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The Neural Basis of Event-Time Introspection

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ABSTRACT

We explored the neural mechanisms allowing humans to report the subjective onset times of conscious events. Magnetoencephalographic recordings of neural oscillations were obtained while human subjects introspected the timing of sensory, intentional, and motor events during a forced choice task. Brain activity was reconstructed with high spatio-temporal resolution. Event-time introspection was associated with specific neural activity at the time of subjective event onset which was spatially distinct from activity induced by the event itself. Different brain regions were selectively recruited for introspection of different event types, e.g., the bilateral angular gyrus for introspection of intention. Our results suggest that event-time introspection engages specific neural networks to assess the contents of consciousness. Subjective event times should therefore be interpreted as the result of complex interactions between introspection and experience networks, rather than as direct reproduction of the individual's conscious state or as a mere post-hoc interpretation.

KEYWORDS

Consciousness – Meta-Consciousness – Decision Making –

High Gamma Oscillations – Magnetoencephalography – Libet

INTRODUCTION

In the seminal study of Libet, Gleason, Wright, & Pearl (1983), healthy human participants had to make introspective judgments about the onset times of their movement decisions while their brain activity was recorded with electroencephalography. The finding that a brain potential related to action preparation starts several hundred milliseconds before the participants introspectively decide to move has had major impact on discussions about the significance of consciousness and free will (Banks & Pockett, 2007; Haggard, 2008). Yet, even though the results were reproduced and extended by independent groups (Haggard & Eimer, 1999; Trevena & Miller, 2002), as well as with fMRI measurements (Soon, Brass, Heinze, & Haynes, 2008), and with single neuron recordings (Fried, Mukamel, & Kreiman, 2011), their implications remain a matter of debate, in particular because it is unknown how we introspect and whether introspective reports are accurate (Klein, 2002; Banks & Pockett, 2007; Danquah, Farrell, & O'Boyle, 2008). Participants in these studies were typically asked to watch a rapidly rotating clock hand, to memorize its position each time they “felt the urge to move”, and to report it after the actual physical movement, and this has been commonly referred to as the *Libet-paradigm*. The Libet-paradigm presumably is associated with numerous concurring cognitive processes, including, among others, movement planning and execution (Deiber et al., 1991; Thaler et al., 1995; Deiber, Ibanez, Sadato, & Hallett, 1996; Gerloff et al., 1998; Ball et al., 1999; Guggisberg, Dalal, Findlay, & Nagarajan, 2007), visual processing (Jastorff & Orban, 2009), working memory (Smith & Jonides, 1998; Muller & Knight, 2006; Bledowski, Rahm, & Rowe, 2009), assessment of time and simultaneity (Battelli, Pascual-Leone, & Cavanagh, 2007; Grondin, 2010), and introspection.

The term *introspection*¹ is generally defined as intermittent re-representation of the contents of consciousness and is separated from a non-introspective form of consciousness responsible for the primary processing of events (Schooler, 2002; Marcel, 2003; Overgaard &

¹ Our usage of the term introspection is synonymous to *meta-consciousness* as defined by Schooler (2002).

Sorensen, 2004; Overgaard et al., 2006), also referred to as *primary consciousness* in this article. In the Libet-paradigm, consciously making a decision or a movement are examples of primary consciousness, whereas re-representing these decisions or movements are instances of introspection.²

In this paper, we focus on this specific cognitive process crucial in the Libet-paradigm, i.e., the introspection of the timing of conscious events such as movement intentions. We hypothesize that participants have to re-represent primarily conscious events such as their movement intentions in order to determine their onset time. We call this process *event-time introspection*. The process of event-time introspection will determine how we have conscious access to, and how we can report, subjective event times, and valuable insights can be gained by examining its neural mechanisms.

Several opposing theoretical models of introspection in general have been proposed, which might also apply to event-time introspection in particular. While we can by far not provide a complete overview, we will outline the main features of three influential groups of hypotheses which make experimentally testable predictions.

(i) According to one model first proposed by Brentano (1874), the introspective awareness, e.g., that I have now the urge to move, arises automatically as a “secondary object” from the primary consciousness of my intention without requiring additional cognition. According to this model, the introspection is identical to primary conscious processing.

² The term *introspection* is used in the context of the Libet-paradigm because of the reflexive character of the task which requires the re-representation of primarily conscious events. Note however, that that event-time introspection does not necessarily require an inward-direction of attention. For instance, when the participants judge the onset time of their perception of external events, they may direct their attention towards the external event rather than towards their internal experience of it. While there are important conceptual differences between inward and outward oriented attention (and probably differences in the corresponding neural processing, see Overgaard et al., 2006), they both require a re-representation of the primary conscious event. Hence, both world- and self-focussed re-representation can be introspective in this sense (Marcel, 2003). Event-time introspection also does not involve a narrative description of more qualitative aspects of experience. It therefore differs from the forms of introspection used in the phenomenologist and meditation tradition, which are more clearly inward-directed towards qualitative aspects of experience.

(ii) In an alternative model, notably proposed by the phenomenologist tradition (Husserl, 1984; Gallagher & Zahavi, 2010) but also in newer work (Jack & Shallice, 2001; Schooler, 2002; Marcel, 2003; Overgaard & Sorensen, 2004; Overgaard et al., 2006), introspection involves a specific conscious act in addition to the conscious processing of the event itself, in that it additionally requires re-representing and attending to the contents of primary consciousness.

(iii) A third model denies that humans have introspective access to their intentions and instead suggests that subjective reports result from an interpretation of perceptual recollections (Lyons, 1986; Carruthers, 2010)³.

Results from previous studies provide some evidence for model (iii). The subjective time of intention reported by human subjects can be manipulated with a short focal TMS pulse that transiently disturbs neural processing, even if this pulse is applied up to 200 ms *after* execution of the corresponding movement (Lau, Rogers, & Passingham, 2007). Moreover, if a deceptive auditory signal is presented 5 to 60 ms *after* the action to signify the movement time later than it actually occurred, subjects also introspectively report the intention onset to occur later in time (Banks & Isham, 2009; Rigoni, Brass, & Sartori, 2010). The speed of the clock used in the Libet paradigm also influences the reported event onset times (Danquah, Farrell, & O'Boyle, 2008). These findings show that introspective reports depend, at least in part, on post-action neural and perceptual processing. However, the question remains what happens at the moment of intention processing and of the subjective event time, i.e., whether humans have introspective access to their intentions.

The above three models of introspection make differing predictions with regards to the neural processes that underlie event-time introspection. Hence, we can empirically test each of them by measuring the neural activations induced by the Libet paradigm with functional imaging. Under model (i), the neural activation induced by Libet-type introspection should be

³ Carruthers (2010) allows introspective access to perceptual events, but denies it for intention.

identical to the activation related to the primary conscious processing of intentions. Under model (ii), introspection of intention onset times should be associated with distinct measurable neural activity responsible for the introspective assessment, which should co-occur in addition to, but roughly at the same time as, the activity related to intention itself. Under model (iii), the subjective assessment of intention onset times should induce neural activity related to interpretation of perceptual data in addition to activity related to intention. This additional activity should peak at times when relevant perceptual information becomes available, e.g., at the time of or after the corresponding movement⁴.

The neural mechanisms observed during event-time introspection have profound consequences on interpretations of subjective event-time reports. Only in the absence of introspection-related activity, i.e., in model (i), can we consider introspective reports as the direct reproduction of conscious intention times. Alternatively, in model (ii), introspective reports would have to be interpreted as the result of complex interactions between intention and introspection processes, whereby the introspection process can additionally influence subjective event times (Schooler, 2002; Marcel, 2003). In case of model (iii), subjective event times would be essentially blind to the conscious processing of intention.

Prior studies on the neural basis of Libet-type introspection do not resolve this issue. Functional magnetic resonance imaging (fMRI) showed activation of the presupplementary motor area (pre-SMA) when subjects introspected the time of their intention to move (Lau, Rogers, Haggard, & Passingham, 2004). Another study showed that patients with lesions in the posterior parietal cortex report the time of their decision to move at the time of the movement rather than some hundred milliseconds before as healthy subjects do (Sirigu et al., 2004), thus suggesting an important role of this brain region for conscious motor intention. However, it is unclear how the divergent results from these previous studies can be integrated into a common framework. In the context of the different models of introspection, neural

⁴ The possibility of activity related to inner speech will be considered in the Discussion.

activity in the SMA and the posterior parietal cortex could each either represent intention, introspection, or other processes related to the Libet-paradigm. Lesion studies and standard fMRI techniques also do not provide information about the time of activation in these areas. It is therefore unclear whether the introspection of movement intentions induces immediate neural activation at the time of decision-making or merely post-hoc processing at the time of sensory feedback from the chosen action. Electroencephalography (EEG) studies found greater and qualitatively different EEG potentials when movement intentions were introspected than when the same subjects moved without introspection (Keller & Heckhausen, 1990), but it is unclear what neural processes these EEG changes represent.

In this study, we probed the spatiotemporal dynamics of neural activity related to introspection of onset times of cognitive events during decision making. We specifically addressed the predictions of the 3 models described above. To this end, we asked the participants to perform two tasks simultaneously: an auditory two-alternative forced choice task and an introspective timing task of the subjective occurrence of events on a visually presented clock (*Figure 1A*). Neural activity was assayed by reconstructing videos of brain activation from magnetoencephalography (MEG), a technique that provides sufficient spatiotemporal resolution to enable a reconstruction of cortical processing at the precise time periods when human subjects introspect and consciously experience cognitive events (Guggisberg, Dalal, Findlay, & Nagarajan, 2007; Dalal et al., 2008; Dalal et al., 2009). We examined oscillatory fluctuations in the high-gamma (65-175 Hz) frequency band as an index of neural activity. Previous electrocorticographic (ECoG) studies have demonstrated that these high-frequency oscillations are spatially more focal and task-specific than slow neural oscillations or event-related potentials (Crone, Miglioretti, Gordon, & Lesser, 1998; Crone et al., 1998; Crone, Boatman, Gordon, & Hao, 2001; Brovelli, Lachaux, Kahane, & Boussaoud, 2005; Canolty et al., 2007), and that they correlate with the fMRI hemodynamic response

(Logothetis et al., 2001; Brovelli, Lachaux, Kahane, & Boussaoud, 2005; Niessing et al., 2005) while having much better time resolution.

In order to discriminate between introspection, decision, and other processes induced by the Libet-paradigm, we applied selective contrasts. Our results are most consistent with model (ii), wherein we observe distinct patterns of neural activity that are specific to event-time introspection, thereby demonstrating the feasibility of careful examination of the neural basis of introspection.

MATERIALS AND METHODS

Subjects

Nine healthy subjects (aged 26-40, 5 female) gave their written informed consent to participate in the experiments. Two subjects had to be excluded from the analyses due to an insufficient number of valid trials (see below). All procedures were approved by the UCSF Committee on Human Research.

Paradigm

The simultaneous auditory two-alternative forced choice task and introspective reporting task are schematically depicted in *Figure 1A*.

For the auditory forced choice task, the subjects were confronted, in each trial, with one of three phonemes /u/, /a/, or /ua/ (duration 325 ms), which were spoken by a male voice and played binaurally through pneumatic earphones. The phonemes /u/ and /a/ instructed the participants to press the left or the right button, respectively (CUED choice condition), and /ua/ to choose and press either button (FREE choice condition). Phonemes rather than sinusoidal tones were used as cues, because previous work had shown that phonemes induce more high-frequency activity in the auditory cortex than tones (Crone, Boatman, Gordon, & Hao, 2001), and therefore provide a better signal for our analysis procedures. Both choice conditions were presented equally often and in a pseudo-randomized order for

each subject. For the CUED condition, the left and right cues were played in pseudo-random order in 50% of the CUED trials each. For the FREE condition, subjects were instructed to press each button about equally often, but to choose spontaneously and avoid predefined response patterns.

For the simultaneous introspective reporting task, subjects watched an analogue clock (Libet, Gleason, Wright, & Pearl, 1983; Lau, Rogers, Haggard, & Passingham, 2004; Sirigu et al., 2004) with a diameter of approximately 5° and a single red clock hand completing a full rotation every 3 s. Each fifth tick was labelled with 0, 5, 10, ..., 55. The participants were instructed to verbally report, after each trial, the position of the clock hand at the time of one of the following three events: "when you heard the phoneme" (PHONEME introspection condition), "when you decided which finger to move" (DECISION introspection condition), or "when you started moving your finger" (MOVEMENT introspection condition). Only one timing judgment had to be made during each trial, and the corresponding instructions were displayed in a distinctive colour at the bottom of the screen. The three introspection conditions were presented in recurring blocks of 40 trials.

