $p = 0.003$, $d = 0.53$) in the Memorization task.

---

[2] Mauchly's test revealed that the assumption of sphericity is violated (p < 0.05). Greenhouse-Geisser correction is applied here and in all results where the sphericity assumption is violated.

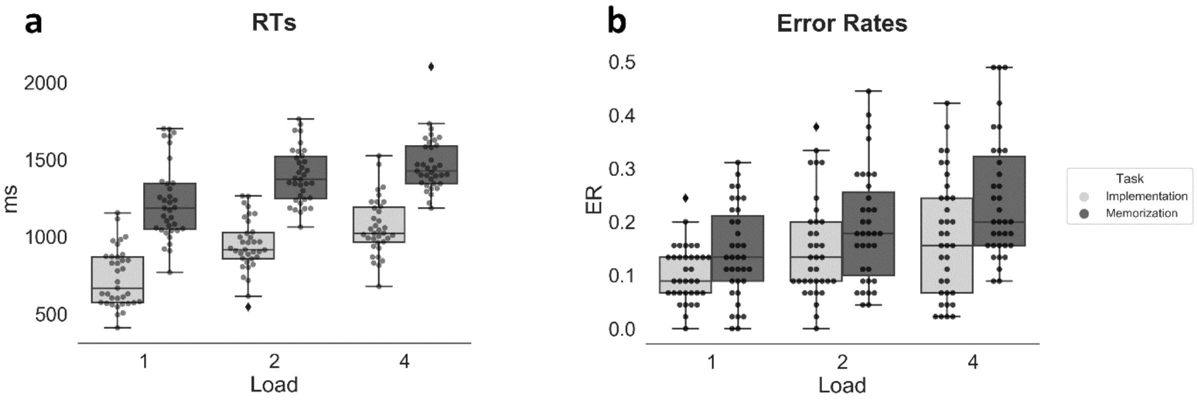

**Figure 2: Behavioral results**. **a**) Reaction times (ms). **b**) Error rates. Both measures confirmed a benefit in performance (i.e., faster RTs and less errors) when the Retro-Cue selected less mappings. In each boxplot, the thick line inside box plots depicts the second quartile (median) of the distribution (n = 35). The bounds of the boxes depict the first and third quartiles of the distribution. Whiskers denote the 1.5 interquartile range of the lower and upper quartile. Dots represent individual subjects' scores.

## *3.2 EEG Results*

### *3.2.1 Contralateral alpha decrease*

As hypothesized, we observed a stronger reduction in alpha power in contralateral compared to ipsilateral electrodes across loads, both in Implementation ($P < 0.001$, cluster-corrected) and Memorization ($P = 0.03$, cluster-corrected) tasks (see Supplementary material for the same analysis performed separately for the two load conditions). The significant clusters spanned the time window around 600 – 800ms. Notably, we did not find any difference between the two tasks (no cluster survived multiple comparison correction, even at a cluster threshold of $P = 0.1$), supporting our hypothesis that the mechanisms allowing for attentional orienting are engaged to a similar extent in the two tasks (Figure 3a). To qualitatively confirm our electrodes selection and the location of the significant effect, contralateral minus ipsilateral half-topographies are reported separately for each task (Figure 3b).

### *3.2.2 Load-dependent alpha increase*

We predicted alpha power to also track the number of items selected by the retro-cue to be relevant for the ongoing task. The repeated measures ANOVA on the averaged alpha power over Pz – POz in the whole CTI (0 – 1800ms) revealed a significant main effect of Load ($F_{2, 68} = 37.92$, $p < 0.001$, $\eta^2_p = 0.53$) (Figure 3c). Specifically, alpha power values increased with the number of retained items (Load 1 vs Load 2: $t = -4.72$, $p < 0.001$ Bonferroni-corrected; Load 2 vs Load 4: $t = -4.91$, $p < 0.001$ Bonferroni-corrected), both in Implementation (Load 1: $M = 1.27$, $SD = 2.10$, Load 2: $M = 1.75$, $SD = 2.11$, Load 4: $M = 2.21$, $SD = 2.23$) and Memorization (Load 1: $M = 1.19$, $SD = 2.16$, Load 2: $M = 1.87$, $SD = 2.27$, Load 4: $M = 2.53$, $SD = 2.34$). Crucially, neither the effects of Task nor the interaction Task x Load were significant (*p*s > 0.2). Scalp topographies of alpha power across the entire CTI are reported separately for each Task and Load condition (Figure 3d).

