RESEARCH ARTICLE

Oscillatory EEG signatures of postponed somatosensory decisions

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Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: GRK1589/1

Abstract

In recent electroencephalography (EEG) studies, the vibrotactile frequency comparison task has been used to study oscillatory signatures of perceptual decision making in humans, revealing a choice-selective modulation of premotor upper beta band power shortly before decisions were reported. Importantly, these studies focused on decisions that were (1) indicated immediately after stimulus presentation, and (2) for which a direct motor mapping was provided. Here, we investigated whether the putative beta band choice signal also extends to postponed decisions, and how such a decision signal might be influenced by a response mapping that is dissociated from a specific motor command. We recorded EEG data in two separate experiments, both employing the vibrotactile frequency comparison task with delayed decision reports. In the first experiment, delayed choices were associated with a fixed motor mapping, whereas in the second experiment, choices were mapped onto a color code concealing a specific motor response until the end of the delay phase. In between stimulus presentations, as well as after the second stimulus, prefrontal beta band power indexed stimulus information held in working memory. Beta band power also encoded choices during the response delay, notably, in different cortical areas depending on the provided response mapping. In particular, when decisions were associated with a specific motor mapping, choices were represented in premotor cortices, whereas the color mapping resulted in a choice-selective modulation of beta band power in parietal cortices. Together, our findings imply that *how* a choice is expressed (i.e., the decision consequence) determines *where* in the cortical sensorimotor hierarchy an according decision signal is processed.

KEYWORDS

beta band, decision making, delayed decisions, intentional decisions, intentional framework, perceptual, response context, somatosensory, vibrotactile, working memory

1 | INTRODUCTION

A key question regarding perceptual decision making concerns the functional role of sensory cortices, association cortices, and motor cortices in the transformation of sensory information into motor actions. Besides the highly influential studies on perceptual decisions in the visual domain (for reviews see Heekeren, Marrett, & Ungerleider, 2008; Gold & Shadlen, 2007), intensive research in the *somatosensory* domain has yielded seminal insights into the processes underlying a sensorimotor transformation from perception via decision to action (see Romo & de Lafuente, 2013, for a comprehensive review). In particular,

employing a vibrotactile sequential frequency comparison (SFC) task, in which monkeys had to decide whether the second of two serially presented vibrations had a higher or a lower frequency than the first one, Romo and colleagues revealed specific activity patterns of single neurons during sensory processing, working memory (WM), and decision making. That is, during stimulus presentation, single neurons in the primary somatosensory cortex encoded the stimulus frequencies (f_1 or f_2) by a monotonically increasing rate code (Salinas, Hernández, Zainos, & Romo, 2000). In the retention interval, that is, during WM maintenance, neurons in prefrontal cortices showed a sustained parametric increase or decrease in firing rates as a function of f_1 (Brody, Hernández, Zainos, & Romo, 2003; Romo, Brody, Hernández, & Lemus, 1999). In the decision phase of the task, firing rates (Hernández, Zainos, & Romo, 2002)

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recorded from medial premotor cortex (MPC), as well as the power of beta band oscillations in corresponding local field potentials (LFPs, Hagens et al., 2011), finally encoded the monkeys' upcoming choices. Further research investigated whether stimulus information (i.e., stimulus frequencies, f_1 and f_2) and choice information (i.e., the signed differences, $f_2 - f_1$) was also maintained in the corresponding brain structures when decisions had to be postponed (Lemus et al., 2007). Indeed, both stimulus frequencies and the signed differences informing choices were indexed by neuronal firing rates of MPC neurons until monkeys reported their choices.

Recent work has started to translate the findings from monkey electrophysiology recordings during the different stages of the SFC task to human electroencephalography (EEG) studies (Spitzer, Wacker, & Blankenburg, 2010; Spitzer and Blankenburg, 2011, 2012; Spitzer et al., 2014; Herding, Spitzer, & Blankenburg, 2016; 2017). In particular, during the retention interval of the task, prefrontal beta band power (20–25 Hz) has been found to scale with the frequency that had to be maintained in WM (i.e., f_1) in analogy to the monkey data (Spitzer et al., 2010; Spitzer & Blankenburg, 2011). Notably, the same modulation of beta band power during WM processing has also been observed for other sensory modalities and different analogue stimulus properties (Spitzer and Blankenburg, 2012; Spitzer et al. 2014), drawing a coherent picture of beta band power representing quantitative WM content in a generic way. Also during the decision phase of the task, beta band power has been suggested to convey task-relevant information, namely, the subjectively perceived outcome of the comparison between f_2 and f_1 (i.e., $f_2 < f_1$ or $f_2 > f_1$; Herding et al., 2016, 2017). Importantly, this choice-indicative signal originated from effector-specific premotor structures, that is, from MPC when responses were reported by button presses (Herding et al., 2016), and from the frontal eye fields (FEF) when saccades were required to indicate decisions (Herding et al., 2017). Together, these findings are well in line with an intentional framework of decision making, which, in essence, proposes that decisions are always formed in terms of intentions to act. Accordingly, decision signals should be found in those brain structures that are involved in the preparation or execution of ensuing decision reports (see Shadlen et al., 2008).

In the current study, we investigated the role of oscillatory EEG signals in the SFC task when decision reports were postponed. In particular, we aimed at extending previous findings concerning WM processing and decision making also to a delayed response setting. We recorded EEG data in two separate experiments. Both experiments deployed the vibrotactile SFC task with delayed decision reports, however, decisions were either associated with a fixed motor mapping or with a mapping onto a color code. With the delayed response design, we intended to probe whether the response delay might constitute an additional retention interval of the task-in that different quantities also need to be maintained in WM during this delay. In particular, we asked the following questions: (a) Does sensory information vanish once a decision has been made, or do we find reactivations of stimulus information during the delay period, as suggested by monkey data? (b) Are participants' choices indexed by upper beta band power originating from relevant premotor areas just as observed for immediate decision

FIGURE 1 Schematic of the task and the overall experimental design. The first stimulus with frequency f_1 ($f_1 = 16, 20, 24$, or 28 Hz) was presented for 250 ms, followed by a retention interval of $1,000$ ms. Subsequently, the second stimulus with frequency f_2 ($f_2 = f_1 \pm 0, 2$, or 4 Hz) was presented for 250 ms, followed by a $2,000$ ms response delay. Thereafter, the response mapping (RM) in form of two colored targets was presented lateral to the fixations cross. Note, that the color of the targets was only relevant in Experiment 2. In Experiment 1 the dots were also presented to ensure consistency over the experiments. After another 500 ms the fixation cross disappeared (response cue; RC) and participants reported their decision [Color figure can be viewed at wileyonlinelibrary.com]

reports (i.e., in an intentional space); or is this information referenced by upper beta band power in prefrontal structures, in analogy to the known prefrontal signature of WM content during the retention interval between f_1 and f_2 ? Additionally, we wanted to pursue the idea of an intentional framework of decision making, and contrasted clearly intentional decisions (i.e., associated with a fixed motor mapping) with more abstract decisions (i.e., based on a color mapping), leading to the final question: (c) How are perceptual decisions processed if no fixed motor mapping is associated with a choice, that is, if participants cannot prepare a specific action as a consequence of their decision, but have to decide in a more abstract space?

We found that answers to all of these questions were related to oscillations in the (upper) beta band (~ 15 – 40 Hz). In particular, the level of beta band power indexed the different task-relevant quantities at different stages of the task. The most probable source locations of the observed effects confirm previous WM findings, and support the general idea of an intentional framework of decision making, even for decisions that are not directly tied to a motor response.