A total of 480 trials were collected for each subject (160 for each introspection condition). For each trial, the clock started to move at a random time point. After an interval varying randomly between 700 and 1800 ms, one of the three cueing phonemes was presented. The subjects made their choice according to the perceived cue and pressed a button while memorizing the clock position at the event corresponding to the current introspection condition. Subjects were asked to press the left or right button as soon as they had made their decision with the index finger of the corresponding hand. After the button press, the clock hand kept moving for 1500 to 2500 ms. Thereafter, the participants had unlimited time to verbally report the memorized clock position, which was logged by the experimenter located outside the magnetically shielded room.

The combined tasks required a high level of concentration and were considered difficult by all participants. Nevertheless, after some initial practice trials which were not included in the analysis, all subjects were able to correctly perform the tasks. Yet, 2 of the 9 recorded subjects had to be excluded, one because of frequent left-right confusions in the CUED choice task, and the other because of a highly unequal left-right choice distribution in the FREE choice task.

Behavioural Analyses

Choice reaction times, i.e., the latency between onset of the cueing phonemes and onset of a button press were measured for each trial and averaged. Differences in reaction time and subjective timing reports between choice and introspection conditions were assessed with a two-way ANOVA for repeated measures. Subjective onset times of all 3 introspected events (phoneme onset, decision, and finger movement) were compared to the onset times of the physical events phoneme presentation and button press using two-tailed paired *t*-tests. Planned comparisons contrasted the subjective times of decision with the subjective phoneme onset and the subjective movement using two-tailed paired *t*-tests.

Recordings and Preprocessing

The participants were seated in a magnetically shielded room, and their MEG was recorded with a 275 channel whole-head CTF Omega 2000 system (VSM MedTech, Coquitlam, BC, Canada), using a sampling rate of 1200 Hz. A third-order synthetic gradient correction was applied to the MEG data (Vrba & Robinson, 2001). Trials with artefacts on visual inspection were excluded from further analysis. Furthermore, trials with obviously erroneous timing judgments of the subjects were also removed. The cut-off for exclusion was fixed at >500ms before or after the corresponding physical event (for PHONEME and MOVEMENT judgments) or >500 ms before or after the average timing judgment of all trials (for DECISION judgments).

Epochs

In order to probe the neural activity underlying introspection, we realigned the recordings of neural activity time locked to the subjective onset of the introspected events reported by the subjects. For this, we created ‘introspection epochs’ (i_p , i_d , and i_m) that were centred on the subjective event onset times and covered a time range from 300 ms before to 300 ms afterwards (*Figure 1B*). Thus, i_p epochs were generated from trials of the PHONEME condition, centred on the reported subjective perception of the phoneme; i_d epochs were created from trials of the DECISION condition, centred on

the reported time of subjective decision; and i_m epochs were created from trials of the MOVEMENT condition, centred on the reported subjective onset time of movement.

In order to differentiate neural processes related to introspection from neural processes related to primary processing of the events, we also used ‘control epochs’ (c_p , c_d , and c_m), during which the task required the same primary processing, but no introspection of the event (see *Figure 1B*). Hence, c_p epochs were centred on the neural events underlying phoneme perception (like i_p epochs), but (in contrast to i_p epochs) were generated from trials of the MOVEMENT condition, during which the subjects made no timing judgment for phoneme perception. The MOVEMENT condition rather than the DECISION condition was used for creation of c_p epochs, because the introspection of this condition was more separated in time from phoneme perception than the introspection of the DECISION condition. In order to ensure similar numbers of control and introspection epochs, we only used trials from one condition for the creation of c_p (and not from both the MOVEMENT and DECISION condition). Similarly, c_d and c_m epochs were centred on the neural events underlying decision making and movement execution, respectively, and generated from trials of the PHONEME condition. Note that although the actual introspection did not occur during the time window of the control epochs, subjects were still exposed to a dual task also during trials from which control epochs were extracted, because they had to introspect another event slightly before or after the control epoch (*Figure 1B*).

Since subjects made no introspection during control epochs, no subjective reports were available to define the centres of these epochs. The centre of control epochs relative to physical phoneme presentation and physical button press were therefore estimated from subjective times reported by each subject during trials *with* introspection of the corresponding event using three different models of event perception. The estimates were derived trial-by-trial from the model with the smallest variance (see *Supplementary Methods*). Control epochs spanned a time range between -300 ms to +300 ms relative to the estimated event onset.

Since the subjective times and the estimates used to define epochs can introduce variance and potential inaccuracies in the reconstructions, we additionally analysed the data with the physical events “phoneme presentation” (for i_p and c_p) and “button press” (for i_m and c_m) as the centres of

introspection and control epochs. No physical epoch definition was possible for i_d and c_d because the time point of decisions is not associated with a corresponding external physical event.

Trials of the FREE and CUED choice condition were combined for the main analyses. In addition, FREE and CUED choices were also assessed separately in order to address the question of whether the neural mechanisms of introspection depend on the type of choice.

Source Localisation

A 3-dimensional voxel grid covering the entire brain with 5 mm resolution was created for each subject and recording, based on a multi-sphere head model of a coregistered structural MRI. Alignment of structural and functional images was ensured by marking 3 prominent anatomical points (nasion and preauricular points) of the subject's head in the MRI images, and localizing 3 fiducials attached to the same points before and after each MEG scan.

Neural activation induced by the task was localised in space and time with a time-frequency beamformer technique, which we have described in detail elsewhere (Guggisberg, Dalal, Findlay, & Nagarajan, 2007; Dalal et al., 2008; Dalal et al., 2009). Neural oscillations in the high-gamma frequency band (65–175 Hz) were used as an index of neural processing (Crone, Miglioretti, Gordon, & Lesser, 1998; Crone et al., 1998; Crone, Boatman, Gordon, & Hao, 2001; Brovelli, Lachaux, Kahane, & Boussaoud, 2005; Canolty et al., 2007). Oscillation power changes from baseline to active time windows in the four frequency bands 65-90, 90-115, 125-150, and 150-175 Hz were processed with an adaptive spatial filter (Sekihara et al., 2001; Vrba & Robinson, 2001; Sekihara, Nagarajan, Poeppel, & Marantz, 2002; Sekihara, Nagarajan, Poeppel, & Marantz, 2004; Sekihara, Sahani, & Nagarajan, 2005); the 60 Hz powerline frequency and harmonics were excluded to reduce interference. The baseline was defined as the time window between 500 ms and 300 ms before onset of the phoneme stimulus, during which the subjects attended to the rotating clock. Active time windows had a duration of 200 ms and were shifted in overlapping steps of 50 ms within the introspection and control epochs. In addition, active windows were shifted within the continuous time range from 200 ms before to 800 ms after phoneme presentation. Separate filter weights were calculated for each time window and for each frequency band (Dalal et al., 2008). This resulted in a time-frequency

decomposition of MEG oscillation power at each voxel of each subject (see *Supplementary Figure 1* for an example).

The *Supplementary Methods* describe how cortical high-gamma oscillations could be distinguished from power changes originating from extracerebral sources such as eye movements or muscle activity.

Contrasts

In order to isolate neural activity related to introspection of phoneme perception ($\mathbf{I_P}$), introspection of decision-making ($\mathbf{I_D}$), and introspection of movement execution ($\mathbf{I_M}$) from activity related to the primary processing of these events (\mathbf{P} , \mathbf{D} , \mathbf{M}), we first contrasted introspection epochs with control epochs of each condition. Hence, at each voxel, time window, and high-gamma frequency band, the power changes during the control epoch (c_p , c_d , or c_m) were subtracted from the activations during the corresponding introspection epoch (i_p , i_d , or i_m), see *Figure 1B* and *Table 1*. In order to assess brain regions that are commonly activated by all 3 timing tasks, a conjunction analysis of all introspection conditions was performed: the area under curve (AUC) of high-gamma band increase at all time windows was calculated and compared between introspection and control epochs. Voxels with significant differences in all 3 (introspection vs. control) comparisons were extracted.

The activity isolated by this first contrast does not necessarily represent event-time introspection per se but can also be elicited by other processes required for the Libet-paradigm such as assessment of time and simultaneity and dual-task interference. In order to control for this concurring activity, we subjected the single-contrast time-frequency maps to a second contrast. The rationale behind this second contrast was that concurring activity can be expected to occur similarly during the introspection epochs of all 3 introspection conditions, whereas the introspective re-representation was expected to be specific to each condition/event. Hence, for each condition, the single-contrast time-frequency map was contrasted against the introspection epoch of another condition: i_m was subtracted from the single-contrast time-frequency map of the PHONEME condition (i_m rather than i_d was used for this second contrast, because this epoch was more separated in time from phoneme perception than

i_d). Similarly, i_p was subtracted for the double contrast of the DECISION and MOVEMENT conditions (*Table 1*).

Since the specifications and time courses of concurring activity could not be known a priori, we created a schematic and simplified model of all activity that might have been ongoing during the time window of introspection and evaluated whether our double contrasts were robust to different specifications and time courses of concurring neural activity. *Figure 1C* gives an overview of the different possible time courses of concurring neural activity that had to be controlled by the contrasts: (i) activity that may have been maintained more or less uniformly throughout each trial including during the baseline time period during which subjects watched the rotating clock, e.g., processing of visual information and motion (V in *Figure 1C*); (ii) activity that may have occurred during the entire task but not during the baseline, e.g., general attention (G); (iii) nonspecific activity that may have occurred only during the time window of introspection, e.g., assessment of time and simultaneity and dual task interference (T); (iv) activity with asymmetric time courses, i.e., activity that might have started before but not continued after the introspection (e.g., expectancy of the task-relevant event, E), or (v) activity that only outlasted but did not precede the time window of introspection (e.g., working memory for storing the introspected time points until the verbal reports, W). Note that we do not make the assumption to know the precise onset, offset, magnitude, or function of the neural processes that were present during the trials, and the model illustrated in *Figure 1C* is clearly overly simplistic. However, we focus our analyses to a limited time window around the subjective occurrence of events. Hence, our analysis does not require precise modelling of onset and offset times of concurring activity, but merely their presence or absence relative to our time window of interest, i.e., whether they started and ended before, during, or after the time window of introspection. The model includes all possible time courses of potentially confounding activity relative to the time window of introspection, no matter whether they precede, accompany, or follow introspection-related activity. We also do not need to know the magnitude or the true presence of each of these concurring activities, because they are either cancelled out or represented with a different polarity in the contrasts.

Table 1 gives an overview of the applied contrasts which finally result in the isolated neural processes of interest (in bold). After the double contrast, only the neural processes related to

introspection were represented with positive high-gamma power changes, whereas all concurring activity was either cancelled out or represented with negative power changes. This configuration enabled us to apply a positive-tailed statistical test which thresholds the resulting activity maps such that only significant positive power changes corresponding to the neural correlates of event-time introspection are retained.

In order to isolate the neural networks mediating the *processing* of the choice-related events **P**, **D**, and **M** from non-specific concurring activity, we contrasted the control epoch of each condition with the introspection epoch of another condition. The introspection epoch that was most separate in time from the given control epoch was selected for each condition. *Table 2* shows that after this contrast, only neural activity related to processing of choice-related events is associated with positive power changes, whereas all non-specific activity is either cancelled out or associated with negative power changes.

Voxel Statistics

A positive-tailed *t*-test for one sample was used to test the time series of each high-gamma frequency band at each voxel against the null-hypothesis of zero power change, such that only voxels and frequency bands with significant *positive* power changes were retained.

The high-gamma frequency band covers a broad range of oscillation frequencies, but task-induced power modulations typically occur only in a subportion thereof. Furthermore, different subjects and different brain regions tend to present different patterns of high-gamma frequencies that are activated during a given task (Hoogenboom et al., 2006). This potentially leads to problems when analyzing activations across different subjects and in different brain regions. If we look at the broad high-gamma band, we risk losing information due to noise and fluctuations in the non-activated frequencies. If, on the other hand, we use narrow bands only, we risk missing activations in neighbouring bands. We overcome this dilemma by statistically combining the 4 analyzed, relatively narrow high-gamma frequency bands (65-90, 90-115, 125-150, and 150-175 Hz) to a single broadband time-series of neural activation (Guggisberg, Dalal, Findlay, & Nagarajan, 2007). Thus, for each subject and at each voxel, the frequency bands that showed significant positive power changes in the

positive-tailed *t*-test mentioned above were selected and averaged in order to obtain a single time-series of power changes in all significant high-gamma frequency bands. By omitting frequencies without significant task-related power modulations, we effectively increase the signal-to-noise ratio and thus increase the sensitivity of subsequent statistical tests. Voxels that did not have significant positive power changes in any of the 4 high-gamma frequency bands were set to 0.