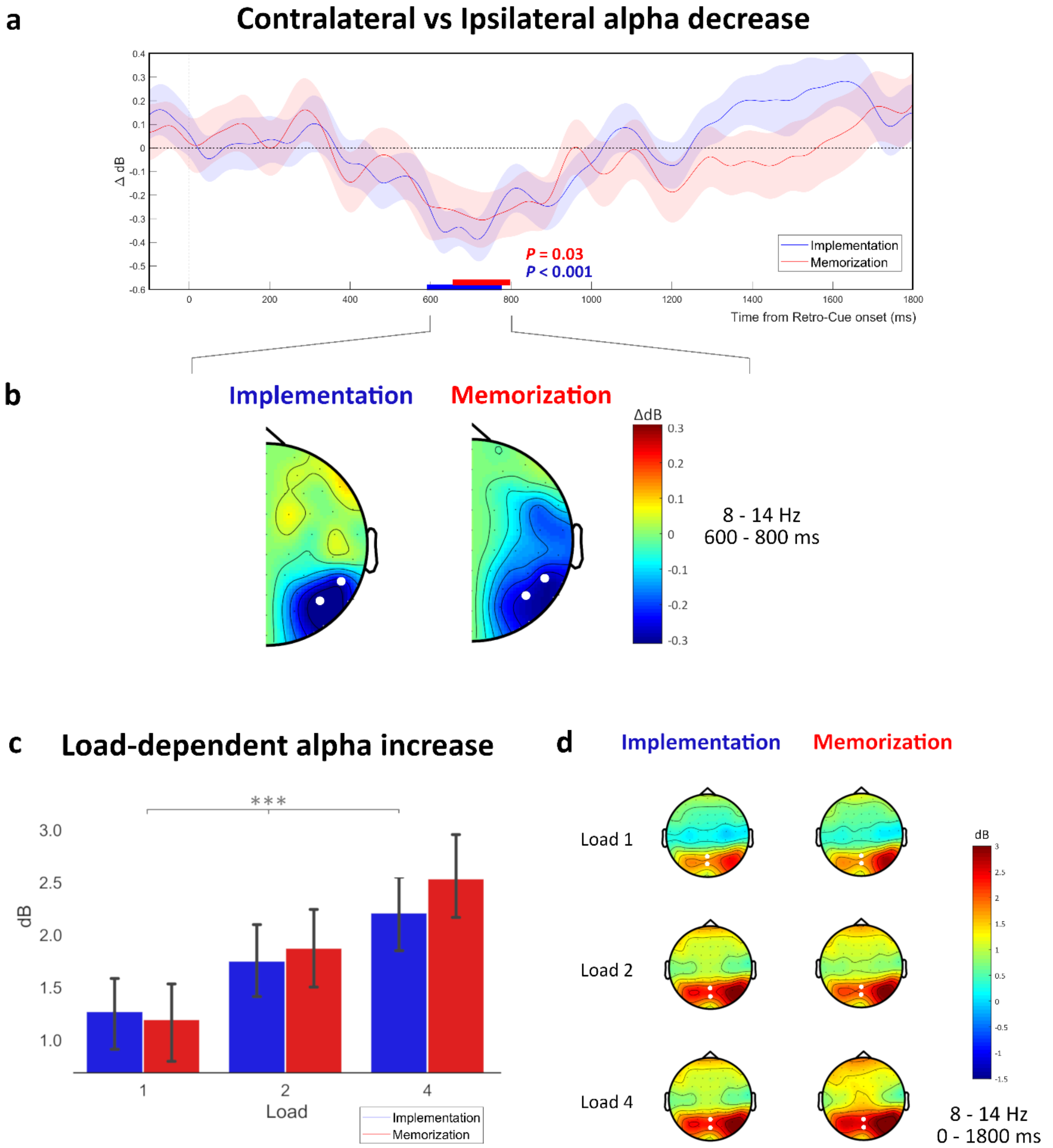

**Figure 3: Alpha power dynamics. a**) Time courses of the difference waves (contralateral minus ipsilateral time course) of alpha power activity between contralateral and ipsilateral electrode clusters (PO8 - P8 and PO7 - P7). Both difference waves show a significant deflection from 600 to 800ms after the onset of the retro-cue. Horizontal lines above the x-axis indicate significant temporal clusters (blue:

Implementation, red: Memorization), obtained with cluster-based permutation testing). Shading represents ± 1 s.e.m., calculated across participants (n = 35). **b**) Half topographies showing differences in alpha power for contralateral minus ipsilateral electrodes collapsed across hemispheres. White dots indicate the a-priori selected electrodes used in the cluster-based permutation analysis. **c**) Alpha power values averaged in the time window 0 – 1800 ms after Retro-Cue onset from electrodes Pz and POz. The asterisks indicate significance values ($p < 0.001$) of the effect of Load in the repeated measures ANOVA. Error bars represents the s.e.m. calculated across participants (n = 35). **d**) Topographies of each Task x Load condition. White dots indicate the a-priori selected electrodes (Pz and POz) from which activity was extracted for the ANOVA.

### *3.2.3 Mid-frontal theta in Implementation*

According to our predictions, we expected to find stronger theta synchronization over mid-frontal electrodes in the Implementation task compared to the Memorization task. The comparison in the time-frequency domain (2 – 30 Hz, 0 – 1800ms) revealed a significant cluster ($P = 0.045$, cluster-corrected) of difference in power between the two tasks at low frequencies (< 5 Hz), spanning from 600 to 1200ms (Figure 4a, b). To further explore this effect, we extracted the average power values from the time window of the significant cluster, separately for each Load condition, in different frequency bands: 'low theta' (2 – 5 Hz) and 'high theta' (6 – 8 Hz). A 2 (Task) x 3 (Load) x 2 (Frequency Range) repeated measures ANOVA revealed a significant main effect of Frequency Range ($F_{1, 34} = 11.02$, $p = 0.002$, $\eta^2_p = 0.24$) and Load ($F_{2, 68} = 4.90$, $p = 0.010$, $\eta^2_p = 0.13$). Crucially, the factor Frequency Range significantly interacted with both Task ($F_{1, 34} = 16.45$, $p < 0.001$, $\eta^2_p = 0.37$) and Load ($F_{1.44, 49.04} = 6.75$, $p = 0.006$, $\eta^2_p = 0.17$). More specifically, differences between the two tasks were significant in the low theta range ($F_{1, 34} = 6.51$, $p = 0.015$) but not in the high theta range ($F_{1,\,34} = 0.15$, $p = 0.699$). On the contrary, a significant effect of Load was found in the high theta range ($F_{2,\,68} = 9.77$, $p < 0.001$), but was not present for low theta range ($F_{2,\,68} = 0.12$, $p = 0.884$). The main effect of Task, the interaction of Task and Load, and the three-way interaction of Task, Load and Frequency Range were not significant (all *p*s > 0.15) (Figure 4c).