2 | MATERIALS AND METHODS

2.1 | Participants

We acquired EEG data from a total of 35 (23 female; 21–40 years old) right-handed participants completing the delayed SFC tasks in two separate experiments (17 in the first experiment, and 18 in the second experiment; see Figure 1). Informed consent was obtained from each participant prior to the experiment. The study was approved by the local ethics committee at the Freie Universität Berlin and was in accordance with the Declaration of Helsinki.

2.2 | Stimuli and task

Both experiments consisted of the same SFC task but varied in the way participants were instructed to report their decisions (see below).

FIGURE 2 Behavioral model based on Bayesian inference accounts for influence of time-order effect on choice behavior. (a) Stimulus set used in both experiment. Each square indicates a stimulus pair. Color code indicates the according physical difference between both frequencies $f_2 - f_1$. Dashed rectangle marks the orthogonal subset of trials, for which f_2 was not correlated with $f_2 - f_1$. (b) Probability to choose $f_2 < f_1$ as a function of f_1 , separately for all physical differences $f_2 - f_1$ (i.e., -4, -2, 0, 2, and 4 Hz), with squares indicating group means of observed data, and lines corresponding to averaged model fits. (c) Grand mean proportions of correct responses (PCRs) as a function of f_1 , separately for non-zero physical differences $f_2 - f_1$ (i.e., -4, -2, 2, and 4 Hz), reveal interaction effect between f_1 and $f_2 - f_1$ (i.e., influence of TOE; see text for details). (d) Average response times (RTs; $\pm$ standard errors of the mean) were not affected by TOE, most likely as a result of the delayed response protocol. Same conventions as in c [Color figure can be viewed at wileyonlinelibrary.com]

Supra-threshold vibrotactile stimuli with a constant peak amplitude were presented to the left index finger using a 16-dot piezoelectric Braille display (4×4 quadratic matrix; 2.5 mm spacing) controlled by a programmable stimulator (Piezostimulator; Quaerosys, Schotten, Germany). The driving signals of the stimuli were generated by modulating the amplitude of a sinusoidal carrier signal (fixed at 133 Hz) using frequencies in the flutter range (i.e., 12–32 Hz; see Figure 2a). Thereby, participants perceived tactile flutter, while possible artifacts in the EEG recordings due to the physical driving signal (i.e., the voltage applied to the stimulator) were constrained to frequencies above 100 Hz, well outside the frequency range of interest (5–45 Hz; e.g., see Tobimatsu et al., 1999). More precisely, the perceived frequency (i.e., the modulation frequency) corresponded to the envelope of the driving signal, while the spectrum of the driving signal only contained two frequency components both above 100 Hz, that is, one at 133 Hz (carrier frequency) and the second one at 133 Hz + modulation frequency. The sound of the Braille display was masked by white noise (~ 80 dB), presented via loudspeakers, throughout the experiments. The experiments were implemented in Matlab (R 2013b; Version 8.2.0.701 The MathWorks), using the Psychophysics Toolbox extensions (Psychtoolbox; Version 3.0.12; Brainard, 1997; Kleiner et al., 2007) and custom Matlab code.

In each trial, two vibrotactile stimuli (250 ms each), separated by a short retention period (1,000 ms), were presented to the participants'

left index finger, while they fixated a cross in the center of a computer screen. The first stimulus could take one of four possible frequencies (f_1 : 16, 20, 24, or 28 Hz; randomly varied). In 75% of the trials, the frequency of the second stimulus (f_2) differed by ± 2 or 4 Hz from f_1 . In the remaining 25% of trials, f_2 was identical to f_1 ($f_2 = f_1$; see Figure 2a for complete stimulus set). These trials were introduced to study decisions independent from any sensory evidence. We did not inform participants that both stimuli could be identical, and asked them to always respond whether $f_2 < f_1$ or $f_2 > f_1$. In both experiments, 2,000 ms after the offset of f_2 , two colored target dots (diameter of 1° visual angle) were displayed to the left and to the right of the fixation cross (12° of visual angle off-center; vertically centered on the screen). One of the targets was blue, whereas the other one was yellow (counterbalanced over sides across trials). After another 500 ms, a response cue was provided (i.e., the fixation cross disappeared), and participants reported their choices by a button press with the right hand (i.e., " $f_2 < f_1$ " or " $f_2 > f_1$ "; see Figure 1). In Experiment 1, the colored targets were irrelevant and participants were instructed to ignore them. Instead, either choice was associated with a specific button press. The exact button-to-choice mapping was counterbalanced across participants. That is, half of the participants were instructed to press the left-arrow button if " $f_2 < f_1$ ", and the right-arrow button if " $f_2 > f_1$ ", whereas the other half of participants was instructed to respond vice versa. Consequently, participants indicated their decisions by applying

a fixed decision-to-motor mapping, allowing for the preparation of a specific action during the response delay. However, the specific actions were dissociated from particular choices across the group. In Experiment 2, participants reported their decisions by selecting a target based on its color (i.e., select blue vs. yellow target). Again, choices were indicated via left- or right-arrow button presses. Since the colored targets only appeared at the end of the response delay (i.e., 2,000 ms after f_2), and the specific spatial configuration was unpredictable (i.e., blue dot was equally likely on either side of the screen), the color mapping prevented the preparation of a specific motor response during the delay phase. Importantly, the association between a specific color (i.e., blue or yellow) and a particular choice (i.e., " $f_2 < f_1$ " or " $f_2 > f_1$ ") was again counterbalanced across participants. Taken together, in both experiments, the visual and tactile stimuli, as well as the responses per se (i.e., left- or right-arrow button press) were identical, while specific actions were dissociated from particular choices. Only the mapping of decisions onto their consequences differed between both experiments in that choices were either a priori linked to a specific motor response (Experiment 1) or not (Experiment 2; flexible link via color mapping). After a short training session of 20 trials, participants performed eight full experimental blocks, each containing 128 trials resulting in a total of 1,024 frequency comparisons.

2.3 | EEG recording

EEG was recorded with a sampling rate of 2,048 Hz (offline down-sampled to 512 Hz) using a 64-channel active electrode system (ActiveTwo; BioSemi; Amsterdam; Netherlands) with electrodes placed according to the extended 10–20 system. Three additional electrodes were used to record the vertical and horizontal electrooculogram (vEOG and hEOG, respectively). Single electrode locations were registered using a stereotactic electrode positioning system (Zebis Medical, GmbH, Isny, Germany) prior to recording.

2.4 | EEG analysis

EEG analyses were performed using SPM8 (Version 6313; Wellcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm), FieldTrip (Version: 09012017; Oostenveld et al., 2011) and custom Matlab code (Matlab R2013b; Version 8.2.0.701).

2.4.1 | Preprocessing

Preprocessing included co-registration of the channels to the individual electrode positions, rejection of noisy channels, average referencing, as well as high-pass filtering (0.5 Hz). Eye-blink artifacts were removed from the EEG by using adaptive spatial filtering based on blink templates obtained from the vEOG (see Ille et al., 2002). The continuous recordings were segmented into epochs from 2,250 ms before the onset of the second stimulus (i.e., 1,000 ms before the onset of the first stimulus) to 500 ms after the response cue. Remaining artifacts were identified by careful visual inspection of the entire EEG data in addition to an automatic marking of segments with amplitudes greater than 150 μ V. In particular, all trials exhibiting horizontal saccades were excluded from the analysis.