Based on the coregistered structural MRI, individual maps were spatially normalised at each time window to standard MNI (Montreal Neurological Institute) voxel space at 5 mm resolution.

The significance of the spatially normalized contrast time-series of power change in the combined high-gamma frequency bands (65-175 Hz) was tested across subjects with statistical non-parametric mapping (SnPM) (Singh, Barnes, & Hillebrand, 2003; Guggisberg, Dalal, Findlay, & Nagarajan, 2007; Dalal et al., 2008). SnPM does not depend on a normal distribution of power change values across subjects, and therefore remains valid after the previous statistical tests at the frequency level. In addition, it allows correcting for the familywise error of testing at multiple voxels. Power change values were thresholded at a corrected $p < 0.05$.

Regions of Interest (ROIs)

Voxel clusters that showed a significant final contrast were selected and defined as ROIs. The mean time course of activation from baseline, of the single contrast, and (in case of introspection related ROIs) of the double contrast was then extracted for each ROI from the individual data of each subject as the average power difference across all its voxels. ROIs that showed no significant activations from baseline or no significant contrast with physical epoch definitions were excluded in order to avoid contrast-related biases or biases due to inaccuracies and variance of subjective reports.

ROI statistics

A two-tailed paired *t*-test was used to test for differences in ROI activation from baseline between FREE and CUED choice conditions as well as between left and right index finger movements. Comparisons were performed for global activations as quantified by the area under curve

of the corresponding ROI time-series as well as for each time point of the ROI time-series with a false discovery rate set at 10% (Genovese, Lazar, & Nichols, 2002).

Software

All analysis algorithms are implemented in our Matlab toolbox NUTMEG (Dalal et al., 2011) version 3.1, which can be freely downloaded from <http://nutmeg.berkeley.edu>. Spatial normalization was done with the toolbox SPM2 for Matlab (<http://www.fil.ion.ucl.ac.uk/spm/software/spm2/>). The algorithms for SnPM were adapted from the toolbox SnPM3 for Matlab (<http://www.sph.umich.edu/ni-stat/SnPM/>). Three-dimensional renderings of the maps were created with mri3dX (<http://cubic.psych.cf.ac.uk/Documentation/mri3dX/>).

RESULTS

Behavioural data

Mean auditory choice reaction time was 749 ms (\pm 158 ms SD) and did not differ between introspection conditions ($F_{2,36}=1.3$, $p=0.29$) or choice conditions ($F_{1,36}=0.9$, $p=0.36$), and their interaction was not significant ($F_{2,36}=0.01$, $p=0.99$). *Figure 2* shows the times of the reported subjective onsets of the choice-related events. The subjective perception of the cueing phonemes occurred on average 20 ms (\pm 68 ms) after the physical onset of the phonemes, with the difference between subjective and physical times not being significant ($p=0.47$). Movements subjectively occurred significantly earlier than the actual onset of the physical button press ($p=0.043$) with an average difference between subjective and objective times of 54 ms (\pm 56 ms), in accordance with previous findings (Haggard, Clark, & Kalogeras, 2002). The subjective decision about which finger to move occurred on average 255 ms (\pm 109 ms) before button press ($p<0.0001$). The subjective time of decision differed

significantly from both subjective phoneme onset ($p=0.0008$) and subjective movement ($p=0.0099$). This behavioural data is comparable to previous studies (Libet, Gleason, Wright, & Pearl, 1983; Lau, Rogers, Haggard, & Passingham, 2004; Sirigu et al., 2004).

Imaging data

The combined forced choice and introspection task induced high-gamma activations from baseline that concerned almost the entire cortex in all introspection conditions (see Supplementary Videos 1-3).

When contrasting introspection epochs against control epochs to isolate neural processes related to the timing task from processes related to the primary processing of these events, we observed significant contrasts in supramodal areas in all introspection conditions (*Figure 3, Supplementary Videos 4-6*). For the PHONEME condition, the largest clusters of significant contrasts were located in left frontal and temporal areas, for the DECISION condition in the parieto-occipito-temporal junction around the angular gyrus of both sides, and for the MOVEMENT condition in the dorsomedial prefrontal cortex (DMPFC) and the supragenual anterior cingulate cortex (SACC).

A conjunction analysis revealed the brain regions that showed significant single contrasts in all 3 timing tasks. As shown in *Figure 4*, this comprised primary visual cortex (V1, Brodmann area 17), left associative visual areas (V3, Brodmann area 19), the right angular gyrus (Ang, Brodmann area 39), the left Cerebellum (Cb), the right middle frontal gyrus (MFG, Brodmann area 6) and the left superior frontal gyrus (SFG, Brodmann area 6).

The individual contrasts of each introspection condition were then subjected to a second contrast in order to isolate activity induced by introspective re-representation per se from other processes induced by the timing task such as assessment of time and simultaneity and dual-task interference (*Table 1 and Figure 1C*). *Figure 5 and Table 3* show the brain areas

that also survived this second contrast and that are therefore specific to the introspective re-representation of a particular event.

Event-time introspection of external auditory stimuli (**I_P**) activated the left inferior and middle frontal gyrus of Brodmann area 46.

Event-time introspection of decision making (**I_D**) was associated with enhanced high-gamma oscillations in bilateral parieto-occipito-temporal junction around the angular gyrus of Brodmann area 39. This is in precise agreement with a previous lesion study which showed that patients with lesions in this area are indeed incapable of reporting the time of their decision to occur before the actual movement see Fig. 4 in Sirigu et al. (2004).

Introspection of the time of movement (**I_M**) was accompanied by a specific activation that comprised the DMPFC (Brodmann area 9) and the SACC (Brodmann area 32), which overlaps with findings of a previous fMRI study (Lau, Rogers, & Passingham, 2006).

Figure 5 also illustrates the activation time courses of the regions with significant double contrast. All regions peaked close to the time of subjective event onset.

Neural activity at the regions involved in introspection (*Figure 5*) significantly differed between the three introspection conditions ($F_{2,162} > 16.0, p < 0.0001$).

The neural networks which showed significant contrasts during control epochs (*Table 2*) and which were therefore specifically recruited for the primary processing of events are indicated in *Figure 6* and *Table 3*.

Phoneme perception (**P**) was associated with activation of the bilateral superior temporal gyrus. This is in accordance with direct recordings of neural high-gamma oscillations from the human cortex (Crone, Boatman, Gordon, & Hao, 2001; Canolty et al., 2007) as well as with fMRI results (Binder et al., 1996; Giraud et al., 2004).

Activations in the SMA and in areas of the superior parietal lobule (SPL, Brodmann area 7) were observed at the time when subjects reported to become aware of their decisions

(D). This confirms existing data suggesting that the SMA mediates movement initiation and selection (Deiber et al., 1991; Thaler et al., 1995; Deiber, Ibanez, Sadato, & Hallett, 1996; Guggisberg, Dalal, Findlay, & Nagarajan, 2007), and that the posterior parietal cortex encodes intentions (Andersen & Buneo, 2002; Guggisberg, Dalal, Findlay, & Nagarajan, 2007).

Movement preparation and execution (**M**) was associated with corresponding activation of bilateral primary motor cortex (M1) and the bilateral inferior parietal cortex (IPL) in Brodmann area 40. Furthermore, an increase in high-gamma oscillations related to movement execution could also be observed bilaterally in the cerebellar hemispheres (Cb), which reconfirms our previous report of high-gamma oscillations in the cerebellum (Dalal et al., 2008). The MEG activations related to **M** are in agreement with direct recordings from the human cortex (Crone, Miglioretti, Gordon, & Lesser, 1998; Sochurkova, Rektor, Jurak, & Stancak, 2006; Dalal et al., 2008) and fMRI studies (Hulsmann, Erb, & Grodd, 2003).

No significant differences between FREE and CUED choices were found when analysing the activation time courses of all introspection and decision related ROIs shown in *Figures 5 and 6*, neither globally ($|t(6)| < 1.82$, $p > 0.12$) nor at single time points (corrected $p > 0.05$). Furthermore, no additional region showed consistent contrasts when FREE and CUED choices were analysed separately.

DISCUSSION

In this study we have reconstructed with high temporal fidelity the sequence of activation of different networks of brain regions involved in perception, decision and movement, as well as those involved in the event-time introspection of these events. The involvement of spatially distinct networks in auditory perception (**P**), decision (**D**) and movement (**M**) is well-established in several imaging studies (Deiber et al., 1991; Binder et al., 1996; Deiber, Ibanez, Sadato, & Hallett, 1996; Hulsmann, Erb, & Grodd, 2003; Giraud et al., 2004; Guggisberg, Dalal, Findlay, & Nagarajan, 2007) and the reconstructions reported here (*Figure 6*) only serve to demonstrate the consistency of this imaging modality to reconstruct such well-known networks. The fundamentally novel finding of this study is that the introspective re-representation of conscious perception, decision, or movement, which is required to make subjective judgments about their onset time, induces specific additional neural activity at the time of subjective event occurrence in networks which are distinct from the brain regions involved in the primary processing of these events. For example, during introspection of the timing of decision (**I_D**), we observe a statistically significant additional increase of neural activity in the bilateral angular gyrus (*Figure 5*). These findings support introspection model (ii) and imply that first-person reports obtained in the Libet-paradigm do not directly reproduce the primary consciousness of an event, but seem to involve the interaction between separate primary consciousness and introspection networks.

In the following, we will first consider potential confounds and alternative explanations of this finding before further addressing its implications.

The observed activity enhancement cannot be ascribed to the primary conscious processing of choice itself, because subjects made conscious decisions in all trials. The contrast between our introspection and control epochs (*Figure 1B*) did not compare between

conscious vs. unconscious processing, but represents the difference between “conscious event processing with introspection” vs. “conscious event processing without introspection” of a given event.

The activity increase can also not be due to concurring processes related to the dual task of introspection and decision making (such as task interference, assessment of simultaneity, general attention, working memory, or others) because they were subtracted out in the applied double contrast. Although the specifications and time courses of this concurring activity could not be known a priori, the contrasts were robust to all possible time courses relative to the time window of introspection (see *Figure 1C* and *Table 1*).

The remaining differences in neural activity might have been confounded due to inaccuracies in the reported introspective times or due to the fact that the onset of events in control epochs had to be estimated. In order to exclude this possibility, we also analyzed the dataset time-locked to the physical onset of the events phoneme presentation and button press. *Supplementary Figure 2* demonstrates that the networks found to be active during phoneme perception (**P**), movement execution (**M**), and their introspection (**I_P**, **I_M**) in the analyses centred on subjective times also showed significant double contrast peaks when the analyses were centred on the corresponding physical events. An eventual systematic bias in the subjective event times can therefore not explain the observed neural activations.

We also controlled for possible confounds that may have been introduced during the subtraction procedures of the double contrast, such as activity differences at baseline or deactivations in the subtracted epochs. All reported regions with significant contrasts showed activation peaks compared to baseline during the time window of introspection or primary processing of the corresponding event (*Figures 5 and 6*).

Finally, the subtraction procedures applied in this study assume a linear additivity of neural processes, which probably does not adequately capture true interactions. Furthermore, the source reconstruction from MEG data introduces some uncertainty. However, the

consistency of the brain activations observed in this study with prior lesion, electrocorticography, and fMRI studies (see Results section), some of which are not subject to these issues, gives some credence that the results are not confounded by methodological problems.

Hence, the introspection related activations shown in *Figure 5* (**I_P**, **I_D**, **I_M**) are highly specific to the act of introspection of a particular event.

These functional imaging results per se would not allow deducing a causal relationship between the observed neural activations and the behavioural act of introspection, i.e., it would be possible that the activations represent, e.g., attention to inner speech or other perceptual data occurring at this time in the sense of model (iii) (Carruthers, 2010), rather than the processing of introspection in the sense of model (ii). However, this possibility is unlikely given evidence from previous studies. Patients with lesions in the angular gyrus are indeed unable to correctly introspect the onset time of their intentions (Sirigu et al., 2004), and there is almost perfect overlap between the common lesion of patients with introspective deficits and the activations reported here. These patients also showed a decrease in an EEG potential before action execution, suggesting that lesions in the angular gyrus reduce introspection-related brain activity at the time of introspection. Moreover, direct electrical stimulation of the cortex in the area of the angular gyrus induces an introspective feeling of having the intention to move (Desmurget & Sirigu, 2009).