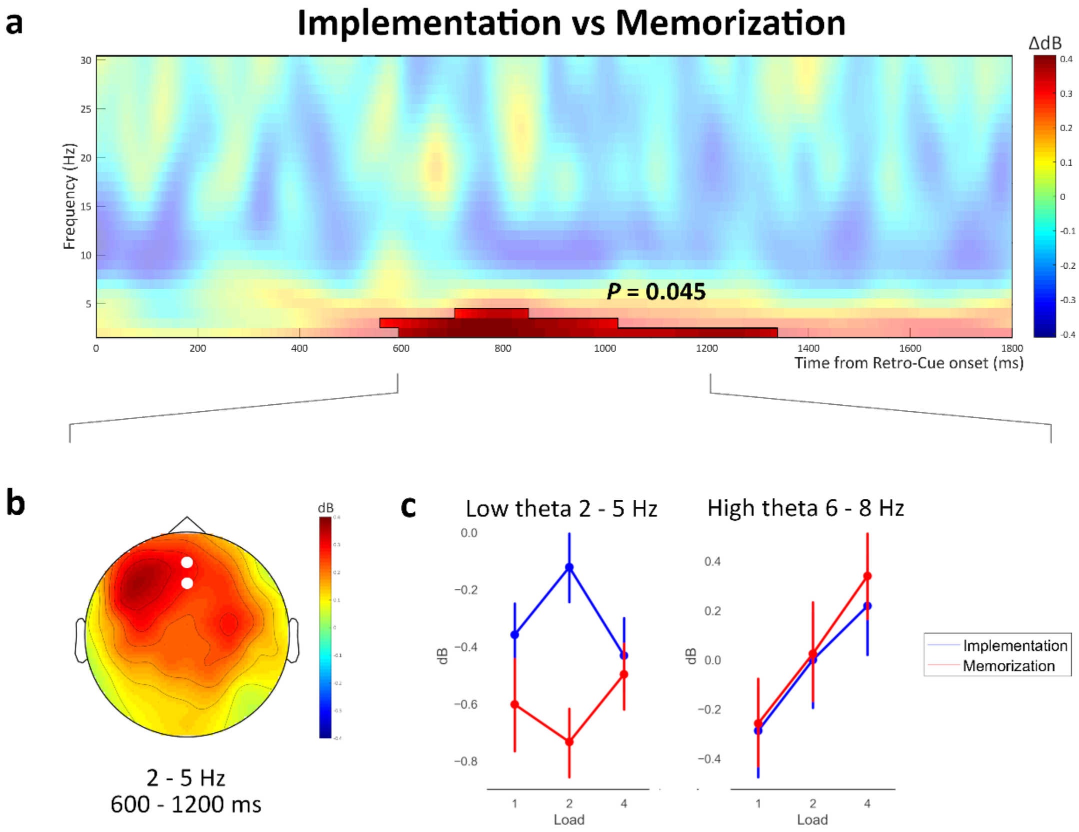

**Figure 4: Oscillatory theta dynamics in Implementation compared to Memorization**. **a**) Time-frequency spectrogram of the difference between Implementation and Memorization, averaged across the electrodes Fz and AFz. The contoured area outlines the significant cluster ($P = 0.045$) obtained with a cluster-based permutation approach. **b**) Scalp topography of the difference in activity in low theta (2 – 5 Hz) between Implementation and Memorization, averaged in the time window 600 – 1200ms. White dots indicate the a-priori selected electrodes (Fz and AFz) used for the cluster-based permutation test. **c**)

Average power values in the time window 600 – 1200ms, separately for low theta (2 – 5 Hz) and high theta (6 – 8 Hz). Error bars represent the s.e.m. calculated across participants (n = 35).

One potential confound when investigating activity in low frequency bands is that this might be reflecting sustained ERPs. We ruled out this possibility by comparing across tasks the Contingent Negative Variation (CNV), a slow negative potential over centro-frontal electrodes during preparation for an upcoming target (Walter et al., 1964). The CNV did not show a differential pattern between Implementation and Memorization (see Supplementary material), suggesting that our frontal activity is better described by low frequency oscillations, rather than a sustained ERP. Furthermore, at the lowest estimated frequency of 2 Hz, the wavelet was two-cycles long, therefore spanning a 1s interval. This is generally assumed to be selective enough to reflect a true oscillations (Cohen, 2014).

### *3.2.4 Motor-related mu and beta suppression in Implementation*

We hypothesized proceduralization to be linked also with an increased engagement of motor and premotor regions, in preparation for the instructed upcoming movement, compared to memorization. Specifically, we predicted a suppression of oscillations in the of mu (8 – 12 Hz) and beta (20 – 30 Hz) frequency ranges, which have been shown to reflect motor cortex activity (Pineda, 2005; Cheyne, 2013; Tzagarakis et al., 2015; Schneider et al., 2017b; Rhodes et al., 2018). To test for this hypothesis, we compared Implementation and Memorization tasks in the time-frequency domain across a large cluster of electrodes over the motor and pre-motor cortices. We found a significant negative cluster ($P < 0.001$, cluster corrected) approximately in the time window 700 – 1600ms, spanning a broad range of frequencies above 8 Hz (Figure 5a). Next, we extracted the average power in the two distinct frequency bands (mu: 8 – 12 Hz and beta: 20 – 30 Hz) between 700 and 1600ms after Retro-Cue onset, separately for each Task and Load condition. These power values were entered in two separate repeated measures ANOVAs, that yielded analogous results in both frequency bands. For mu, we found a significant main effect of Task ($F_{1, 34} = 6.61$, $p = 0.015$, $\eta^2_p = 0.16$) and of Load ($F_{1.70, 57.93} = 32.60$, $p < 0.001$, $\eta^2_p = 0.49$). Mu suppression was stronger for Implementation compared to Memorization task, and for lower compared to higher Loads (Implementation, Load 1: $M = 0.21$, $SD = 1.51$, Load 2: $M = 0.55$, $SD = 1.29$, Load 4: $M = 1.53$, $SD = 1.48$; Memorization, Load 1: $M = 0.46$, $SD = 1.57$, Load 2: $M = 1.10$, $SD = 1.67$, Load 4: $M = 1.60$, $SD = 1.50$). Similarly, for beta the results revealed significant differences between the two tasks ($F_{1, 34} = 5.23$, $p = 0.028$, $\eta^2_p = 0.13$) and across Loads ($F_{2, 68} = 7.90$, $p < 0.001$, $\eta^2_p = 0.19$). Again, beta suppression was stronger in Implementation and for lower Loads (Implementation, Load 1: $M = -0.27$, $SD = 0.69$, Load 2: $M = -0.21$, $SD = 0.49$, Load 4: $M = 0.01$, $SD = 0.63$; Memorization, Load 1: $M = -0.11$, $SD = 0.67$, Load 2: $M = 0.04$, $SD = 0.64$, Load 4: $M = 0.13$, $SD = 0.67$). For both frequency ranges, the interaction of Task x Load did not reach significance ($p$s > 0.35) (Figure 5b, c). To qualitatively estimate the topographies of these effects, scalp maps are depicted, separately for each Task and Load (Figure 5d, e).