2.4.2 | Induced activity

To minimize the influence of stimulus-evoked activity (i.e., phase-locked), and hence, to examine purely induced activity (i.e., non-phase locked), the event-related potential (ERP; i.e., the average evoked potential) associated with each stimulus pair was subtracted from according single-trial data prior to time-frequency transformation (e.g., see Klimesch et al., 1998). In particular, the ERP for a certain f_1 – f_2 pairing was subtracted from the EEG data of those trials that contributed to the ERP (e.g., all trials with $f_1 = 20$ Hz and $f_2 = 22$ Hz). Time-frequency (TF) representations of corresponding single-trial spectral power between 5 and 45 Hz (resolved in steps of 1 Hz) were computed every 50 ms by applying a Morlet wavelet-transformation with a sliding window of seven cycles length (i.e., TF bin = 50 ms $\times$ 1 Hz). Changes of spectral power are reported as event-related (de)synchronizations (ERD/ERS) in the separate frequency bins that were resolved (Pfurtscheller & Aranibar, 1977). That is, ERD/ERS provide a measure for the percentage change in spectral power relative to a pre-stimulus baseline (–2,000 ms to –1,300 ms, for parametric effects by f_1 ; –1,000 ms to 0 ms, for parametric effects of f_2 , f_2 – f_1 , & choice). To restrain inter-trial and inter-subject variability, time frequency data were convolved with a 3 Hz $\times$ 300 ms Gaussian smoothing kernel (Kilner et al., 2005).

2.4.3 | Statistical analysis

We used the framework of general linear models (GLM) to implement different single-trial factorial designs for repeated measures, depending on the factors of interest (i.e., f_1 , f_2 , f_2 – f_1 , or choices). The resulting parameter estimates (i.e., TF maps of average spectral power for each factor of interest) were weighted with specific contrast weights. To analyze parametric effects of f_1 , we implemented a one-factorial design with four factor levels representing the four possible f_1 conditions (16, 20, 24, and 28 Hz), and tested for a parametric modulation in the resulting TF maps using a linear contrast vector (f_1 -contrast: [–0.75 –0.25 0.25 0.75]). Possible parametric effects of f_2 were investigated analogously (i.e., one-factorial design; five factor levels for possible f_2 : 18, 20, 22, 24 and 26 Hz; linear contrast vector: [–1 –0.5 0 0.5 1]), however, only using a subset of trials in which f_2 and f_2 – f_1 were independent. In the full stimulus set, factors f_2 and f_2 – f_1 were necessarily correlated (Pearson's $r = .535$, $p = .015$), since the stimulus set was designed to decorrelate f_1 from the differences f_2 – f_1 to prevent participants from anticipating how to decide already after f_1 (and both f_1 and f_2 cannot be decorrelated from f_2 – f_1 at the same time). More precisely, the highest values of f_2 (28, 30, and 32 Hz) were always associated with $f_2 > f_1$ trials, whereas the lowest f_2 values (12, 14, and 16 Hz) only occurred in $f_2 < f_1$ trials. Therefore, we excluded trials with those extreme f_2 values from subsequent analyses to avoid confounding the signed differences (f_2 – f_1) with f_2 -stimulus information and vice versa (see Figure 2a, orthogonal subset). Analyzing only data from this subset prevented us from confounding the signed differences (f_2 – f_1) with f_2 -stimulus information and vice versa. To investigate decision effects, i.e. oscillatory signals coding the difference between f_2 and f_1 , we estimated subjectively perceived frequency differences

(SPFDs) as a refined measure for the quantity on which decisions are based in the SFC task (see Herding et al., 2016, 2017). In brief, we modeled participants' choices in the framework of Bayesian inference, motivated by the observation that participants do not seem to compare f_2 with the physical value of f_1 (see Hellström, 1985, 2003), but rather with a value slightly shifted towards the mean of all presented stimulus frequencies (see Preuschhof et al., 2010; Ashourian & Loewenstein, 2011; Karim et al., 2012; Sanchez et al., 2014). This characteristic choice pattern is the result of the so called time-order error (or time-order effect; TOE), which refers to the observation that the presentation order of two sequentially presented stimuli has an influence on the discriminability of both stimuli (see Fechner, 1860; Hellström, 1985). In our model, we introduced a mean-biased version of f_1 , which we call f_1' , to account for the impact of the TOE on choice behavior (i.e., choice pattern as if comparing f_2 to a mix of f_1 and the mean of all presented stimuli). In particular, f_1' is defined as the expected value of the posterior distribution of f_1 when using a Gaussian prior centered over all presented frequencies. Three free parameters (the variance of the likelihood distribution of f_1 , the variance of the prior distribution, and an overall response bias) were estimated in this model based on each participant's choices (further details in Herding et al., 2016). The SPFDs were then defined as the differences $f_2 - f_1'$ for each stimulus pair, yielding 16 individually refined difference measures for each participant (as compared to four objective differences: -4 , -2 , 2 , and 4 Hz). Based on all observed SPFD values (differences of log-transformed frequency values), we defined six levels of SPFD (i.e., $[-0.18]$; $[-0.18 \text{ to } -0.09]$; $[-0.09 \text{ to } 0]$; $[0 \text{ to } 0.09]$; $[0.09 \text{ to } 0.17]$; $[> 0.17]$) to allow for a sensible grouping of data across participants while maintaining subjective information. We specified the levels symmetrically around a SPFD of zero (corresponding to chance-level performance), and in such a way that each participant had at least one stimulus pair for each level. For incorrect trials, we separated trials only into two classes (due to low trial numbers for some levels of SPFD) with $\text{SPFD} < 0$ and $\text{SPFD} > 0$, that is, $f_2 < f_1$ and $f_2 > f_1$. We used these discrete levels of SPFDs to implement a one-factorial design with six factor levels corresponding to the above-defined levels of SPFDs. The six TF maps resulting from GLM estimation (i.e., average spectral power per SPFD level) were contrasted using participant-specific contrast vectors defined by the median of individual SPFDs per factor level.

Up to this point, all analyses were calculated using correct trials from comparisons with $f_2 \neq f_1$, and all trials with $f_2 = f_1$ (no correct/incorrect judgment possible). To investigate effects of choices on spectral power, we also included incorrect trials as an additional factor into the analysis, leading to a one-factorial design with eight levels (i.e., six levels for correct trials + two levels for incorrect trials, see above). We contrasted the resulting TF maps using a categorical choice contrast, instead of a linear contrast as before, in order to reveal true choice effects (i.e., chose " $f_2 > f_1$ " vs. chose " $f_2 < f_1$ "). In particular, since such a choice modulation should be expressed as opposing modulations by SPFDs in correct and incorrect trials, we assessed choice effects by applying a categorical interaction contrast between both factors (i.e., $\text{SPFDs} \times \text{correct/incorrect}$: $[-1/3 \ -1/3 \ -1/3 \ 1/3 \ 1/3 \ 1/3 \ 1 \ -1]$).

On the group-level, contrast images were tested for significant effects using a cluster-based permutation test (Maris & Oostenveld, 2007). For effects of f_1 , f_2 , and $f_2 - f_1'$ we compared the summary statistics of the observed data (one-sample t test pooling across participants from both experiments; $n = 35$) with a distribution of summary statistics obtained from 1,000 randomly sign-flipped permutations. For choice effects, we followed the same procedure, but computed the respective tests for each experiment individually. A cluster was defined as a group of adjacent TF bins that all exceeded a cluster-defining threshold of $p_{\text{threshold}} < .005$ (uncorrected). Clusters that exceeded a family-wise error (FWE)-corrected threshold of $p_{\text{cluster}} < .05$ (corrected for time, frequency, and channels) were considered to be statistically significant. Due to strong a priori assumptions on the topographical distribution of signals encoding quantity information for parametric WM (or delay activity) effects of f_1 , f_2 and $f_2 - f_1'$, we applied FWE-correction only for right frontal electrodes (AF4, F2, F4, F6, FC6, FC4, FC2; e.g., see Spitzer et al., 2010; Spitzer and Blankenburg, 2011). For choice effects, we corrected over all electrodes.