Taken together, the activations shown in *Figure 5* most probably correspond to the neural mechanisms of assessing the contents of consciousness during event-time introspection.

Our findings have implications on at least 3 levels, each of which will be discussed in the following. First, they present evidence for the existence of neural networks responsible for event-time introspection. Second, they provide a basis for the interpretation of introspective

data and allow explaining why event-time introspection can sometimes be biased. Third, they suggest that measurements of brain activity can be influenced by neural activity related to introspection.

Introspection Networks

How are networks responsible for event-time introspection organized?

Figure 5 demonstrates that the spatial location of activity enhancement associated with event-time introspection depends on whether the introspection concerns perceptual, intentional, or action events. Thus, each cognitive event seems to be introspectively assessed by its own specific network, which is in turn spatially separate from primary consciousness networks.

In addition, the Libet timing task recruits an overarching network that is common to all 3 types of events examined in this study (*Figure 4*). These regions participate in the assessment of time and simultaneity and in the processing of the dual task, but are probably not involved in the re-representation of a particular conscious event type. The activation of primary and associative visual areas is not surprising given the visual presentation of the clock. In agreement with previous studies (Battelli, Pascual-Leone, & Cavanagh, 2007; Grondin, 2010), we also observe right angular gyrus, cerebellar, and frontal activation during the timing task.

Activation in introspection networks peaks at the time of subjective event onset (*Figure 5*, second and third column). This seems to correspond to the time when activity in areas responsible for primary processing of these events exceeds a certain threshold (*Figure 5*, second and third column).

In accordance with previous studies (Lau, Rogers, Haggard, & Passingham, 2004; Sirigu et al., 2004), we found the SMA and the bilateral angular gyrus to be implicated in

introspective awareness of the decision time. However, the findings reported here suggest that the two areas assume different functions. The SMA represents the conscious decision and intention to move (Lau, Rogers, Haggard, & Passingham, 2004) whereas the angular gyri seem to be of primordial importance for the re-representation of the conscious decision to move during introspection. The angular gyri enhance their activity only when the time of intentions is introspected. Moreover, subjects with lesions in this area lose their capability to correctly introspect the onset time of their decisions, whereas they keep their ability to make the decisions themselves (Sirigu et al., 2004). This dissociation suggests that the introspective assessment of decisions, but *not* the decisions themselves, are mediated by the angular gyri.

Further evidence for different roles of the SMA and angular gyri comes from studies that applied direct electrical stimulation to the cortex (Desmurget & Sirigu, 2009). Electrical stimulation of the angular gyri induces the impression of having the desire to move, which is rather unspecific with regard to which movement is to be performed and not accompanied by the actual movement, even with strong stimulation intensities (Desmurget et al., 2009). In contrast, electrical stimulation of the SMA provokes an urge to move a specific body part in a specific direction and even a physical movement with stronger stimulation intensities (Fried et al., 1991). The difference between the endogenous aspect of parietal stimulations and the obligatory motor preparation character of SMA stimulations fits well with the model of introspection introduced here.

A different proposition for divergent roles of SMA and angular gyri in conscious intention has previously been advanced by Desmurget & Sirigu (2009), who suggest that the posterior parietal cortex around the angular gyri is responsible for the primary processing of conscious intentions whereas the SMA releases the movement. According to this proposition, the angular gyri process intentions which seem to be directly reportable in the sense of model (i). Conversely, our findings suggest that it is the SMA that processes intentions. The (meta-

)awareness of intentions encoded in the angular gyri seems to result from an introspective re-assessment rather than from the primary formation of these intentions.

To address the question of whether introspection networks adjust to the decision context, we compared the activation time courses of two different choice conditions. Although differences could be observed when the activations induced by FREE and CUED choices were compared at all voxels, they did not concern the regions responsible for introspection and decision-making at the time of subjective event occurrence. This suggests that the same introspection networks are recruited for all types of auditory choice.

The introspection paradigm used in our and other studies (Lau, Rogers, Haggard, & Passingham, 2004; Sirigu et al., 2004) concerned only the *timing* of cognitive events, which raises the question whether the results might be generalized to other types of introspection. The findings reported by Desmurget et al. (2009) provide some evidence that this could be the case. Parietal stimulation in the area of the angular gyri did not induce impressions of intended movement *times*, but of conscious movement intentions in general. Furthermore, previous studies have also observed neural correlates of introspection during perceptual (Overgaard et al., 2006) and self-confidence tasks (Fleming et al., 2010).

Overgaard et al. (2006) have observed EEG differences when human subjects performed a visual perception task in an “introspective state of mind” with an inward-direction of attention to subjective experience as compared to a “non-introspective state of mind” with an outward-direction of attention to external stimuli. This earlier study therefore also supports the notion that introspection is associated with its own neural substrate. In contrast to this earlier study, our participants were not necessarily in an introspective state of mind, since they had to attend to both external stimuli and internal intentions. For the introspection of phoneme

onset times, subjects may even have attended to the co-occurrence of two external events only. The fact that we still observed introspection-related activities in our study suggests that all re-representations of the contents of consciousness require separate neural processing, even if they are not inward-directed. Nevertheless, the event-time introspection of external events such as phonemes may involve different neural processing than event-time introspection of internal events such as intentions.

Value and Limitations of Event-time Introspection

There is a long-standing controversy around the scientific usage of introspection (Jack & Shallice, 2001; Jack & Roepstorff, 2002; Lutz, Lachaux, Martinerie, & Varela, 2002; Schooler, 2002; Marcel, 2003; Velmans, 2007). The findings reported here give insight into some aspects of the black box of event-time introspection and therefore allow drawing some preliminary conclusions with regards to its meaning. Introspection-related neural activity was found to occur at the subjective time of events, thus suggesting that introspection networks obtain immediate information about event processing in primary consciousness networks rather than mere post-hoc interpretation, and this seems to be the case not only for sensory and motor events but also for intention. In this regards, introspection seems to be a valid tool for assessing subjective events.

However, the finding that introspection depends on its own neural substrate raises a caveat when interpreting introspective data. Subjective reports do not directly reproduce processing in networks representing the introspected event, but instead result from complex interactions with introspection networks (Schooler, 2002; Marcel, 2003). This confirms a notion that was originally advanced by Immanuel Kant, who proposed that introspection “exhibits to consciousness even ourselves only as we *appear* to ourselves, not as we *are* in ourselves” (Kant, 1787/1996, emphasis added).

This study focussed on the time range around the subjective occurrence of introspected events. However, previous studies have shown that introspective reports do not only depend on *introspection* processes described above, but also on post-action activity (Lau, Rogers, & Passingham, 2007; Banks & Isham, 2009; Rigoni, Brass, & Sartori, 2010), which we tentatively name *interpretation* processes. During *introspection*, specific networks collect information about ongoing primary processing of events. The *interpretation* process may then integrate available information from introspective and also other networks possibly leading to judgments about the intentions behind an action. This may include the analysis of perceptual data in the sense of model (iii). It may also involve temporal back-referral mechanisms which seem to be necessary to account for the delay until a given event reaches consciousness (Libet, 2004).

The TMS results suggest that *interpretation* is mediated by the SMA, although other areas may also be involved (Rigoni, Brass, & Sartori, 2010). The SMA therefore seems to have a double role: it represents intention before the corresponding action is executed and is then reactivated after the action to contribute to the interpretation of introspective data. Indeed, activation of the SMA has not only been observed during action selection, but also *after* internally generated actions (Cunnington, Windischberger, Robinson, & Moser, 2006; Guggisberg, Dalal, Findlay, & Nagarajan, 2007).

This two-stage model of introspection and interpretation allows explaining biased subjective reports at various levels. Since the neural mechanisms of introspection have resource constraints, they are susceptible to interference with other ongoing neural activity. Hence, introspection may be disturbed by concurring tasks that require neural resources in close temporal proximity to the act of introspection, as it has indeed been observed in several previous studies (Moutoussis & Zeki, 1997; Eagleman & Sejnowski, 2000; Haggard, Clark, & Kalogeras, 2002; Stetson, Cui, Montague, & Eagleman, 2006; Corallo, Sackur, Dehaene, & Sigman, 2008) and also in this study for subjective movement onset. The resulting error can

be in the order of ~50ms. The introspection process can also misrepresent the primary conscious experience (Schooler, 2002; Marcel, 2003). In patients (e.g., commissurotomy patients, who lack neural connections between the left and the right hemisphere, Gazzaniga, 2000), erroneous introspections may result from conditions that selectively disturb the collection or transmission of data during the introspection stage but leave the subsequent interpretive processes unaffected. The resulting judgment will be based on incomplete introspective data and hence inaccurate. Finally, interference can also occur during post-action interpretation (Lau, Rogers, & Passingham, 2007; Banks & Isham, 2009; Rigoni, Brass, & Sartori, 2010).

Introspection Influences Measurements of Brain Activity

The findings reported here also raise the possibility that the early component of the brain potential that was reported to precede subjective intentions by (Libet, Gleason, Wright, & Pearl, 1983) is, at least in part, produced by neural activity related to introspection rather than movement preparation. Indeed, it has been shown that the Bereitschaftspotential is greater in amplitude when subjects make introspections about the time of their volition than when they move without introspection (Keller & Heckhausen, 1990), and that it becomes almost indiscernible in patients that cannot introspect their volition due to a lesion in the angular gyri (Sirigu et al., 2004). The Bereitschaftspotential is therefore not a good marker to indicate cortical motor preparation.

Other studies have reported significantly lateralized brain activity associated with unilateral movements which preceded the subjective onset of intentions (Haggard & Eimer, 1999). We explored whether neural activity related to introspection might also be lateralized. To this end, we compared the reconstruction of high-gamma brain oscillations induced by left finger movements with the activity induced by right finger movements in lateral hemispheric regions exhibiting significant double contrasts. Only activity in the primary motor cortex and

the IPL of both sides ($p < 0.028$), but not the angular gyrus of either side ($p > 0.23$), showed significant differences between left and right hand movements in our analyses (see *Supplementary Figure 3*). Thus, when focusing on high-gamma oscillations, we did not find a contribution of introspection areas to lateralization of brain activity in the tasks applied in this study. This, however, does not exclude lateralized activity in other frequency bands.

We analyzed the time course of lateralized high-gamma activity in the primary motor cortex as a robust marker of cortical movement preparation. In our two-alternative forced choice paradigm, the earliest high-gamma activation differences in M1 between left vs. right hand choices were observed at 194 ms (± 74 ms) before movement onset (see *Supplementary Figure 4*), which is not significantly different from the subjective intention onset at 255 ± 109 ms ($t(6) = 1.1$, $p = 0.32$). Hence, when using more specific markers of cortical movement preparation than the Bereitschaftspotential in a two-alternative forced choice paradigm, we did not observe a delayed onset of conscious awareness. However, pattern recognition algorithms can decode intentions from fMRI activity in prefrontal and parietal areas up to 10 s before reported conscious awareness (Haynes et al., 2007; Soon, Brass, Heinze, & Haynes, 2008), and hence long before the activation differences in the primary motor cortex found here. It is therefore probable that we could find earlier predictors for the future decisions also in our data.

CONCLUSIONS

This study shows that event-time introspection induces specific neural activations at the time of neural processing of the introspected event, suggesting that during introspection, healthy humans recruit specific neural networks to access relevant neural processes in primary consciousness networks. With regards to the interpretation of studies using event-time

introspection, this study provides some evidence, although incomplete, that healthy humans do not merely use post-hoc interpretations of sensory feedback for introspective reports, but have online introspective access to neural processing of the events. On the other hand, the reported subjective event times can be influenced by the neural processes required for introspection and do therefore not directly reflect the primary conscious state. Measurements of spatially distributed brain activity such as the Bereitschaftspotential can be influenced by activity related to introspection. A one-to-one comparison of spatially distributed neural and introspective onset times as done in the Libet-paradigm is therefore problematic.

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TABLE LEGENDS

Table 1. Overview of the contrasts applied to the data epochs in order to isolate the neural processes related to introspection.

Epochs and neural processes are shown schematically in *Figure 1*. After the double contrast, only the neural processes of interest (in bold) were represented with positive power changes, whereas all other activity was either cancelled out or represented with negative power changes. A positive tailed statistical test was then applied to threshold the maps.

Table 2. Overview of the contrast applied to the control epochs in order to isolate the neural processes related to the processing of choice.

Epoch and neural process labels as in *Table 1* and *Figure 1*.

Table 3. Anatomical locations of brain areas with significant contrasts.