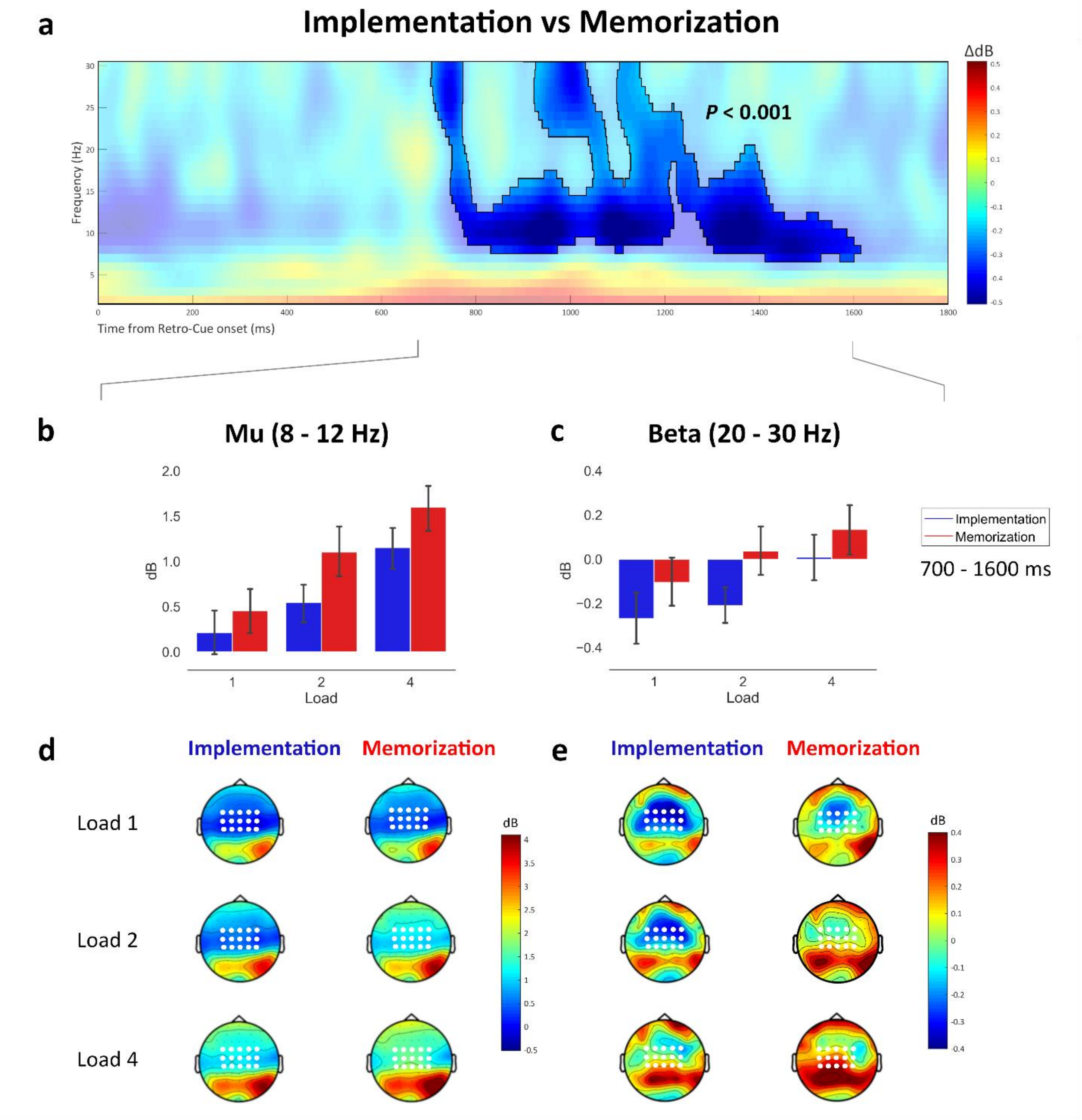

**Figure 5: Motor-related mu and beta suppression**. **a**) Time-frequency spectrogram of the difference between Implementation and Memorization, averaged across a cluster of a-priori selected centro-parietal electrodes. The contoured area outlines the significant cluster (*P* < 0.001) obtained with a cluster-based permutation approach. **b**) and **c**) Average power values in the time window 700 – 1600ms after Retro-Cue onset, separately for the two frequency bands of interest. Error bars represent the s.e.m., computed across participants (n = 35). **d**) and **e**) Scalp topographies for each Task x Load condition, averaged in the time

window 700 – 1600ms, separately for the two frequency bands of interest. White dots indicate the electrodes from which the power amplitude was extracted for the cluster-based permutation and the ANOVAs.

## 4. Discussion

In the present study, we investigated the temporal dynamics underlying novel instruction implementation. In line with our predictions and the framework proposed by Myers and colleagues (2017), we observed an analogous unfolding of early attentional mechanisms between tasks, reflected in similar patterns of alpha power dynamics. Crucially, Implementation and Memorization showed dissociable oscillatory features starting after alpha suppression, suggesting that Implementation-specific processes are occurring after the relevant items are prioritized. These mechanisms are likely involved in the reformatting of the selected S-R mappings, a process requiring the exertion of cognitive control and resulting in the preparation of the instructed motor plan.