2.4.4 | Source reconstruction

The cortical sources of amplitude modulations observed on the scalp level were localized using the 3D source reconstruction routines provided by SPM8 (Friston et al., 2006). Based on the individually recorded electrode positions for each participant, a forward model was constructed using an 8,196-point cortical mesh of distributed dipoles perpendicular to the cortical surface of a template brain (cf. Friston et al., 2008). The lead field of the forward model was computed using the three-shell boundary elements method EEG head model available in SPM8. Conventional minimum norm priors under group constraints (Litvak & Friston, 2008) were used to invert the forward model. For each condition, the results of model inversion were summarized in a 3D image that reflected spectral source amplitude in the TF window of interest. Relevant contrasts of these 3D images served as an estimate for participant-specific source locations and were used for group level statistical analysis (see Litvak et al., 2011).

More precisely, the most likely sources of the different effects were localized using the preprocessed stimulus-locked induced EEG data (i.e., in the time domain). Additionally, the data were bandpass filtered in the frequency range of the relevant TF cluster identified on the scalp level (± 1 Hz to ensure that no information is lost at the cluster borders). The 3D images summarizing each condition were computed over TF windows that were tightly bound to the extent of corresponding clusters, that is, temporally and with respect to the frequency range without the ± 1 Hz margin at the cluster borders. To identify cortical sources in which the respective amplitude was modulated by f_1 , f_2 , $f_2 - f_1'$, or by choice, the 3D images were weighted by a contrast vector in analogy to the sensor space analysis. Source estimates were analyzed on the group level using conventional t tests. The results of this mass-univariate statistical test are displayed at a significance level of $p < .05$ (uncorrected) to indicate the most probable sources of the effects observed at the scalp-level. Note that we did not apply any spatial priors or explicit masking for source estimation. However, the model inversion under group constraints might be seen as

applying an implicit group mask, since individual sources are constrained to lie within an optimal subset of all possible source locations given the overall group data (see Litvak & Friston, 2008). Anatomical reference for source estimates was established on the basis of the SPM anatomy toolbox (version 2.2c; Eickhoff et al., 2005).

3 | RESULTS

3.1 | Behavior

Proportions of correct responses (PCRs) were analyzed using a two factorial 2×4 ANOVA including the between-subject factor *Experiment* (two levels) and the within-subject factor *f1-frequency* (four levels; 16, 20, 24, and 28 Hz). We used Greenhouse-Geisser correction to adjust for degrees of freedom, and hence, p values for violated assumptions of sphericity. Table 1 and Figure 2c show the PCRs across *f1-frequencies* for the two experiments. There was no main effect for the factor *Experiment* ($F(1, 33) = 0.71, p = .4$), but a significant main effect for *f1-frequency* ($F(2.18, 71.65) = 11.92, p < .001$). Within-subject contrasts revealed that performance accuracy was significantly lower for $f1 = 16$ and 28 Hz compared to $f1 = 20$ and 24 Hz. No interaction between both factors was observed ($F(2.1, 71.65) = 0.28, p = 0.77$). We repeated this analysis substituting the within-subject factor *f1-frequency* by the factor *f2-f1* (four levels; $-4, -2, 2$, and 4 Hz). Also here, we used Greenhouse-Geisser correction to adjust for degrees of freedom, and hence, p values for violated assumptions of sphericity. This analysis showed that, as could be expected, the factor *f2-f1* had a significant impact on participants' performance accuracies ($F(1.55, 51.24) = 24.56, p < .001$). Within-subject contrasts revealed that performance accuracy was significantly lower for $f2-f1 = 2$ and -2 Hz compared to $f2-f1 = -4$ and 4 Hz, picturing that larger frequency differences are easier to perceive as compared to smaller differences between $f2$ and $f1$. There was neither a main effect for the factor *Experiment* ($F(1, 33) = 0.8, p = .38$), nor an interaction effect between *Experiment* $\times$ *f2-f1* ($F(1.55, 51.24) = 0.3, p = .83$). As usually observed in sequential comparison tasks, choice behavior of participants was heavily influenced by the TOE (see Fechner, 1860; Preuschhof et al., 2010; Ashourian & Loewenstein, 2011; Karim et al., 2012; squares in Figure 2c). Briefly, the TOE refers to the observation that the temporal order of stimulus presentation matters in a sequential comparison paradigm. We could formally show the influence of the TOE as an interaction between the factors *f1* and *f2-f1* (i.e., 4×4 ANOVA; $F(2.5, 85) = 96.05, p < .001$; pooled data over both experiments). This finding implies that participants seemed to have over- respectively underestimated low and high $f1$ ("low" and "high" relative to the mean of all presented stimuli). That is, participants tended to choose " $f2 < f1$ " more often for low $f1$ as compared to high $f1$, even when both stimuli were identical, that is, $f1 = f2$ (see Figure 2b). This choice pattern concisely summarizes the influence of the TOE on decisions in any sequential comparison task, and can be modeled by the assumption that participants compare $f2$ not only with the physical value of $f1$, but also with the mean frequency of all previously presented stimuli (or rather, with a mixture of $f1$ and the mean stimulus frequency; see Ashourian &

TABLE 1 Behavioral results

A Percent of correct responses in % (SEM)				
<i>f1</i> (Hz)	16	20	24	28
Experiment 1	63.9 (2.6)	72.5 (1.8)	71.8 (2)	65.5 (2.3)
Experiment 2	65.5 (3)	74.8 (2.1)	72.9 (2.4)	69.4 (2.4)
<i>f2-f1</i> (Hz)	-4	-2	2	4
Experiment 1	71.3 (3.1)	61.3 (3.1)	62.1 (2.5)	75.5 (2.7)
Experiment 2	75.7 (3.1)	62 (1.9)	64.6 (2.2)	77.7 (2.8)
B Response times in ms (SEM)				
<i>f1</i> (Hz)	16	20	24	28
Experiment 1				
correct	334 (14)	337 (16)	334 (15)	336 (16)
incorrect	335 (15)	338 (16)	335 (18)	339 (16)
Experiment 2				
correct	323 (20)	319 (20)	319 (20)	323 (20)
incorrect	322 (20)	322 (20)	323 (20)	319 (20)
<i>f2-f1</i> (Hz)	-4	-2	2	4
Experiment 1				
Correct	336 (15)	336 (15)	340 (17)	334 (16)
Incorrect	339 (18)	340 (18)	343 (16)	347 (17)
Experiment 2				
Correct	319 (20)	322 (19)	320 (20)	323 (21)
Incorrect	322 (20)	324 (19)	314 (19)	334 (22)

Note: **A** Mean discrimination performance and **B** average median response times (correct and incorrect) for each *f1* and each *f2-f1* condition in experiments 1 and 2. Standard errors of the mean (SEM) are depicted in brackets.

Loewenstein, 2011; Herding et al., 2016). Importantly, our behavioral model based on Bayesian inference (i.e., $f2-f1'$) was able to account for the observed choice behavior (see lines in Figure 2a-c), and clearly outperformed a model that assumed choices based on the physical differences $f2-f1$ (Bayes factors > 3 for 33/35 participants).