Abbreviations: IFG, inferior frontal gyrus; MFG, middle frontal gyrus; Ang, Angular Gyrus; DMPFC, dorsomedial prefrontal cortex; SACC, supragenual anterior cingulate cortex; Sup Temp, superior temporal cortex; SMA, supplementary motor area; SPL, superior parietal lobule; M1, primary motor cortex; Cb, Cerebellum; IPL, inferior parietal lobule.

FIGURE LEGENDS

Figure 1.

A Paradigm. The participants introspectively assessed the timing of different events during an auditory two-alternative forced choice task. In each trial, subjects watched a rotating analogue clock, heard an auditory cue (megaphone), chose between the left or the right button either according to the cue or freely (mental event symbolized by a light bulb), and then pressed the chosen button with the index finger of the corresponding side (hand symbol). In different introspection conditions, subjects assessed the position of the clock at the time point of one of these three events (thought bubbles) and reported it after the clock stopped moving (speech bubble).

B Epochs. Introspection epochs (continuous squares) were centred on the subjective times of phoneme perception (i_p), decision (i_d), or movement (i_m). During control epochs (dashed squares), subjects made no introspection when they heard the phonemes (c_p), made their decision (c_d), or moved their fingers (c_m).

C Neural Processes of interest (black bars) in this study concerned the processing of choice-related events (phoneme perception, **P**; decision, **D**; movement execution, **M**) or their introspection (**I_P**, **I_D**, **I_M**). They were isolated from other task-induced neural activations (grey bars) with subtraction procedures. Concurring neural processes may have occurred during the time window of introspection only (T, e.g., assessment of time and simultaneity, dual task interference). Other processes may have been present also before (E, e.g., expectancy of the task-relevant event) or after introspection (W, e.g., working memory), or may have both preceded and outlasted the time window of introspection (V, e.g., vision and motion processing; G, e.g., general attention and motor preparedness). *Tables 1 and 2* demonstrate that all these concurring neural processes, if present, could be removed by the contrasts.

Figure 2. Average (\pm standard deviation) times of subjective onsets of the 3 events are shown relative to the times of physical phoneme presentation and physical button press.

The asterisks indicate the level of statistical significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Figure 3. Brain regions with significant high-gamma band (65-175 Hz) activations induced by the Libet timing task.

The colour overlays indicate significant contrasts between introspection and control epochs (first contrast in Table 1). The time window with the highest power difference is shown for each condition: 100 ms after the subjective onset time of phoneme perception for the PHONEME condition (top), 50 ms before the subjective onset time of the decision for the DECISION condition (middle), and 50 ms before the subjective onset time of

the finger movement for the MOVEMENT condition (bottom). The temporal evolution of the contrasts across all time windows is shown in *Supplementary Videos 4-6*.

Figure 4. Common network recruited by the Libet timing task for all event types.

The figure shows a conjunction analysis of the area under curve of all single contrasts shown in *Figure 3*. The marked regions were significantly more active when subjects had to determine the onset time of phoneme perception, intention, or movement as compared to the primary processing of these events. They are therefore associated with the assessment of time and simultaneity and possibly with other concurring processes.

Abbreviations: V1, primary visual cortex; V3, associative visual area; Ang, right angular gyrus; Cb, cerebellum; MFG, right middle frontal gyrus; SFG, left superior frontal gyrus.

Figure 5. Spatiotemporal reconstruction of neural activations induced by the re-representation of specific conscious events during event-time introspection.

First column Brain regions that showed significant double contrasts related to introspection of phoneme onset (**I_P**), intention onset (**I_D**) or movement onset (**I_M**). **Second column** Mean (\pm standard error) activation time course from baseline of the brain areas marked in the first column, relative to the physical onset time of the cueing phonemes. The grey staircase plots indicate the cumulative distribution of average subjective event onset times of all subjects relative to physical phoneme onset. **Third column** Activation time course relative to subjective event onset time. **Fourth column** Time course of the contrast between introspection and control epochs relative to subjective event onset time. **Last column** Time course of double contrast relative to subjective event onset time. *Abbreviations* as in Table 3.

Figure 6. Spatiotemporal reconstruction of activations induced by the primary processing of perceptual, intentional, and motor events.

First column Brain regions that showed significant contrasts related to the primary processing of phoneme perception (**P**), decision-making (**D**), movement execution (**M**). **Second column** Mean (\pm standard error) activation time course from baseline of the brain areas marked in the first column, relative to the physical onset time of the cueing phonemes. The grey staircase plots indicate the cumulative distribution of average subjective event onset times of all subjects relative to physical phoneme onset. **Third column** Activation time course relative to subjective event onset time. **Fourth column** Time course of the contrast isolating the choice-related processes from concurrent activity, relative to subjective event onset time. *Abbreviations* as in Table 3.

Tables

Table 1. Overview of the contrasts applied to the data epochs in order to isolate the neural processes related to introspection.

<i>Contrast Level</i>	<i>Label</i>	<i>Subtracted Epochs</i>	<i>Subtracted Neural Processes</i>	<i>Remaining Neural Processes</i>
Activation	i_p'	$i_p - baseline$	V+G+E+W+T + P + I_P - V	G+E+W+T+ P + I_P
	i_d'	$i_d - baseline$	V+G+E+W+T + D + I_D - V	G+E+W+T+ D + I_D
	i_m'	$i_m - baseline$	V+G+E+W+T+ M + I_M - V	G+W+E+T+ M + I_M
	c_p'	$c_p - baseline$	V+G+E+ P - V	G+E+ P
	c_d'	$c_d - baseline$	V+G+W+ D - V	G+W+ D
	c_m'	$c_m - baseline$	V+G+W+ M - V	G+W+ M
First Contrast	i_p^*	$i_p' - c_p'$	G+E+W+T+ P + I_P - (G+E+ P)	W+T+ I_P
	i_d^*	$i_d' - c_d'$	G+E+W+T+ D + I_D - (G+W+ D)	E+T+ I_D
	i_m^*	$i_m' - c_m'$	G+E+W+T+ M + I_M - (G+W+ M)	E+T+ I_M
Double Contrast	i_p^{**}	$i_p^* - i_m'$	W+T+ I_P - (G+W+E+T+ M + I_M)	I_P -G-E-M-I _M
	i_d^{**}	$i_d^* - i_p'$	E+T+ I_D - (G+E+W+T+ P + I_P)	I_D -G-W-P-I _P
	i_m^{**}	$i_m^* - i_p'$	E+T+ I_M - (G+E+W+T+ P + I_P)	I_M -G-W-P-I _P

Epochs and neural processes are shown schematically in *Figure 1*. After the double contrast, only the neural processes of interest (in bold) were represented with positive power changes, whereas all other activity was either cancelled out or represented with negative power changes. A positive tailed statistical test was then applied to threshold the maps.

Table 2. Overview of the contrast applied to the control epochs in order to isolate the neural processes related to representation of choice.

<i>Contrast Level</i>	<i>Label</i>	<i>Subtracted Epochs</i>	<i>Subtracted Neural Processes</i>	<i>Remaining Neural Processes</i>
First	c_p^*	$c_p' - i_m'$	G+E+ P - (G+W+E+T+ M + I_M)	P -W-T-M-I _M
Contrast	c_d^*	$c_d' - i_p'$	G+W+ D - (G+E+W+T+ P + I_P)	D -E-T-P-I _P
	c_m^*	$c_m' - i_p'$	G+W+ M - (G+E+W+T+ P + I_P)	M -E-T-P-I _P

Epoch and neural process labels as in *Table 1* and *Figure 1*.

Table 3. Anatomical locations of brain areas with significant contrasts.

<i>Neural Process</i>	<i>Label</i>	<i>Brodmann Area</i>	<i>MNI Coordinates</i>	<i>Cluster Size [nr of voxels]</i>
I_P	IFG/MFG L	46	-55 45 10	7
I_D	Ang L	19/39	-40 -85 35	25
	Ang R	39/19	45 -75 30	29
I_M	DMPFC	9	10 45 30	86
	SACC	32	5 40 20	
P	Sup Temp R	22	75 -15 0	11
	Sup Temp L	22	-75 -45 10	15
D	SMA L/R	6	15 5 80	53
	SPL L/R	7	10 -70 70 -10 -65 65	10
M	M1 L	4	-30 -25 60	86
	M1 R	4	35 -30 55	47
	Cb L		-30 -85 -45	22
	Cb R		45 -75 -55	4
	IPL L	40	-45 -50 45	73
	IPL R	40	45 -55 55	8

Abbreviations: IFG, inferior frontal gyrus; MFG, middle frontal gyrus; Ang, angular gyrus; DMPFC, dorsomedial prefrontal cortex; SACC, supragenual anterior cingulate cortex; Sup Temp, superior temporal cortex; SMA, supplementary motor area; SPL, superior parietal lobule; M1, primary motor cortex; Cb, Cerebellum; IPL, inferior parietal lobule.

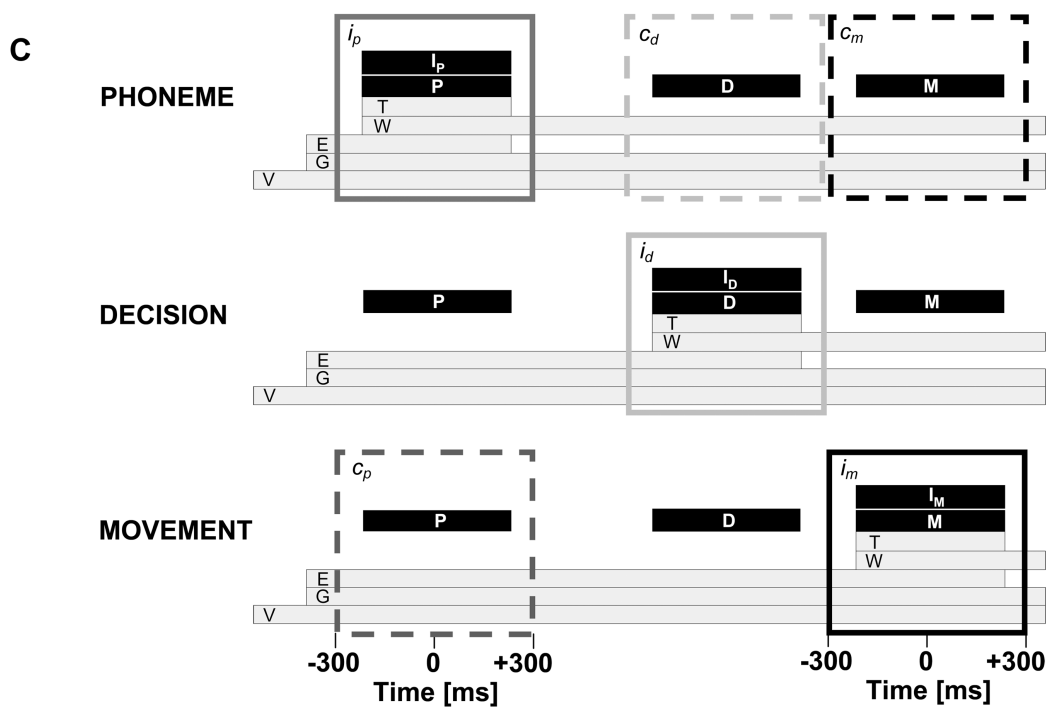
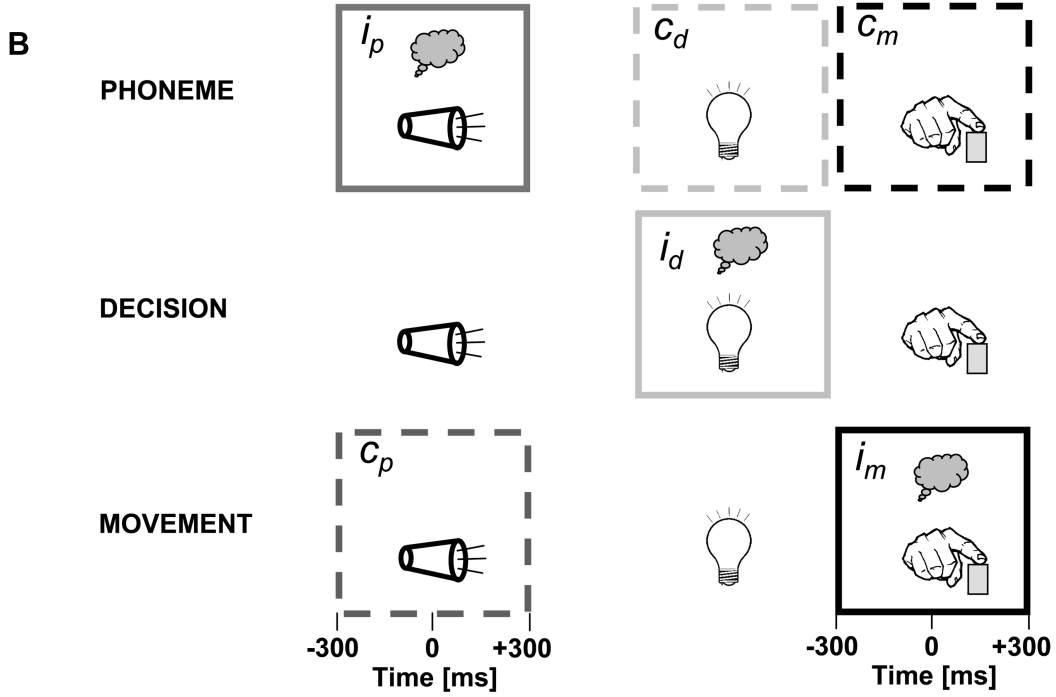
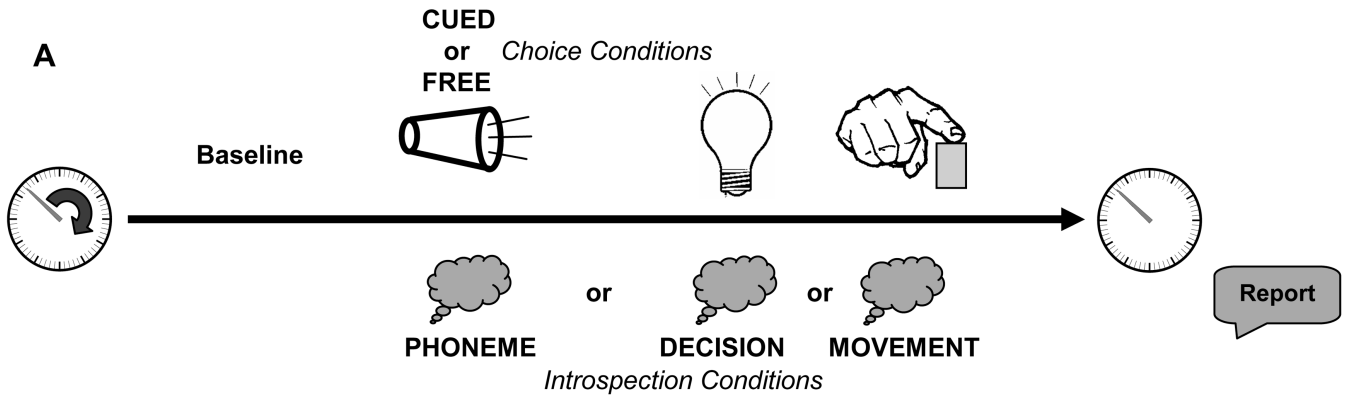