### *4.1 Low frequencies oscillations for S-R binding in Implementation*

Based on previous research, we predicted low frequency oscillations over frontal sensors to be associated with the proactive reformatting of the S-R mapping into an action-oriented code. The crucial contribution of the PFC in quickly converting symbolic instructions into task-sets for prospective action has been widely established in several fMRI studies (Brass et al., 2009; Cole et al., 2010; Ruge and Wolfensteller, 2010; Dumontheil et al., 2011; Hartstra et al., 2011; González-García et al., 2017; Palenciano et al., 2019b). Activation of prefrontal areas was associated with the creation and activation of procedural condition-action rules from the instructed mappings, a process that is thought to involve cognitive control (Brass et al., 2017). Analogously, the need for top-down control over complex goal-directed cognitive operations is traditionally linked with oscillations in the theta frequency range over prefrontal cortices (Cavanagh and Frank, 2014; Cooper et al., 2019). Moreover, recent influential models of large-scale brain interactions attribute to theta the crucial role of orchestrating information exchange between distant areas by synchronizing their firing pattern (Fries, 2005, 2015; Lisman and Jensen, 2013; McLelland and VanRullen, 2016; Verguts, 2017). We assumed the Implementation task in our experiment to require a more extensive allocation of cognitive control, given the need to manipulate the declarative representations of the selected S-R mappings into their procedural counterparts, leading to increased power in low frequencies over frontal sensors (Itthipuripat et al., 2013). As expected, we found a significant cluster of frontal activity dissociating the two tasks. Interestingly, this cluster was restricted to frequencies below 5 Hz. While the higher theta band (6 – 8 Hz) tracked the number of selected items (Onton et al., 2005), slower oscillations were sensitive to the task. Recent studies found that switching internal attention between items in WM for prospective use was associated with an increase in delta/low-theta oscillations (de Vries et al., 2018, 2019c). We found low theta activity to be different between tasks and sustained during the CTI. This suggests that its role might go beyond the exertion of short-lasting top-down control over attentional prioritization, but also encompasses the reformatting of the prioritized memoranda into behavior-guiding representations. This is possible for the Implementation task, while in the Memorization task the prioritized representation(s) can only be used as a template to guide the upcoming task (Olivers et al., 2011; Olivers and Eimer, 2011; de Vries et al., 2019a). Although not significant, the pattern of low theta activity suggests a different contribution of this frequency in the Implementation task across loads, possibly reflecting capacity limits in the proceduralization process.

Therefore, the stronger activity in Implementation likely reflects the inherently more extensive reformatting process of proceduralization, which we assume involves a theta-driven binding between the stimulus and its corresponding motor plan. The Memorization task also requires the prioritization and the binding of stimulus and response, but this would engage theta dynamics to a lesser extent, given the impossibility to activate a motor plan.

### *4.2 Motor preparation in Implementation is reflected in mu and beta suppression*

Previous fMRI studies showed that the proactive proceduralization of novel instructions is accompanied by increased neural activity in pre-motor areas, suggesting motor preparation (Ruge and Wolfensteller, 2010; Hartstra et al., 2011, 2012; Muhle-Karbe et al., 2017; Bourguignon et al., 2018). This motor involvement is thought to boost instruction implementation by enabling mental simulation of the overt application of the instructed mappings (Brass et al., 2017). Motor imagery has been associated with suppression in mu and beta bands over motor cortices (Pfurtscheller and Neuper, 1997; McFarland et al., 2000; Pineda, 2005; Pfurtscheller et al., 2006; Cheyne, 2013). Consistently, we found these markers to be larger in Implementation compared to Memorization, already during the CTI. While in both tasks participants had to perform an overt motor response at the end of the trial, only during Implementation they could proactively start preparing their response to the upcoming target. This rules out the possibility that the observed differences reflect more general mechanisms of unspecific motor energization, temporal estimation or target expectancy (Van Elswijk et al., 2007; Nobre and Van Ede, 2018; Wiener et al., 2018). Moreover, we found mu and beta dynamics to be sensitive to load: the lower the number of relevant mappings, the stronger the suppression. This finding supports the assumption that proceduralization is subject to capacity limitations and proceduralizing less mappings leads to stronger procedural representations and motor activation (Liefooghe et al., 2012). Engagement of motor regions is also occurring during Memorization, although to a lesser extent, as revealed by the observed Load effect. One possibility is that our responses, despite being bilateral and more abstract than the traditional 'left' and 'right', are automatically processed also when held declaratively, causing motor activation (Bundt et al., 2015). Overall, our results suggest that preparing to execute novel mappings involves the activation of a specific motor plan corresponding to the instructed response.

### *4.3 Alpha-mediated attentional orienting is analogous in Implementation and Memorization*

We observed no task-dependent modulation in the dynamics of alpha oscillations. Activity in the alpha frequency band has been consistently associated with attentional processing (van Ede, 2017). In particular, posterior alpha power decreases over electrodes contralateral to the attended hemifield, both in perceptual and in WM tasks (Sauseng et al., 2005; Jensen and Mazaheri, 2010; Poch et al., 2017). In our experiment, participants were encouraged to focus on the selected items and discard the unselected ones. Coherently, in both tasks we found after the retro-cue a significant suppression of alpha oscillations contralateral to the attended hemifield. The most influential model proposed to account for this phenomenon is referred to as *Gating by Inhibition* (Jensen and

Mazaheri, 2010). According to it, top-down alpha modulation of sensory cortices allows for the inhibition of irrelevant inputs, contributing to the creation of a functional network optimized to perform the task (Mazaheri et al., 2014; Van Diepen et al., 2019). Our clusters of alpha lateralization extended around 600 – 800ms after retro-cue. This dynamic is consistent with previous findings on retrospective attention orienting, showing modulations within 500 and 1000ms (Wallis et al., 2015; Wolff et al., 2015, 2017; Mok et al., 2016; Poch et al., 2017, 2018). The effectiveness of the selection process is further supported by load-dependent centro-posterior alpha power modulation (Jensen, 2002). The time course of alpha power has been observed to be sensitive to the number of items retained during a WM task. In both our tasks, alpha increased with load. Crucially, lateralized and load-dependent alpha activity was not different between tasks, confirming that the information provided by the retro-cue is used to analogously orient attention and select the items that are likely to be probed, independently of task demands.