Further, we looked at the variation of response times (RTs) in dependence of our experimental factors. First, we calculated a three-factorial $2 \times 4 \times 2$ ANOVA with factors *Experiment* (two levels), *f1-frequency* (four levels; 16, 20, 24, and 28 Hz), and *Accuracy* (two levels; correct vs. incorrect responses). In this analysis, RTs were not affected systematically by any of these factors (all $p > .41$). Again, we reanalyzed the same ANOVA substituting the within-subject factor *f1-frequency* by the factor *f2-f1* (four levels; $-4, -2, 2$, and 4 Hz). We only found a trend for the main effect of the factor *Accuracy* ($F(1, 33) = 3.33, p = .07$), indicating that participants responded more slowly in incorrect decisions. Apart from that, there was no systematic effect of any of the factors on RTs (all $p > .12$), most likely as a result of the delayed response protocol. As participants formed their decisions already during the response delay, RTs could not capture any

FIGURE 3 Overall changes in evoked and induced power throughout the paradigm with respect to prestimulus baseline interval (1,000 ms). (a) Grand mean of somatosensory steady-state evoked potentials (SSEPs) for an exemplary stimulus pair ($f_1 = 20$ Hz, $f_2 = 24$ Hz) pooled across electrodes Fz, F2, FCz, CP6, CP4, P4, and P6 (see inset). (b) Grand mean of changes in induced power pooled across electrodes C3, C5, CP5, CP3, C4, C6, CP6, CP4, and POz (see inset). Beta band power (15–25 Hz) decreases during tactile stimulus presentation in bilateral central electrodes, followed by a contralateral rebound. Alpha band power (8–13 Hz) in occipital electrodes increases during the working memory interval [Color figure can be viewed at wileyonlinelibrary.com]

variations in decision time between conditions, but only reflected how fast participants were able to react to the response cue (i.e., the offset of the fixation cross).

3.2 | Electroencephalography

In a first step, we validated our EEG data by checking for classic EEG signatures in response to tactile stimulations. In particular, we confirmed that only during stimulus presentation, evoked power (i.e., the time-frequency representation of event-related potentials) over contralateral somatosensory areas increased exclusively in those frequencies that corresponded to the presented stimulus frequency (Figure 3a; e.g., see Tobimatsu et al., 1999; Spitzer et al., 2010; Herding et al., 2016). Moreover, we also observed the typical decrease and the following rebound in induced beta band power over somatosensory areas as a result of tactile stimulation (Figure 3b; e.g., Jasper & Andrews, 1938; Pfurtscheller, 1981; Bauer et al., 2006; Spitzer et al., 2010; Ludwig et al., 2016; Herding et al., 2016).

3.2.1 | Parametric effects of f_1

Figure 4a shows parametric effects of f_1 during the retention interval and the response delay pooled over both experiments. Here, we identified two significant clusters. First, in the retention interval after the offset of f_1 and before the onset of f_2 , beta band power (15–20 Hz) exhibited a parametric modulation by f_1 from -800 to -400 ms in electrodes AF4, F2, and F4 ($p_{\text{cluster}} = .04$, FWE-corrected over a priori defined set of electrodes; Figure 4a,c). That is, the higher the f_1 -frequency, the higher the beta band power in these prefrontal electrodes during the retention interval (Figure 4b). During the response delay, we found a similar modulation by f_1 , 650–900 ms after the onset of f_2 in

prefrontal electrodes AF4, F4, F6, FC6, and FC4 ($p_{\text{cluster}} = .02$, FWE-corrected over a priori defined set of electrodes; Figure 4a–c). Of note, when applying a more liberal cluster-defining threshold ($p_{\text{threshold}} < .01$), the observed frontal cluster also extended to parietal electrodes, forming one large cluster, however, only during the retention interval between f_1 and f_2 ($p_{\text{cluster}} = .03$, FWE-corrected for whole scalp; see Figure 4c). The topographical distributions (extracted from the marked time-frequency windows) confirm that the signal for both of these parametric effects during WM and response delay was mostly carried by right prefrontal electrodes (Figure 4c). Source reconstructions revealed that the modulation by f_1 most likely originated from the right prefrontal cortex (PFC) both during the WM interval (Brodmann area 46; MNI peak-coordinates: 23, 57, 20; 597 voxels) as well as during the response delay (Brodmann area 45; MNI peak-coordinate: 50, 34, 7; 742 voxels). During the WM interval, additional sources were found in primary somatosensory cortex (SI; Brodmann area 3b, 1, and 2; MNI peak-coordinate: 36, -33 , 55; 695 voxels) and superior parietal lobe (SPL; Brodmann area 7A; MNI peak-coordinates: 21, -57 , 60; 485 voxels).

3.2.2 | Parametric effects of f_2

Figure 4d shows parametric effects of f_2 during the response delay pooled over the two experiments. Including all trials of the orthogonal subset in the analysis, we did not find any significant power modulation by f_2 . To increase the signal-to-noise ratio, we excluded trials with $f_2 = f_1$ from further analysis, as in these trials, frequencies cannot be successfully discriminated. We identified a significant cluster indicating a positive parametric modulation by f_2 in electrodes AF4, F2, F4, and F6 ($p_{\text{cluster}} = .04$, FWE-corrected over a priori defined set of electrodes) in the frequency range from 30 to 35 Hz, 1,600 to 1,800 ms after

FIGURE 4 Upper beta band power is modulated by f_1 , f_2 , and the subjectively perceived frequency differences (SPFDs) f_2-f_1' during retention interval and response delay in the vibrotactile SFC task. (a) Time-frequency (TF) representation of group statistics testing a parametric modulation of induced power by f_1 in correct trials, averaged over a priori defined electrodes (black & white dots in c). The significant TF clusters ($p_{\text{retention}} = .04$; $p_{\text{delay}} = .02$; FWE-corrected over a priori defined set of right frontal electrodes) are marked by dashed rectangles. (b) Time-courses of oscillatory power in the frequency range from 15 to 20 Hz for the four f_1 stimulus frequencies (16, 20, 24, and 28 Hz) averaged over electrodes within the predefined region of interest (ROI; black and white dots in c). (c) Upper: Topographical scalp distributions of the two marked time-frequency windows in the retention interval and the delay (dashed rectangles in a). Lower: 3D source localization for the parametric modulation by f_1 for the indicated time-frequency windows (dashed rectangles). Color saturation reflects cortical depths with less saturated source patches indicating deeper source locations. (d) Same as (a) for modulations by f_2 ($p_{\text{cluster}} = .04$; FWE-corrected over a priori defined right frontal electrodes). (e) Time-courses of oscillatory power in the frequency range between 30 and 35 Hz for the five f_2 stimulus frequencies of the orthogonal subset (18, 20, 22, 24, and 16 Hz) averaged over electrodes within the right prefrontal ROI. (f) Same as (c) for effects of f_2 . (g) Same as (a) for modulations by SPFDs f_2-f_1' ($p_{\text{cluster}} = .04$; FWE-corrected over a priori defined right frontal electrodes). (h) Time-courses of oscillatory power in the frequency range between 15 and 25 Hz separately for six discrete levels of SPFDs averaged across electrodes within the ROI (see Section 2 for details). (i) Same as (c) for effects of f_2-f_1' [Color figure can be viewed at wileyonlinelibrary.com]

the onset of f_2 . However, the observed prefrontal effect should be taken with care, as it is mainly driven by an overall very low beta band power for $f_2 = 18$ Hz throughout the retention interval (Figure 4e). Moreover, the cluster peak appears markedly later than for the modulations by f_1 and f_2-f_1' (Figure 4a,d,g). Nevertheless, the significant cluster seems to be overall the result of a parametric modulation by f_2 , and despite the late peak latency, the cluster already starts at the same time as the modulations by f_1 and f_2-f_1' . Source reconstruction localized the modulation by f_2 again to the right IFG (Brodmann area 45; MNI peak-coordinate: 51, 31, 3; 107 voxels; Figure 4f). When applying the same, more liberal threshold that was used to reveal the parietal extension of the modulation by f_1 (i.e., $p_{\text{threshold}} < .01$), no significant cluster was found on the whole-scalp level.