Figure 1

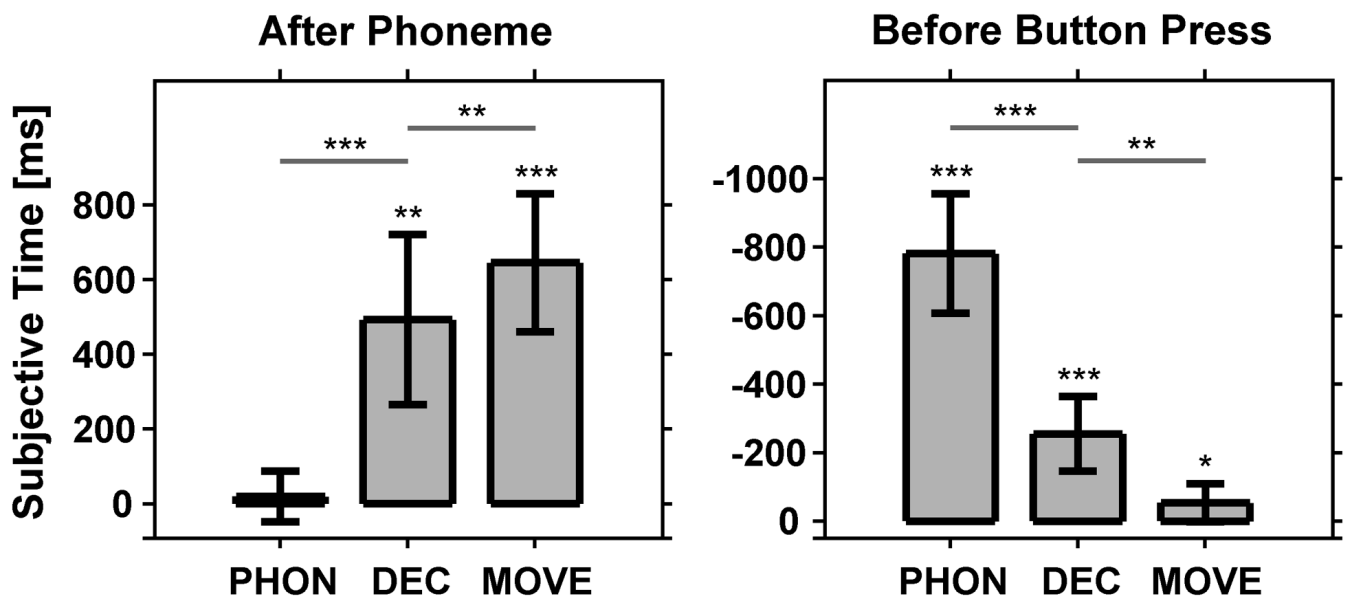
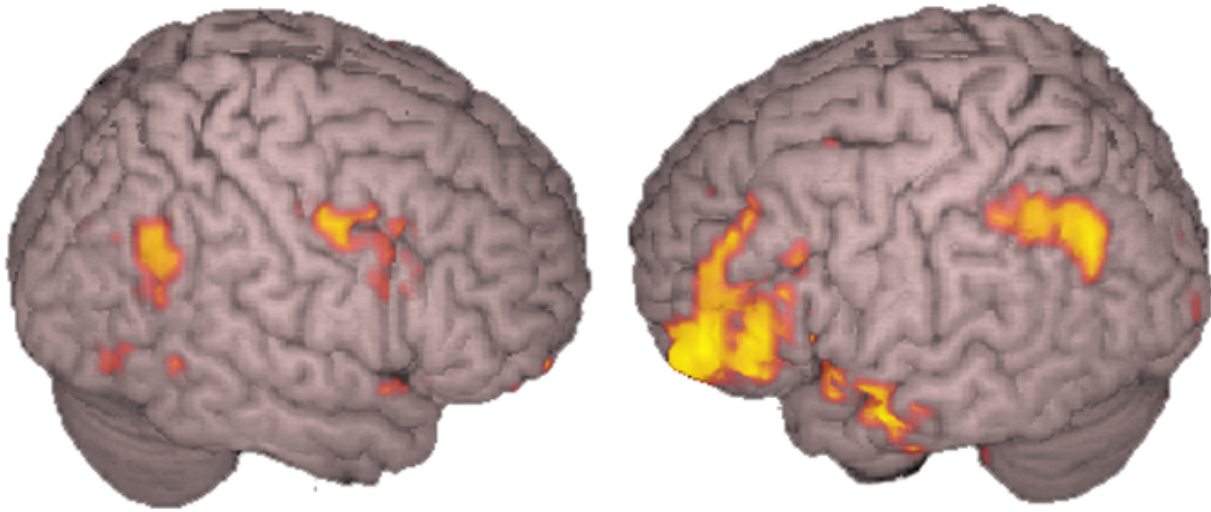
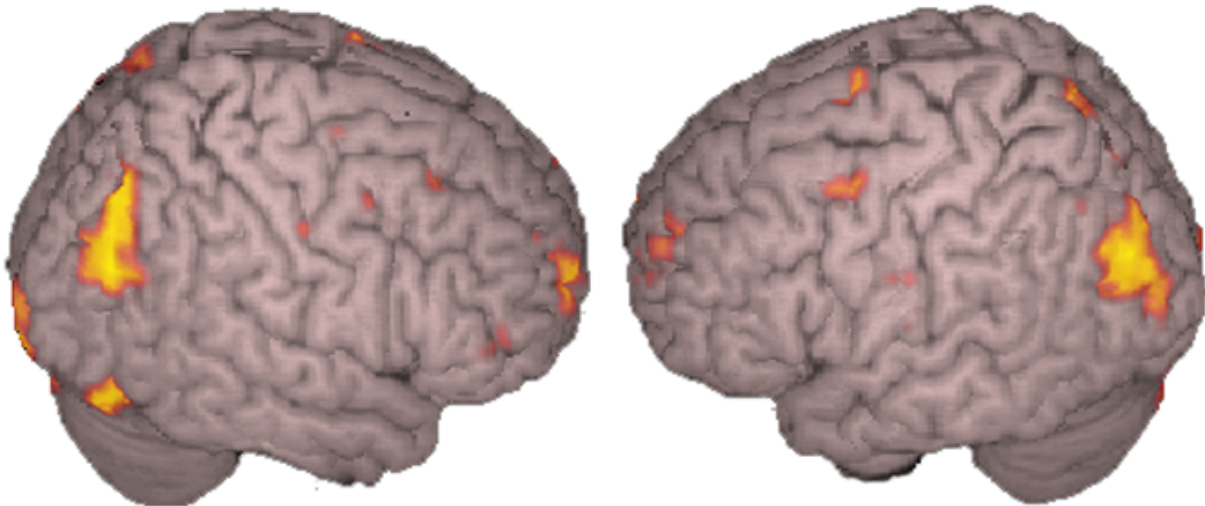