## 5. Conclusions

Our study shed light for the first time on the oscillatory dynamics associated with the retrospective prioritization and proceduralization of novel instructions. We showed that alpha-mediated mechanisms of attentional orienting are in place to prioritize the relevant items, independently from the upcoming task demands. Conversely, other neural features were sensitive to the task. The implementation of novel mappings, as opposed to their declarative maintenance, is characterized by increased power in low frequencies and by stronger suppression of mu and beta activity. We interpreted the former to be a signature of the allocation of cognitive control for the successful binding of stimulus and response into a behavior-optimized procedure, and the later to reflect the motor preparation of the instructed motor responses by means of motor imagery. Crucially, these differences were found during the CTI, supporting the idea that under appropriate task conditions, proceduralization can occur proactively in preparation for the upcoming response execution demands.

Future research should investigate how proceduralization affects the underlying neural representation of the instructed mapping, under the assumption that it is recoded from a declarative to a procedural format, and how prefrontal regions mediate this reformatting process. Moreover, future studies should explore the capacity limits of proceduralization: whether they are caused by the concurrent activation of interfering motor plans or by a failure in recoding more instructions into procedures is still an open question to be addressed.

## REFERENCES

Bhandari A, Duncan J (2014) Goal neglect and knowledge chunking in the construction of novel behaviour. Cognition 130:11–30.

Bonnefond M, Jensen O (2012) Alpha oscillations serve to protect working memory maintenance against anticipated distracters. Curr Biol 22:1969–1974.

Bourguignon NJ, Braem S, Hartstra E, De Houwer J, Brass M (2018) Encoding of Novel Verbal Instructions for Prospective Action in the Lateral Prefrontal Cortex: Evidence from Univariate and Multivariate Functional Magnetic Resonance Imaging Analysis. J Cogn Neurosci 26:1–15.

Brady TF, Konkle T, Alvarez GA, Oliva A (2013) Real-world objects are not represented as bound units: Independent forgetting of different object details from visual memory. J Exp Psychol Gen 142:791–808.

Brass M, Liefooghe B, Braem S, De Houwer J (2017) Following new task instructions: Evidence for a dissociation between knowing and doing. Neurosci Biobehav Rev 81:16–28.

Brass M, Wenke D, Spengler S, Waszak F (2009) Neural Correlates of Overcoming Interference from Instructed and Implemented Stimulus-Response Associations. J Neurosci 29:1766–1772.

Brodeur MB, Guérard K, Bouras M (2014) Bank of Standardized Stimuli (BOSS) Phase II: 930 New Normative Photos Paterson K, ed. PLoS One 9:e106953.

Bundt C, Bardi L, Abrahamse EL, Brass M, Notebaert W (2015) It wasn’t me! Motor activation from irrelevant spatial information in the absence of a response. Front Hum Neurosci 9.

Capilla A, Schoffelen J-M, Paterson G, Thut G, Gross J (2014) Dissociated α-Band Modulations in the Dorsal and Ventral Visual Pathways in Visuospatial Attention and Perception. Cereb Cortex 24:550–561.

Cavanagh JF, Frank MJ (2014) Frontal theta as a mechanism for cognitive control. Trends Cogn Sci 18:414–421.

Cheyne DO (2013) MEG studies of sensorimotor rhythms: A review. Exp Neurol 245:27–39.

Cohen MX (2014) Analyzing neural time series data: theory and practice. MIT Press.

Cohen MX, Donner TH (2013) Midfrontal conflict-related theta-band power reflects neural oscillations that predict behavior. J Neurophysiol 110:2752–2763.

Cole MW, Bagic A, Kass R, Schneider W (2010) Prefrontal dynamics underlying rapid instructed task learning reverse with practice. J Neurosci 30:14245–14254.

Cole MW, Laurent P, Stocco A (2013) Rapid instructed task learning: A new window into the human brain’s unique capacity for flexible cognitive control. Cogn Affect Behav Neurosci 13:1–22.

Cooper PS, Karayanidis F, McKewen M, McLellan-Hall S, Wong ASW, Skippen P, Cavanagh JF (2019) Frontal theta predicts specific cognitive control-induced behavioural changes beyond general reaction time slowing. Neuroimage 189:130–140.

de Vries IEJ, Slagter HA, Olivers CNL (2019a) Oscillatory Control over Representational States in Working Memory. Trends Cogn Sci.

de Vries IEJ, Van Driel J, Karacaoglu M, Olivers CNL (2018) Priority Switches in Visual Working Memory are Supported by Frontal Delta and Posterior Alpha Interactions. Cereb Cortex 28:4090–4104.

de Vries IEJ, van Driel J, Olivers CNL (2019b) Decoding the status of working memory representations in preparation of visual selection. Neuroimage 191:549–559.

de Vries IEJ, van Driel J, Olivers CNL (2019c) Decoding the status of working memory representations in preparation of visual selection. Neuroimage 191:549–559.

Delorme A, Makeig S (2004) EEGLAB : an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J Neurosci Methods 134:9–21.

Demanet J, Liefooghe B, Hartstra E, Wenke D, De Houwer J, Brass M (2016) There is more into ‘doing’ than ‘knowing’: The function of the right inferior frontal sulcus is specific for implementing versus memorising verbal instructions. Neuroimage 141:350–356.

Dumontheil I, Thompson R, Duncan J (2011) Assembly and use of new task rules in fronto-parietal cortex. J Cogn Neurosci 23:168–182.

Duncan J, Emslie H, Williams P, Johnson R, Freer C (1996) Intelligence and the Frontal Lobe: The Organization of Goal-Directed Behavior. Cogn Psychol 30:257–303.