That the modulation of beta band power by f_2 was observed in a higher frequency range (~ 30 – 35 Hz) as compared to the modulation by f_1 (~ 15 – 20 Hz) might be in part related to typically observed variability in the modulated frequencies (see Spitzer et al., 2010; Spitzer &

Blankenburg, 2011, 2012; Ludwig et al., 2016; ~ 15 – 30 Hz power modulated by f_1 during WM), or might hint at differences on a more detailed level between both effects (e.g., differences in the generating mechanisms). However, the important message here should be that spectral power in the beta band seems to reflect different task-relevant quantities at different stages of the vibrotactile SFC task (see also modulations by f_2-f_1' and choices described below).

3.2.3 | Parametric effects of SPFDs

Figure 4g shows parametric effects of subjectively perceived frequency differences (SPFDs) between f_2 and f_1 (f_2-f_1') pooled over all participants from both experiments. We identified a significant cluster ($p_{\text{cluster}} < .04$, FWE-corrected over a priori defined set of electrodes) in the response delay in the frequency range from 16 to 29 Hz, 600 to 900 ms after the offset of f_2 in electrodes F6, FC4, and FC2, indexing a positive modulation of beta band power by SPFDs (Figure 4g,h). The sources of this cluster were also localized to the right IFG (Brodmann

FIGURE 5 Upper beta band power is modulated by participants' choices, with the location of modulation depending on the consequence of the decision. (a–c) Participants were provided with a motor mapping a priori (Experiment 1). (a) Time-frequency (TF) representation of group statistics testing a modulation by choices in correct as well as in incorrect trials. Spectral power between 30 and 40 Hz was modulated by choices $\sim 1,000$ ms after f_2 in frontal electrodes indicated in c ($p_{\text{cluster}} = .01$, FWE-corrected). (b) Time-courses of oscillatory power in the frequency band corresponding to the identified TF cluster in (a) (30–40 Hz), separately for six discrete levels of SPFDs for correct trials (solid lines), and two classes for incorrect trials (dashed lines; see text for details). (c) Upper: Topographical scalp distribution corresponding to the TF cluster identified in (a) (dashed rectangle), with white dots indicating electrodes spanning the cluster. Lower: 3D source reconstruction of the TF cluster displayed in (a). Color saturation reflects cortical depths with less saturated source patches, indicating deeper source locations. (d–f) Same conventions as in a–c for data from Experiment 2, in which participants were not provided with a motor mapping a priori, but mapped their decisions onto a color code. (d) Spectral power between 27 and 32 Hz was modulated by choices $\sim 1,400$ ms after f_2 in parietal electrodes indicated in f ($p_{\text{cluster}} = .04$, FWE-corrected). (e) Time-courses of oscillatory power in frequency band corresponding to TF cluster in (d). Same conventions as in (b). (f) Upper: Topographical scalp distribution corresponding to the TF cluster identified in (d) (dashed rectangle). Lower: 3D source reconstruction of the TF cluster displayed in (d). Color saturation reflects cortical depth as in (c) [Color figure can be viewed at wileyonlinelibrary.com]

area 45; MNI peak-coordinate: 47, 35, 2; 388 voxels; Figure 4i). Again, applying a more liberal threshold ($p_{\text{threshold}} < .01$) for an explorative analysis on the whole-scalp level did not reveal any statistically significant clusters.

3.2.4 | Choice effects

Figure 5 shows the effects of choices for either experiment. In the beginning, we sought to find effects in trials with $f_2 \neq f_1$, and to confirm any observed modulation by choices in trials with $f_2 = f_1$. The analysis of trials with $f_2 = f_1$, however, did not reveal any significant choice modulations, possibly because this analysis only comprised 25% of all trials (max. 256 trials per participant), which was likely not enough data to find significant effects of this kind. Nevertheless, as our Bayesian model predicted small but non-zero SPFDs, even for trials with $f_2 = f_1$ (i.e., no physical difference), we were able to divide these trials as well into “correct” and “incorrect” trials (i.e., trials with positive SPFDs and choice “ $f_2 > f_1$ ”/“ $f_2 < f_1$ ” were classified as correct/incorrect, whereas trials with negative SPFDs and choice “ $f_2 > f_1$ ”/“ $f_2 < f_1$ ” were classified as incorrect/correct). These trials could thus also be grouped into the known SPFD classes, allowing for a combined analysis with all the other trials (i.e., $f_2 \neq f_1$ & $f_2 = f_1$ trials together). Choice effects reported in the following were computed on all trials, irrespective of whether they were correct or incorrect. That is, the time-frequency maps display the group statistics of the interaction contrast

between the sign of the SPFD (i.e., $f_2 < f_1$ /“ $f_2 > f_1$ ”) and correct/incorrect decisions. In other words, this analysis only reveals modulations of spectral power by the sign of the differences between f_1 and f_2 , if the modulations happen in opposite directions for correct and incorrect trials. Hence, any identified effects are intimately linked to the participants' behavior.

In *Experiment 1*, there was a significant cluster ($p_{\text{cluster}} = .01$, FWE-corrected) in eleven (pre)frontal electrodes (see Figure 5c), strongest in electrodes F1 and F2, highlighting a modulation of spectral power by choices in frequencies from 30 to 40 Hz at a time around 750 to 1,050 ms after the onset of f_2 (Figure 5a). In particular, the power in this frequency range was always higher for “ $f_2 > f_1$ ” choices as compared with “ $f_2 < f_1$ ” choices, irrespective of whether choices were correct or incorrect (Figure 5b). Source reconstruction localized this choice modulation to the left medial premotor cortex (MPC; Brodmann area 6; MNI peak coordinate: $-19, 4, 53$; 80 voxels; Figure 5c).

In *Experiment 2*, we found a significant cluster ($p_{\text{cluster}} = .04$, FWE-corrected) in seven parietal electrodes (see Figure 5f), strongest in CP1, CPz, and CP2. This cluster was evident in a frequency range between 27 and 32 Hz around 1,200 and 1,550 ms after the offset of f_2 (Figure 5d). In particular, choices of “ $f_2 > f_1$ ” were again associated with higher spectral power than choices of “ $f_2 < f_1$ ”, regardless of whether choices were correct or not (Figure 5e). A source reconstruction suggested the posterior parietal cortex (PPC) in the left hemisphere (Inferior Parietal

Lobe; Bordman area: 39; MNI peak coordinate: $-36, -71, 38$; 69 voxels; Figure 5f) as the most likely origin of the choice modulation in this experiment.