Figure 2

Introspection of phoneme perception > phoneme perception



Introspection of decision making > decision making



Introspection of movement execution > movement execution

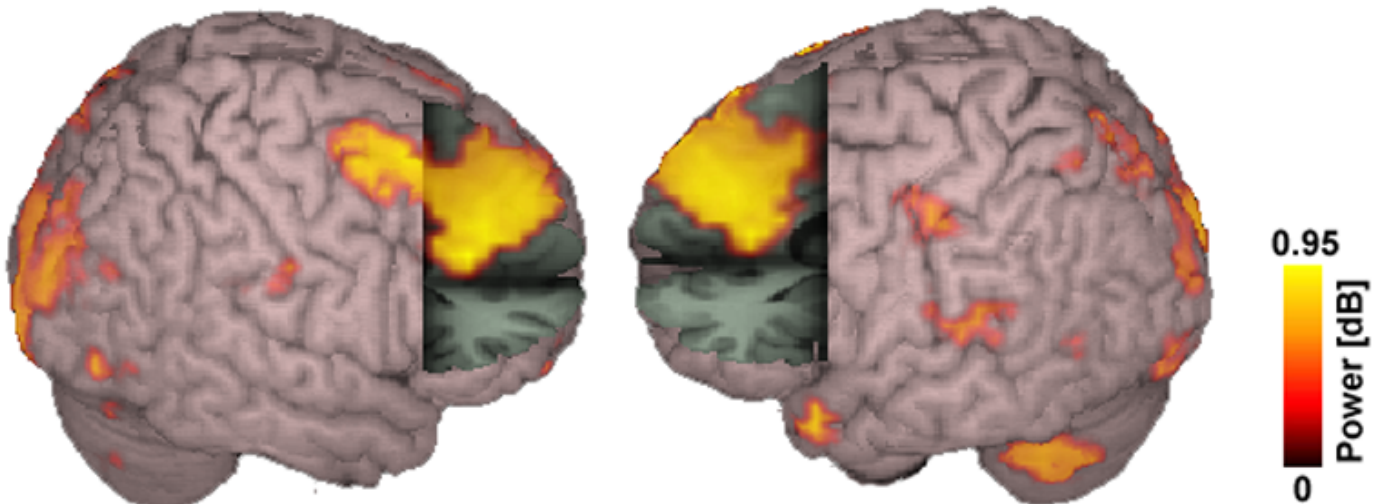


Figure 3

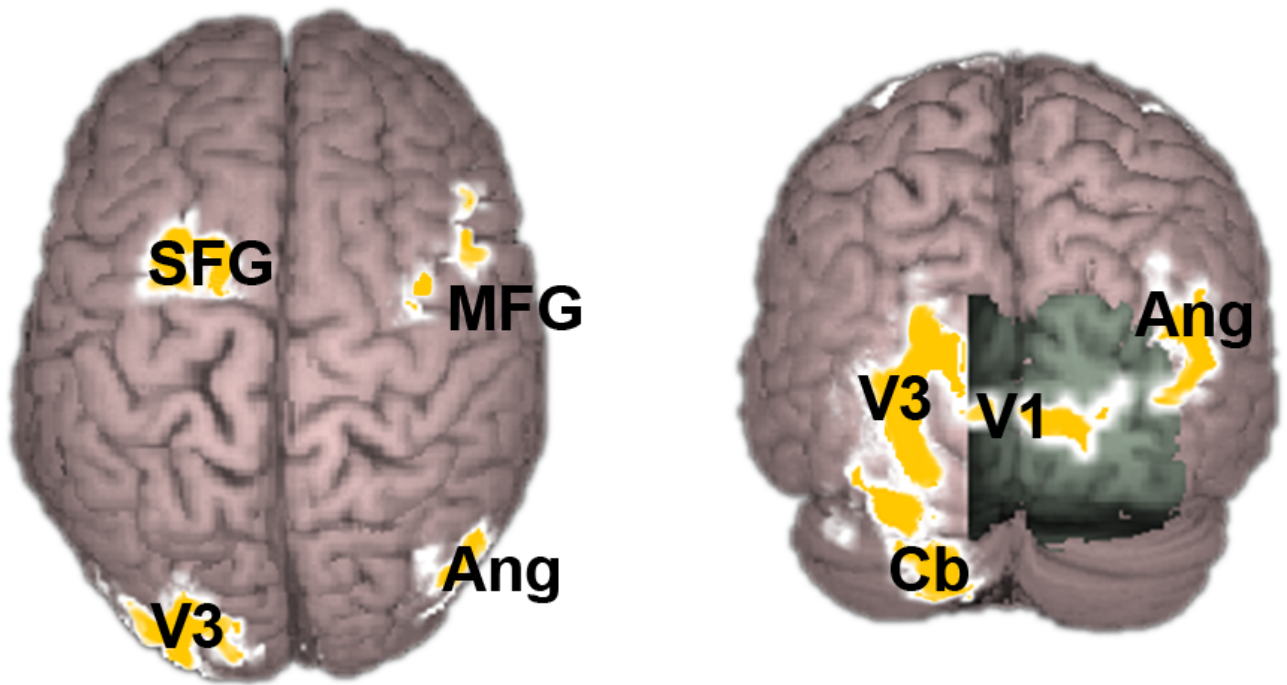


Figure 4

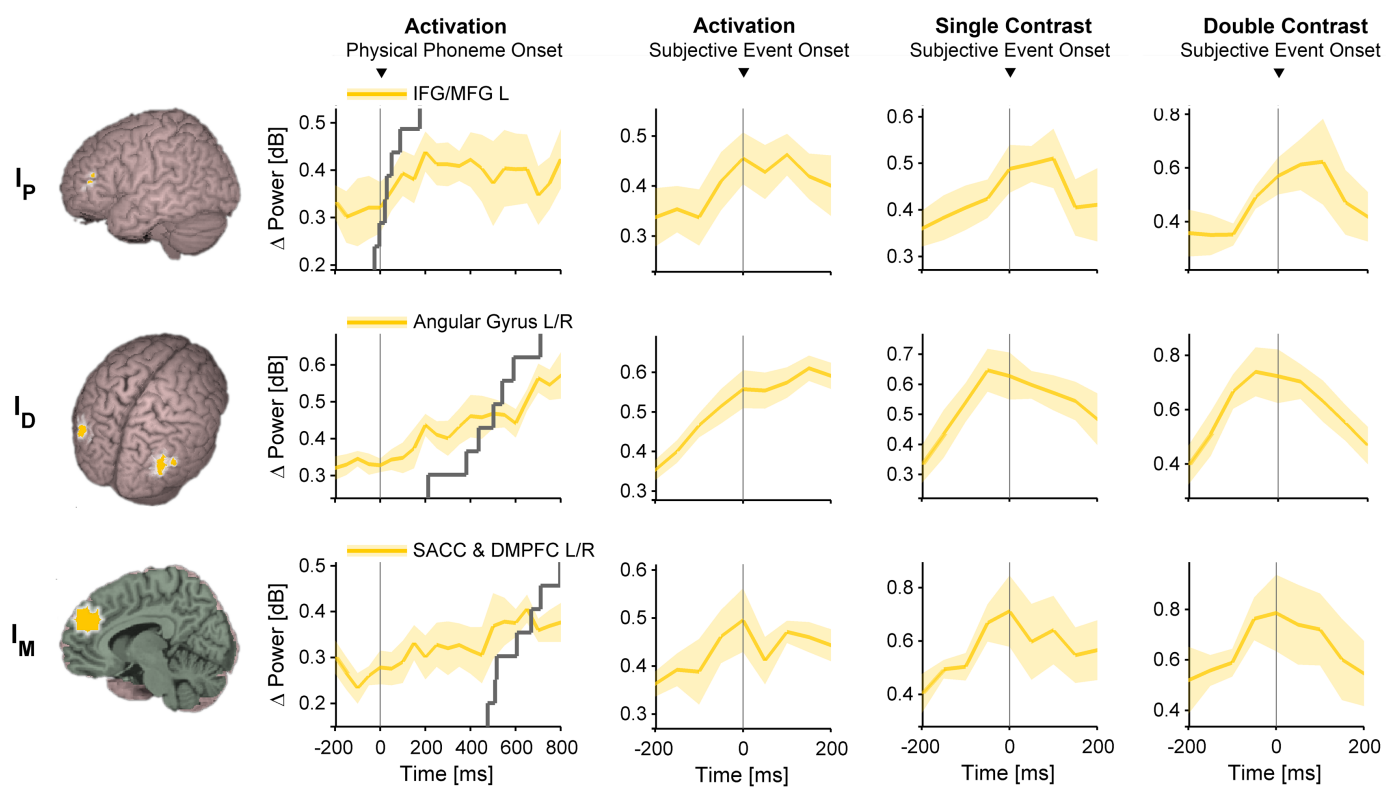


Figure 5

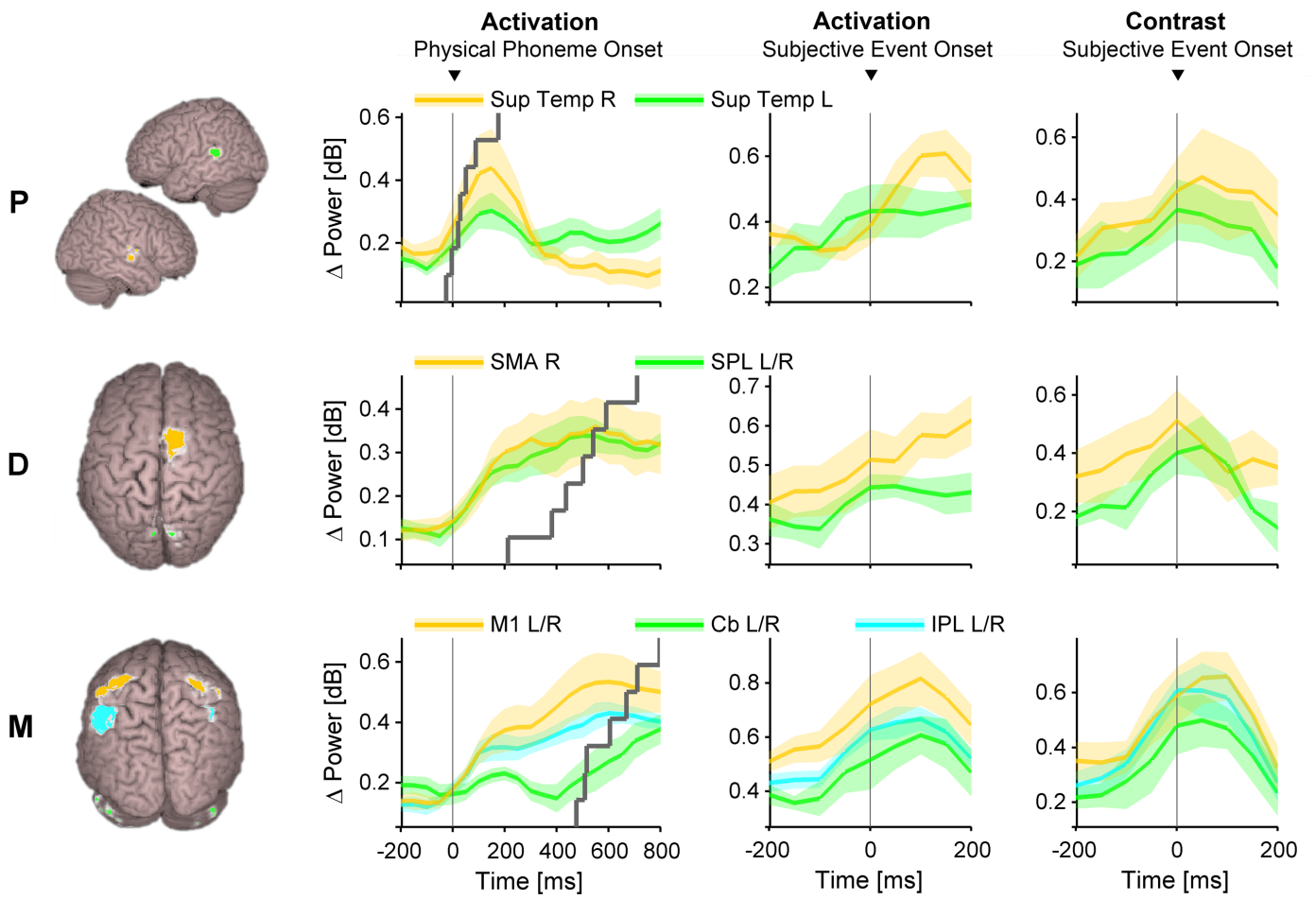


Figure 6

Supplementary Material

The Neural Basis of Event-Time Introspection

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SUPPLEMENTARY METHODS

Creation of control epochs

Since subjects made no introspection during control epochs (c_p , c_d , and c_m), no subjective reports were available to define the centres of these epochs. We were, however, able to *estimate* the corresponding onset times from the reports made by a given subject during trials *with* introspection of the corresponding event. For example, although subjects made no introspection of the phoneme onset time during c_p epochs, we were able to estimate the centres of these epochs from a model of event introspection built from other trials *with* introspection of phoneme onset.

The following 3 models A of individual event perception were therefore calculated based on the subjective timing reports R given by the subjects during trials *with* introspection of the corresponding event:

$$A_1 = R - S \tag{1}$$

$$A_2 = R - B \tag{2}$$

$$A_3 = (R - S) / (B - S) \tag{3}$$

where S represents the time of physical phoneme (stimulus) presentation and B the time of the physical button press. According to model A_1 , the events subjectively occurred a given time interval after the physical phoneme presentation, regardless of the time of button press. According to model A_2 , the events occurred a given time interval before the physical button press, regardless of the time of phoneme presentation. According to model A_3 , the events occurred after a given proportion of the time span between phoneme presentation and button press. In order to evaluate which model was most appropriate to estimate the onset of each event for each subject, we calculated the variance of each model across trials *with* corresponding timing judgments. The average of the model with the smallest variance was then selected to estimate the occurrence R^* of a given event and for a given subject also in trials *without* corresponding timing reports.

$$R^* = S + \bar{A}_1 \quad (4)$$

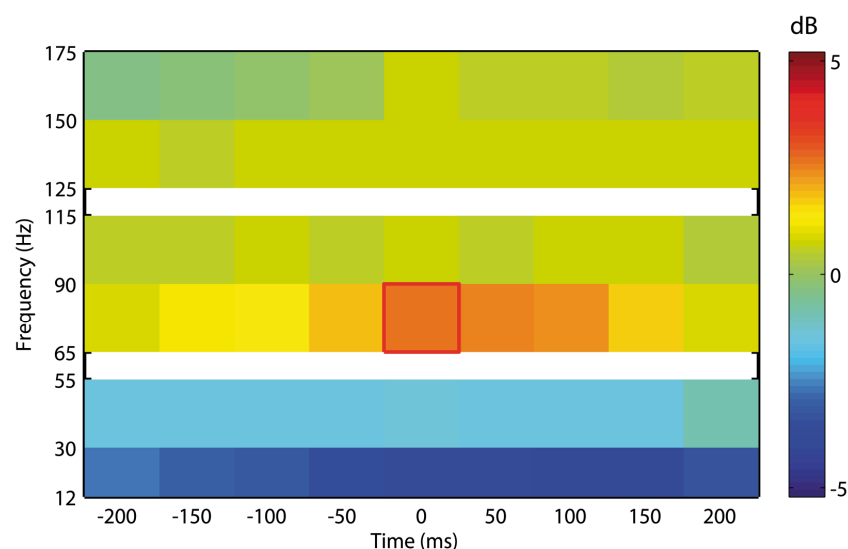
$$R^* = B + \bar{A}_2 \quad (5)$$

$$R^* = S + (B-S) \bar{A}_3 \quad (6)$$

For phoneme perception, model A_1 yielded the smallest variance in 5 out of 7 subjects, model A_2 in the remaining 2 subjects. For the subjective event of decision-making, model A_2 was found to be most appropriate in 3 subjects, model A_3 in 3 subjects, and model A_1 in 1 subject. For the subjective time of button press, model A_3 gave the best approximation in 5 subjects, model A_2 in 2 subjects. Thus, the subjective onset time R^* of each event *without* introspection was estimated relative to the time of physical phoneme presentation and/or physical button press from an optimal model of the average subjective times reported in trials *with* introspection. These estimated times were then used to define the centre of the corresponding control epochs.