Fries P (2005) A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. Trends Cogn Sci 9:474–480.

Fries P (2015) Rhythms for Cognition: Communication through Coherence. Neuron 88:220–235.

González-García C, Arco JE, Palenciano AF, Ramírez J, Ruz M (2017) Encoding, preparation and implementation of novel complex verbal instructions. Neuroimage 148:264–273.

González-García C, Formica S, Liefooghe B, Brass M (2020) Attentional prioritization reconfigures novel instructions into action-oriented task sets. Cognition 194:104059.

González-García C, Formica S, Wisniewski D, Brass M (2019) Frontoparietal action-oriented codes support novel task set implementation. bioRxiv:830067.

Gould IC, Rushworth MF, Nobre AC (2011) Indexing the graded allocation of visuospatial attention using anticipatory alpha oscillations. J Neurophysiol 105:1318–1326.

Griffin G, Holub A, Perona P (2007) Caltech-256 Object Category Dataset. Available at: https://authors.library.caltech.edu/7694/.

Groppe DM, Makeig S, Kutas M (2009) Identifying reliable independent components via split-half comparisons. Neuroimage 45:1199–1211.

Hartstra E, Kühn S, Verguts T, Brass M (2011) The implementation of verbal instructions: An fMRI study. Hum Brain Mapp 32:1811–1824.

Hartstra E, Waszak F, Brass M (2012) The implementation of verbal instructions:

Dissociating motor preparation from the formation of stimulus-response associations. Neuroimage 63:1143–1153.

Itthipuripat S, Wessel JR, Aron AR (2013) Frontal theta is a signature of successful working memory manipulation. Exp Brain Res 224:255–262.

Jasp Team (2019) JASP (Version 0.11.1)[Computer software]. Available at: https://jasp-stats.org/.

Jensen O (2002) Oscillations in the Alpha Band (9-12 Hz) Increase with Memory Load during Retention in a Short-term Memory Task. Cereb Cortex 12:877–882.

Jensen O, Mazaheri A (2010) Shaping Functional Architecture by Oscillatory Alpha Activity: Gating by Inhibition. Front Hum Neurosci 4:1–8.

Klem GH, Lüders HO, Jasper HH, Elger C (1999) The ten-twenty electrode system of the International Federation. The International Federation of Clinical Neurophysiology. Electroencephalogr Clin Neurophysiol Suppl 52:3–6.

Konkle T, Brady TF, Alvarez GA, Oliva A (2010) Conceptual distinctiveness supports detailed visual long-term memory for real-world objects. J Exp Psychol Gen 139:558–578.

Liefooghe B, Wenke D, De Houwer J (2012) Instruction-based task-rule congruency effects. J Exp Psychol Learn Mem Cogn 38:1325–1335.

Lisman JE, Jensen O (2013) The Theta-Gamma Neural Code. Neuron 77:1002–1016.

Manza P, Hau CL V., Leung H-C (2014) Alpha Power Gates Relevant Information during Working Memory Updating. J Neurosci 34:5998–6002.

Marchesotti S, Bassolino M, Serino A, Bleuler H, Blanke O (2016) Quantifying the role of motor imagery in brain-machine interfaces. Sci Rep 6:24076.

Maris E, Oostenveld R (2007) Nonparametric statistical testing of EEG- and MEG-data. J Neurosci Methods 164:177–190.

Mazaheri A, van Schouwenburg MR, Dimitrijevic A, Denys D, Cools R, Jensen O (2014) Region-specific modulations in oscillatory alpha activity serve to facilitate processing in the visual and auditory modalities. Neuroimage 87:356–362.

McFarland DJ, Miner LA, Vaughan TM, Wolpaw JR (2000) Mu and Beta Rhythm Topographies During Motor Imagery and Actual Movements. Brain Topogr 12:177–186.

McLelland D, VanRullen R (2016) Theta-Gamma Coding Meets Communication-through-Coherence: Neuronal Oscillatory Multiplexing Theories Reconciled. PLoS Comput Biol 12:e1005162.

Milner B (1963) Effects of Different Brain Lesions on Card Sorting: The Role of the Frontal Lobes. Arch Neurol 9:90–100.

Mok RM, Myers NE, Wallis G, Nobre AC (2016) Behavioral and Neural Markers of Flexible Attention over Working Memory in Aging. Cereb Cortex 26:1831–1842.

Muhle-Karbe PS, Duncan J, De Baene W, Mitchell DJ, Brass M (2017) Neural Coding for Instruction-Based Task Sets in Human Frontoparietal and Visual Cortex. Cereb Cortex 27:1891–1905.

Myers NE, Stokes MG, Nobre AC (2017) Prioritizing Information during Working

Memory: Beyond Sustained Internal Attention. Trends Cogn Sci 21:449–461 Available at: http://dx.doi.org/10.1016/j.tics.2017.03.010.

Myers NE, Walther L, Wallis G, Stokes MG, Nobre AC (2015) Temporal Dynamics of Attention during Encoding versus Maintenance of Working Memory: Complementary Views from Event-related Potentials and Alpha-band Oscillations. J Cogn Neurosci 27:492–508.

Neuper C, Pfurtscheller G (2001) Event-related dynamics of cortical rhythms: Frequency-specific features and functional correlates. Int J Psychophysiol 43:41–58.

Nobre AC, Van Ede F (2018) Anticipated moments: Temporal structure in attention. Nat Rev Neurosci 19:34–48.

Olivers CNL, Eimer M (2011) On the difference between working memory and attentional set. Neuropsychologia 49:1553–1558.

Olivers CNL, Peters J, Houtkamp R, Roelfsema PR (2011) Different states in visual working memory: When it guides attention and when it does not. Trends Cogn Sci 15:327–334.

Onton J, Delorme A, Makeig S (2005) Frontal midline EEG dynamics during working memory. Neuroimage 27:341–356.

Oostenveld R, Fries P, Maris E, Schoffelen J-M (2010) FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. Comput Intell Neurosci 2011.