4 | DISCUSSION

In the present study we investigated oscillatory EEG correlates of decision making in the vibrotactile SFC task with delayed responses. We introduced different response mappings in two separate experiments to explore the influence of decision consequences on relevant choice signals. We also focused on oscillatory signatures of WM processing, and probed whether individual stimulus information, alongside of choice information, was maintained during the delay phase of this task. During the main retention interval, that is between $f1$ and $f2$, we observed a parametric modulation of spectral power in right prefrontal beta band oscillations (15–25 Hz) by the frequency of the first stimulus ($f1$). During the ensuing response delay (or “second retention interval”), parametric power modulations by $f1$, $f2$, as well as by the estimated subjectively perceived frequency differences (SPFDs; $f2-f1'$) were also evident in right prefrontal electrodes, spanning similar frequencies (15–35 Hz). Depending on the response mapping, we moreover found different cortical sources of choice-selective modulations in the upper beta band (~ 25 –40 Hz). These sources indicated that choices mapped onto a specific action (Experiment 1) were represented in premotor areas. In contrast, choices associated with a mapping onto a color code (Experiment 2) were processed in parietal areas. Notably, all observed choice-related power modulations were inverted for *incorrect* trials, underpinning the behavioral relevance of the respective signals.

4.1 | Maintenance of stimulus information throughout the task

Memory-based perceptual decisions entail the comparison of an active representation of sensory information with previously presented sensory information maintained in WM (Hayden & Pasternak, 2013). For memory-based decisions in the somatosensory domain, the vibrotactile SFC task has been extensively used to study the underlying neural processes in monkeys (Romo et al., 1999; Hernández et al., 2010; for review see Romo & de Lafuente, 2013) and in humans (Li Hegner et al., 2010; Pleger et al., 2006; Spitzer et al., 2010; 2014; Spitzer & Blankenburg, 2011; 2012). Specifically, during the retention phase of the task, the PFC has been implicated by animal work (e.g., Romo et al., 1999), as well as by several human EEG studies (e.g., Spitzer et al., 2010; Spitzer & Blankenburg, 2011), to index the content that has to be maintained in WM, that is, $f1$. In overall agreement with the monkey literature, and directly replicating the previous EEG studies, we found that the power of beta band oscillations in prefrontal electrodes was modulated by $f1$ during the retention interval of the task. Other studies have generalized this effect to visual and auditory WM (Spitzer & Blankenburg, 2012) as well as to different analogue stimulus features (Spitzer et al., 2014). In line with the common notion that besides PFC also parietal cortex encodes quantitative information (e.g., see Nieder & Dehaene, 2009), we found that the modulation of beta band power by

$f1$ during the WM phase of the task also extended to parietal areas. At the same time, recent work has identified load-dependent modulations of beta band power in somatosensory areas within the parietal lobe (van Ede et al., 2017), suggesting a recruitment of modality specific early sensory cortices during WM processing (e.g., see D'Esposito & Postle, 2015). However, the parietal extension of the beta band modulation in the current study was only found with a more liberal statistical approach, and has not been reported in other studies that applied the same paradigm (e.g., Spitzer et al., 2010, 2014; Spitzer & Blankenburg, 2011, 2012). Moreover, content-specific modulations in early sensory cortices during WM processing, especially in the somatosensory domain, are still highly controversial (e.g., see Leavitt et al., 2017). Future work will need to reveal whether a content-specific signature during WM processing in parietal beta band power can be robustly recorded in human EEG data. If so, it remains to be shown whether such a parietal content-specific modulation originates from posterior parietal parts in line with the notion of quantitative information processing in these areas (e.g., Nieder & Dehaene, 2009), or rather from early somatosensory cortices as suggested by a sensory recruitment theory of WM (e.g., see D'Esposito & Postle, 2015; van Ede et al., 2017). Taken together, consistent reports of content-specific modulations of upper beta band power suggest that oscillations in this frequency range might reflect an internal estimate of an abstract quantity ascribed to the relevant stimulus feature held in WM (see also Spitzer & Blankenburg, 2011; Spitzer et al. 2014).

In previous studies, participants usually reported their decision right after the presentation of the second stimulus. Only a few studies in monkeys investigated how stimulus information and decision evidence are further processed in cases where the decision report is delayed, i.e. when a decision has to be stored in WM (e.g., Lemus et al., 2007; Hernández et al., 2010; Haegens et al., 2011). Here, an interesting question is whether only information about the decision is maintained in WM or if stimulus information, on which the decision was based, is stored alongside, for example, to reevaluate the decision. If such stimulus information was also retained during the decision delay, one could expect to observe similar effects as those indexing the maintenance of $f1$ (see above). Indeed, we observed a parametric modulation of prefrontal beta band power as a function of $f1$ and $f2$ during the response delay. Further, a ROI-based analysis indicated that decisional evidence in the form of SPFDs ($f2-f1'$) was also represented in right prefrontal beta band power. The present findings thus complement earlier studies of the delayed SFC task, in which firing rates in monkeys' medial premotor cortex (MPC) monotonically encoded $f1$, $f2$, and $f2-f1$ (Lemus et al., 2007). Our results further extend the original findings by Spitzer et al. (2010) in multiple ways: we show that the maintenance of $f2$ and a reactivation of $f1$ during the forced response delay induced the same parametric modulations of beta band power as $f1$ in the (initial) retention interval. Further, we show that this modulation was not only evident for single stimulus features but also for dynamic combinations of quantitative estimates such as the subjectively perceived differences between $f2$ and $f1$. From an ecological perspective, maintaining stimulus information over the course of the response delay is an appealing concept (even though decisions have

been already formed after the presentation of f_2 , and responses can possibly be prepared), because time resources are exploited, and the flexibility to adapt to changing affordances is preserved (Lemus et al., 2007).

4.2 | Oscillatory choice signals are represented in the space of their consequences

In the field of perceptual decision making, two main hypotheses about the neural implementation of decision formation have evolved over the last decades. On the one hand, the intentional framework views decision making as a selection between a limited set of affordances or intentions, processed in areas related to motor planning (Cisek & Kalaska 2010; Shadlen et al. 2008). On the other hand, a modality-transcending general decision module is assumed, supposedly located in the dorsolateral prefrontal cortex (Heekeren et al., 2008) or in the anterior insular (Ho et al., 2009; Liu & Pleskac, 2011). Curiously, the findings obtained in the vibrotactile SFC paradigm (reviewed in Romo & de Lafuente, 2013) have rarely been linked to either of these two conceptual frameworks, possibly because most of the work with the SFC task focused exclusively on decision reports by button presses. In the context of button press responses, however, the available results appear to be in favor of an intentional framework of decision making. Choice-selective signals were consistently reported in recordings from premotor areas that are known to be involved in the preparation of the according decision reports (e.g., Hernández et al., 2002, 2010; Romo et al., 2004; Haegens et al., 2011; Herding et al., 2016). Conversely, firing rates in PFC were also shown to reflect upcoming choices (Jun et al. 2010; Hernández et al., 2010), which might be interpreted in favor of a general decision module. However, in two recent EEG studies, we provided more evidence for an intentional interpretation of perceptual decisions by showing that the same choice signal appears to originate from different effector-specific premotor structures, depending on the response modality (Herding et al., 2016, 2017). That is, we found a choice-indicative modulation of upper beta band power (i.e., increased beta band power for " $f_2 > f_1$ " choices as compared to " $f_2 < f_1$ " choices; see also Haegens et al., 2011) most likely originating from MPC when responses were reported by button presses, and with a source in FEF when saccades were used to indicate responses. In the current study, we further corroborated the idea of an intentional framework of decision making. We extended the aforementioned findings to postponed decision reports in the vibrotactile SFC task, but notably, only when choices were associated with a fixed motor mapping (Experiment 1). In line with previous animal studies (Lemus et al., 2007; Haegens et al., 2011), we could hence show that choice information was also maintained in premotor areas during a forced response delay. In particular, we found the same choice signal in upper beta band power that was previously only associated with immediate decision reports in the vibrotactile SFC task (see Herding et al., 2016, 2017). Interestingly, a recent study in rats substantiated a causal role of frontal motor cortices for maintaining choice information (Goard et al., 2016). In a memory-guided visual decision task, the authors showed that after optogenetic inhibition of frontal motor cortices, but not of

parietal or sensory areas, maintenance of choice information was disrupted.