Source Localisation and Extracerebral Artefacts

The time-frequency beamformer technique used to localise the sources of neural oscillation changes produced a time-frequency decomposition of neural activity at each voxel of each subject. A typical example is shown in *Supplementary Figure 1*.



Supplementary Figure 1. Example of a time-frequency decomposition of MEG power at a precentral voxel of a single subject.

The color of each square represents the MEG power change at the precentral voxel, in the corresponding time window and frequency band. Note that a power increase in high-gamma frequency bands (>65 Hz) was associated with a power decrease in the beta (12-30 Hz) and gamma (30-55 Hz) bands. This pattern is typical for task-induced changes of oscillations in cortical networks. In contrast, confounding power increases originating from extracerebral sources such as saccades or muscle activity would have concerned beta and gamma bands as well.

High-frequency EEG and MEG oscillations can potentially be confounded by electromagnetic power originating from extracerebral sources such as eye/lid movements (Bardouille, Picton, & Ross, 2006; Yuval-Greenberg et al., 2008) or muscle activity (Whitham et al., 2008). Although we did not directly record electrooculograms or electromyograms in this study, we controlled for contamination due to extracerebral artefacts of the results presented here: (i) Muscular and ocular sources induce power increases in a broad frequency range including the alpha, beta, gamma, and high-gamma bands (Bardouille, Picton, & Ross, 2006; Yuval-Greenberg et al., 2008; Whitham et al., 2008). In contrast, the high-gamma band power increases we observed were accompanied by power decreases in the beta and sometimes even the gamma band (see *Supplementary Figure 1*), which corresponds to the typical cortical response to task-related activations (Crone, Miglioretti, Gordon, & Lesser, 1998; Crone et al., 1998; Crone, Boatman, Gordon, & Hao, 2001; Edwards et al., 2005; Brovelli, Lachaux, Kahane, & Boussaoud, 2005; Hoogenboom et al., 2006; Canolty et al., 2007). (ii) All trials were visually inspected and trials with artefacts were excluded from the analysis procedures. (iii) The adaptive spatial filter used to identify the sources of MEG power modulations in this study eliminates extracerebral power modulations (Sekihara, Nagarajan, Poeppel, & Marantz, 2004; Nagarajan, Attias, Hild, & Sekihara, 2006) or localizes them to extracerebral sources such as the orbit (Bardouille, Picton, & Ross, 2006) or the skull. (iv) The activations reported

here are in close accordance with results from fMRI and lesion studies, which are not susceptible to artefacts due to eye movements or muscle activity.

SUPPLEMENTARY RESULTS

Supplementary Videos

Supplementary Videos 1-3 show the temporal evolution of significant neural *activations* during the tasks as compared to baseline. The indicated times are relative to the onset of physical phoneme presentation.

Supplementary Video 1: Activations during the PHONEME introspection condition.

Supplementary Video 2: Activations during the DECISION introspection condition.

Supplementary Video 3: Activations during the MOVEMENT introspection condition.

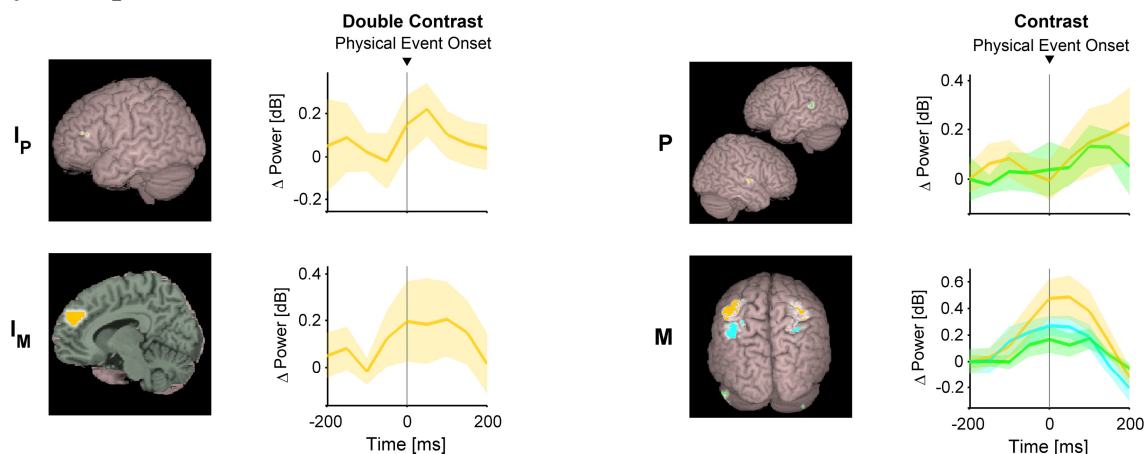
Supplementary Videos 4-6 show the temporal evolution of significant contrasts between introspection and control epochs, corresponding to activations induced by the introspection task. The indicated times are relative to the subjective onset times reported by the subjects.

Supplementary Video 4: Contrasts induced by the PHONEME introspection task.

Supplementary Video 5: Contrasts induced by the DECISION introspection task.

Supplementary Video 6: Contrasts induced by the MOVEMENT introspection task.

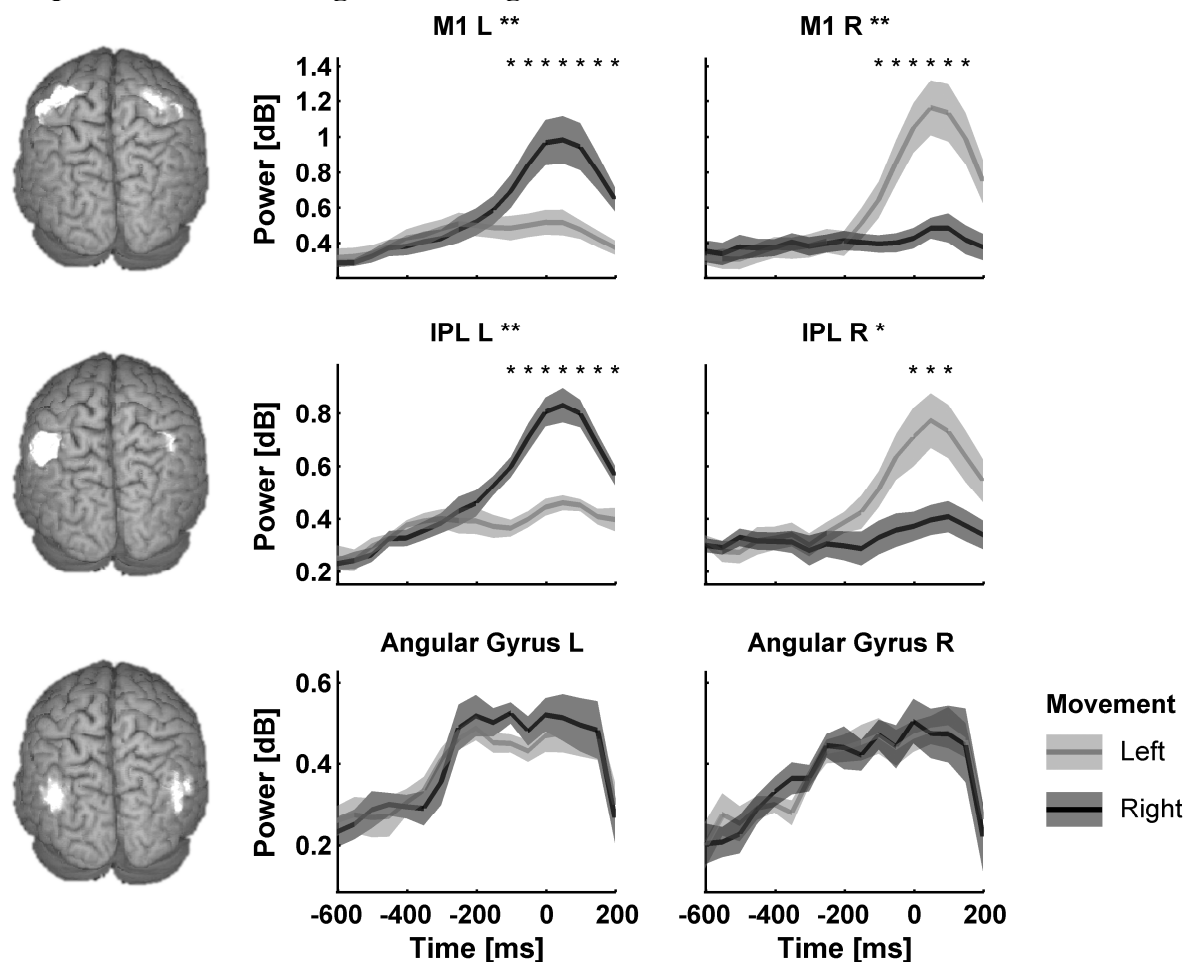
Physical epoch definitions



Supplementary Figure 2. Spatiotemporal reconstruction of high-gamma oscillation changes relative to physical events.

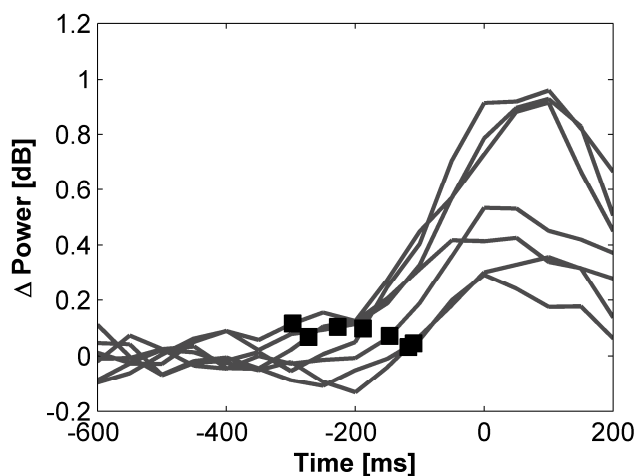
The same analysis procedures were used as for the data shown in *Figures 5 and 6*, but the analysis epochs were centered on the physical events phoneme onset (for P and I_P), or onset of button press (for M and I_M) rather than on the time of subjective event perception. No reanalysis was possible for D and I_D , because decisions are not associated with a corresponding external physical event. Note that the similar contrasts were also found in the analyses centered on physical events. This demonstrates that the results in *Figures 5 and 6* are not artifacts due to inaccuracies of the subjective reports.

Comparison of left and right index finger movements



Supplementary Figure 3. Lateralization of high-gamma activity.

The activation time course of left and right finger movements is shown in regions that showed significant introspection and representation related double contrasts and which were located in the hemispheric convexity. Time 0 corresponds to the time of physical button press. Asterisks inside the diagram boxes indicate significant differences between left and right finger movements at the corresponding time window. Asterisks in the labels indicate significant global differences as quantified by the area under curve of their respective time series (* $p < 0.05$, ** $p < 0.01$). Neural activity in the angular gyri (related to introspection of the decision time) does not significantly contribute to lateralization of high-gamma oscillations. In contrast, lateralized activity could be observed in the primary motor cortex (M1) and the inferior parietal lobule (IPL), which are both involved in movement execution. The earliest significant differences were found in the time window starting 200 ms before button press and ending at 0 ms.



Supplementary Figure 4. Individual onset of movement preparation in the primary motor cortex.

The curves indicate the power difference in the bilateral primary motor cortex (M1) between left and right finger movements of all subjects:

$$\frac{(M1_{\text{left}}^{\text{RightFinger}} - M1_{\text{left}}^{\text{LeftFinger}} + M1_{\text{right}}^{\text{LeftFinger}} - M1_{\text{right}}^{\text{RightFinger}})}{2}$$

The onset of movement preparation relative to the time of button press was defined as the point at which the power difference exceeds the 95% confidence interval of the fluctuations between -600 and -400 ms. It is marked with a black square for each subject.

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