Palenciano AF, González-García C, Arco JE, Pessoa L, Ruz M (2019a) Representational organization of novel task sets during proactive encoding. J Neurosci:0725–19.

Palenciano AF, González-García C, Arco JE, Ruz M (2019b) Transient and Sustained Control Mechanisms Supporting Novel Instructed Behavior. Cereb Cortex 29:3948–3960.

Perrin F, Pernier J, Bertrand O, Echallier JF (1989) Spherical splines for scalp potential and current density mapping. Electroencephalogr Clin Neurophysiol 72:184–187.

Pfurtscheller G, Brunner C, Schlögl A, Lopes da Silva FH (2006) Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. Neuroimage 31:153–159.

Pfurtscheller G, Neuper C (1997) Motor imagery activates primary sensorimotor area in humans. Neurosci Lett 239:65–68.

Pineda JA (2005) The functional significance of mu rhythms: Translating ‘seeing’ and ‘hearing’ into ‘doing’. Brain Res Rev 50:57–68.

Poch C, Carretie L, Campo P (2017) A dual mechanism underlying alpha lateralization in attentional orienting to mental representation. Biol Psychol 128:63–70.

Poch C, Valdivia M, Capilla A, Hinojosa JA, Campo P (2018) Suppression of no-longer relevant information in Working Memory: An alpha-power related mechanism? Biol Psychol 135:112–116.

Popov T, Popova P, Harkotte M, Awiszus B, Rockstroh B, Miller GA (2018) Cross-frequency interactions between frontal theta and posterior alpha control mechanisms foster working memory. Neuroimage 181:728–733.

Rhodes E, Gaetz WC, Marsden J, Hall SD (2018) Transient Alpha and Beta Synchrony Underlies Preparatory Recruitment of Directional Motor Networks. J Cogn Neurosci 30:867–875.

Rihs TA, Michel CM, Thut G (2007) Mechanisms of selective inhibition in visual spatial attention are indexed by α-band EEG synchronization. Eur J Neurosci 25:603–610.

Rihs TA, Michel CM, Thut G (2009) A bias for posterior α-band power suppression versus enhancement during shifting versus maintenance of spatial attention. Neuroimage 44:190–199.

Rohenkohl G, Nobre AC (2011) Alpha oscillations related to anticipatory attention follow temporal expectations. J Neurosci 31:14076–14084.

Ruge H, Wolfensteller U (2010) Rapid formation of pragmatic rule representations in the human brain during instruction-based learning. Cereb Cortex 20:1656–1667.

Sauseng P, Klimesch W, Stadler W, Schabus M, Doppelmayr M, Hanslmayr S, Gruber WR, Birbaumer N (2005) A shift of visual spatial attention is selectively associated with human EEG alpha activity. Eur J Neurosci 22:2917–2926.

Schneider D, Barth A, Getzmann S, Wascher E (2017a) On the neural mechanisms underlying the protective function of retroactive cuing against perceptual interference: Evidence by event-related potentials of the EEG. Biol Psychol 124:47–56.

Schneider D, Barth A, Wascher E (2017b) On the contribution of motor planning to the retroactive cuing benefit in working memory: Evidence by mu and beta oscillatory activity in the EEG. Neuroimage 162:73–85.

Souza AS, Oberauer K (2016) In search of the focus of attention in working memory: 13 years of the retro-cue effect. Attention, Perception, Psychophys 78:1839–1860.

Thut G, Nietzel A, Brandt SA, Pascual-Leone A (2006) Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. J Neurosci 26:9494–9502.

Tzagarakis C, West S, Pellizzer G (2015) Brain oscillatory activity during motor preparation: Effect of directional uncertainty on beta, but not alpha, frequency band. Front Neurosci 9:1–13.

Van Diepen R, Foxe JJ, Mazaheri A (2019) The functional role of alpha-band activity in attentional processing: The current zeitgeist and future outlook. Curr Opin Psychol.

van Dijk H, Schoffelen J-M, Oostenveld R, Jensen O (2008) Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. J Neurosci 28:1816–1823.

van Ede F (2017) Mnemonic and attentional roles for states of attenuated alpha oscillations in perceptual working memory: A review. Eur J Neurosci:1–7.

van Ede F, Chekroud SR, Stokes MG, Nobre AC (2019) Concurrent visual and motor selection during visual working memory guided action. Nat Neurosci 22:477–483.

Van Elswijk G, Kleine BU, Overeem S, Stegeman DF (2007) Expectancy induces dynamic modulation of corticospinal excitability. J Cogn Neurosci 19:121–131.

Verbeke P, Verguts T (2019) Learning to synchronize: How biological agents can couple neural task modules for dealing with the stability-plasticity dilemma Franklin NT, ed. PLOS Comput Biol 15:e1006604.

Verguts T (2017) Binding by random bursts: A computational model of cognitive control. J Cogn Neurosci.

Wallis G, Stokes M, Cousijn H, Woolrich M, Nobre AC (2015) Frontoparietal and Cingulo-opercular Networks Play Dissociable Roles in Control of Working Memory. J Cogn Neurosci 27:2019–2034.

Walter WG, Cooper R, Aldridge VJ, McCallum WC, Winter AL (1964) Contingent negative variation : An electric sign of sensori-motor association and expectancy in the human brain. Nature 203:380–384.

Wenke D, Gaschler R, Nattkemper D, Frensch PA (2009) Strategic influences on implementing instructions for future actions. Psychol Res Psychol Forsch 73:587–601.

Wiener M, Parikh A, Krakow A, Coslett HB (2018) An intrinsic role of beta oscillations in memory for time estimation. Sci Rep 8:1–17.

Wolff MJ, Ding J, Myers NE, Stokes MG (2015) Revealing hidden states in visual working memory using electroencephalography. Front Syst Neurosci 9:1–12.

Wolff MJ, Jochim J, Akyürek EG, Stokes MG (2017) Dynamic hidden states underlying working-memory-guided behavior. Nat Neurosci 20:864–871.