Besides premotor structures, the PPC has been strongly implicated in the formation of perceptual decisions, especially in the visual domain, and when responses were reported by saccades (for review see Gold & Shadlen, 2007). Specifically, firing rates of single neurons in PPC (i.e., in lateral intraparietal area; LIP) were shown to reflect accumulating evidence for oculomotor decisions, peaking at the time of the decision report (e.g., Shadlen & Newsome, 2001; Roitman & Shadlen, 2002). Recently, Bennur and Gold (2011) demonstrated that LIP appears to index evidence for subsequent choices also when decisions were dissociated from a specific oculomotor action. The authors applied a variant of the classic random dot motion (RDM) task, in which choices (i.e., perceived motion direction) were associated with a color mapping similar to the one used in our study (e.g., if leftward motion, choose red target). Monkeys were trained to make a saccade to one of two visual targets based on the targets' colors, which were only revealed before, during, or after stimulus presentation. Crucially, firing rates of LIP neurons encoded sensory evidence for a decision (i.e., perceived net motion) even before the colors of the targets were disclosed, i.e., before a specific action could be prepared. Only after the motor mapping was shown firing rates in LIP started to encode the direction of the subsequent saccade as known from previous work (e.g., Shadlen & Newsome, 2001; Roitman & Shadlen, 2002). In line with these insights, we found the usual choice-indicative modulation of upper beta band power also when choices were associated with a color mapping that concealed a specific motor action (Experiment 2), crucially, with a most-likely source in PPC. That is, the lack of a specific motor mapping led to a relocation of a known choice signal from premotor cortices (Experiment 1) to PPC (Experiment 2).

Whereas the signal in MPC lends itself to a straightforward interpretation (i.e., informing a subsequent button press), an interpretation of the choice-informative signal in PPC is more speculative. Beyond a role in perceptual decision making, the PPC has long been known to show spatial specificity, both to encode the location of visual stimuli as well as to guide movements toward spatial goals (e.g., Andersen, 1995; Colby & Goldberg, 1999). In particular, the PPC has been suggested to implement bottom-up driven saliency maps of the surrounding space to guide spatial attention (e.g., see Itti & Koch, 2000), or relatedly, to implement intentional maps as to plan movements (on a cognitive level) within this space (e.g., see Andersen & Buneo, 2002; Andersen & Cui, 2009). The suggestion of the PPC implementing priority maps, which extend the notion of saliency maps by incorporating top-down signals, can be seen as a combination of both views (e.g., Bisley & Goldberg, 2010). In particular, these priority maps have been suggested not to present intentions per se, but rather to guide the intentions for movement planning. With the given color mapping in our task, the outcome of the comparison between f_1 and f_2 can be seen as to inform an intention to select a target whose location is not yet determined, that is, select the one target dot (out of two targets at fixed locations) with a specific color. Importantly, the subjective comparison outcome determines the color of the dot that has to be selected. In other words, the comparison between f_1 and f_2 provides the information that allows

formulating an intention to act in the given context. From this perspective, we assume that the observed beta band signal in PPC signifies the information (i.e., the decision outcome) that can be used to construct a priority map to guide behavior (i.e., the decision report) in our task. Note that our findings do not exclude the presence of other more detailed evidence signals in PPC. We only argue that the level of upper beta band power does not seem to indicate fine-grained evidence, but rather the categorized decision outcome (see also Herding et al., 2016, 2017). Moreover, note that not observing a modulation of premotor beta band power by the original comparison outcome (i.e., " $f_2 < f_1$ " or " $f_2 > f_1$ ") even after revealing the colored choice targets does not imply that premotor areas have not been involved in the decision report per se when a color-mapping was required. The lack of such a modulation in premotor areas rather suggests that premotor areas do not have, or rather do not need, access to the original comparison outcome, as the final decision report is solely based on where the to-be-chosen color appeared.

Together, our findings suggest that the information that determines a decision (here, the categorized comparison outcome) is processed in cortical areas that implement the consequences of that decision, i.e., in PMC when a motor mapping is provided, and in PPC when a mapping onto visuospatial features (i.e. color and location of the target) is required. A parsimonious interpretation of this observation would be that the same cascade of neural processes underlies the unfolding decision in both scenarios. By providing different response mappings in Experiments 1 and 2, we could catch a glimpse of the sensorimotor transformation at different stages of the process. Namely, at those stages in which the next step of the transformation (i.e., the decision consequence) needs to be implemented. In particular, at the stage of motor preparation when a specific motor mapping was provided (i.e., in PMC; Experiment 1), or at a more abstract stage—before motor preparation—when a specific motor response could not be anticipated (i.e., in PPC; Experiment 2). Accordingly, monkeys' FEF seem to have access to evolving decisional evidence only when a specific motor mapping is provided for a decision report (Gold & Shadlen, 2003): microstimulation of FEF reliably evoked an involuntary saccade of the monkeys before they could indicate their choices in an RDM task. Importantly, this evoked saccade was deflected toward the later chosen response targets, only when a specific motor mapping was provided in advance. However on the other hand, Katz et al. (2016) questioned the causal role of LIP for decisions under these circumstances, challenging the idea of a mere serial processing stream from parietal to frontal areas. The authors showed that a pharmacological inactivation of LIP had no effect on decision performance in an RDM task, whereas area MT (i.e., source of the sensory evidence) proved to be indispensable. Hence, when a choice is directly associated with a specific action, LIP activity seems to be largely irrelevant for a decision (Katz et al., 2016), whereas FEF appears to encode choices solely under these conditions (Gold & Shadlen, 2003). Taken together, these results suggest that premotor areas (i.e., FEF) and PPC (i.e., LIP) play distinct roles in decision making, possibly dissociated by the level of abstractness or the complexity in the resulting action consequence. Accordingly, and in line with previous monkey data (Bennur & Gold, 2011), we here provide further evidence

for such a dissociation: a choice signal in PPC but not in premotor structures when no direct motor mapping is provided. In sum, we suggest that instead of having observed the sensorimotor transformation at different stages of one serial processing stream, the different response mappings might have provoked different routes for the sensorimotor transformation.

To conclude, we systematically investigated the influence of different response mappings (motor mapping vs. color mapping) in postponed decisions based on vibrotactile frequency comparisons. We found that overall, stimulus information, decisional evidence, and choices were represented in beta band power throughout the task, that is, also after the presentation of the second stimulus, suggesting that beta band power might index different task-relevant quantities during respective stages of the task (i.e., f_1 , f_2 , f_2-f_1' , and categorized comparison outcome). In particular, we found that choices that could be mapped onto specific actions were encoded in premotor areas involved in the planning and preparation of the according motor response. Conversely, choices that were not associated with a specific action, but rather required a more abstract response mapping, were encoded in posterior parietal regions. In sum, our findings are well in line with an intentional framework of decision making, and clearly emphasize that the consequences of a decision (i.e., how it is expressed) determine where the crucial information that informs this decision (i.e., what it is based on) is processed.

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How to cite this article: Ludwig S, Herding J, Blankenburg F. Oscillatory EEG signatures of postponed somatosensory decisions. *Hum Brain Mapp*. 2018;39:3611–3624. <https://doi.org/10.1002/hbm.24198>